



**Neogene Tonnoidean
Gastropods of Tropical and
South America: Contributions
to the Dominican Republic
and Panama Paleontology
Projects and Uplift of the
Central American Isthmus**

A. G. Beu



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NEOGENE TONNOIDEAN GASTROPODS OF TROPICAL AND SOUTH AMERICA: CONTRIBUTIONS TO THE DOMINICAN REPUBLIC AND PANAMA PALEONTOLOGY PROJECTS AND UPLIFT OF THE CENTRAL AMERICAN ISTHMUS

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ABSTRACT

The 142 species of tonnoidean gastropods recorded from the Neogene to Recent faunas of tropical America (Mexico, and a few taxa from Florida and California, south to Ecuador and Brazil) are revised, along with the 12 species of Neogene to Recent Personidae and Ranellidae occurring in Chile and Argentina. Taxa included are: (1) BURSIDAE: *Bursa*, 11 species, including the eastern Atlantic species *B. scrobilator* (Linnaeus, 1758) in the Pliocene and Pleistocene of tropical America; *Aspa marginata* (Gmelin, 1791), an eastern Atlantic species recorded in the Pliocene-Pleistocene of Limón, Costa Rica; *Crossata*, with one eastern Pacific species (California to Peru); *Marsupina*, five species, including *M. judensis* n. sp. (Miocene, Punta Judas, Costa Rica). (2) PERSONIDAE: *Distorsio*, 12 species, including *D. biangulata* n. sp. and *D. jungi* n. sp. (both Miocene, Cantaure, Venezuela); *Personopsis*, one Recent species. (3) RANELLIDAE, RANELLINAE: *Argobuccinum*, one species; *Fusitriton*, three species; *Halgyrineum*, one species; *Priene*, one Chilean species; *Ranella*, three species, including *R. chilena* n. sp. (Oligocene-Miocene, Chile); *Ameranella*, one species. (4) RANELLIDAE, CYMATIINAE: *Cabestana*, one living southwestern Atlantic species; *Charonia*, three species; *Crassycymatium crassicornatum* n. gen., n. sp. (Oligocene-Miocene, Chile); *Cymatium*, four species; *Gelagna*, one species; *Gutturium*, one species; *Linatella*, one species; *Monoplex*, 31 species, including *M. gatunicus* n. sp. (Miocene, Panama), *M. jackwinorum* n. sp. (Miocene, Venezuela), *M. longispira* n. sp. (Miocene, Dominican Republic), *M. panamensis* n. sp. (Miocene-Pliocene, both coasts of Panama), and two species left unnamed; *Ranularia*, three species; *Reticutriton*, five species, one left unnamed; *Septa*, two species, including *S. landaui* n. sp. (Miocene-Pliocene, Dominican Republic); *Turritriton*, four species; *Sassia*, seven species, including *S. warreni* n. sp.; *Cymatiella*, one species, *C. vokesorum* n. sp. (the last two both Miocene-Pliocene, Dominican Republic). (5) CASSIDAE, CASSINAE: *Cassis*, 12 species, including *C. altispira* n. sp. (Plio-Pleistocene, Dominican Republic, Atlantic Costa Rica, and Panama) and *C. costulifera* n. sp. (Pliocene, Atlantic Costa Rica, and Panama); *Cypraeacassis*, six species, including *C. cantaurana* n. sp. (Miocene, Cantaure, Venezuela); *Galeodea*, one species; *Sconsia*, six species. (6) CASSIDAE, OOCORYTHINAE: *Dalium*, two species; *Oocorys*, one species. (7) CASSIDAE, PHALIINAE: *Echinophoria*, three species; *Semicassis*, five species. (8) TONNIDAE: *Eudolium*, one species; *Malea*, nine species, including two unnamed; *Tonna*, two species. Although *Ficus* is now included in the superfamily Ficoidea, and most tropical American Ficoidea are not included here, the three *Ficus* species in the Dominican Republic are described in an Appendix: *F. bernardi* n. sp., *F. gibsonsmithi* n. sp., and *F. lisselongata* n. sp.

Neosconsia ecuadoriana Olsson, 1942 (Pliocene, Ecuador), is transferred to the family Buccinidae. The Argentinean Oligocene/Miocene species *Ocenebra* (?) *rada* (Ihering, 1907), *Xymene obliterated* (Cossmann, 1899), and *Urosalpinx* (*sensu lato*) *dautzenbergi* (Ihering, 1897) are transferred to the family Muricidae. *Ipunina vladimiri* Nielsen & Frassinetti, 2008 (Litiopidae; formerly thought to be an *Oocorys* species), is recorded from Cantaure, Venezuela. *Charonia sequenzae* (Aradas & Benoit, 1870) is a fourth Recent *Charonia* species limited to the eastern Mediterranean Sea.

The occurrences of the atlantiphile species *Linatella caudata* (Gmelin, 1791) in Armuelles Formation (Early Pleistocene), Burica Peninsula, Pacific Panama, and of the paciphile species *Malea ringens* (Swainson, 1822) in the Moín Formation (latest Pliocene-earliest Pleistocene), Limón, Atlantic Costa Rica, indicate that a shallow seaway still allowed intermittent transport of planktotrophic molluscan larvae between the eastern Pacific and the western Atlantic during latest Pliocene-earliest Pleistocene time. For much of Late Pliocene and Early Pleistocene time, the Central American Isthmus would have alternated between a land bridge during glacial periods of low sea level and a shallow seaway during interglacial periods of high sea level, until rising above sea level permanently at around 2 Ma.

Taxonomic decisions made herein include type locality designations for *Bursa asperrima* Dunker, 1862 (Hawaii), *B. grayana* Dunker, 1862 (off of Mucuripe, Fortaleza, Brazil), *Triton ranelloides* Reeve, 1844 (Sagami Bay, Japan), *Ranella rugosa* G. B. Sowerby II, 1835 (Perlas Islands, Panama Bay), *Ranella coriacea* Reeve, 1844 (Île Gorée, Sénégal), *Ranella ampullacea* Valenciennes, 1858 (Chiloé Island, Chile), *Buccinum caudatum* Gmelin, 1791 (Bohol Island, Philippines), *Fusus cutaceus* Lamarck, 1816 (Bohol Island, Philippines), *Cassidaria cingulata* Lamarck, 1822 (Bohol Island, Philippines), *Triton amictum* Reeve, 1844a (off of Isla San José, Perlas Islands, Panama Bay), *Triton ficoides* Reeve, 1844 (Gorée, Sénégal), *Fusus wiegmanni* Anton, 1838 (Venado Island, Panama), *Triton cynocephalum* (Lamarck, 1816 (Bahia, Brazil), *Triton moritinctus* Reeve, 1844 (Bahia, Brazil), *Triton gibbosus* Broderip, 1833 (Panama Bay), and *Cassis abbreviata* Lamarck, 1822 (Barbados). The type

locality of *Triton constrictus* Broderip, 1833, is corrected from St. Elena to Manta, Ecuador. Lectotype designations are made for *Ranella caelata* Broderip, 1833, *Murex scrobilator* Linnaeus, 1758 (with type locality designation of Palermo, Sicily), *Ranella ventricosa* Broderip, 1833, *Buffo spadiceus* Montfort, 1810, *Ranella granulata* Lamarck, 1816 (with type locality designation of off of Cayenne, Guiana), *Ranella nana* Broderip & G. B. Sowerby I, 1829, *Ranella albofasciata* G. B. Sowerby II, 1841, *Distorsio gatunensis* Toulou, 1909, *Tritonium thersites* Philippi, 1887, *Triton cancellatus* Lamarck, 1816 (with type locality designated as Maldonado, Uruguay), *Neptunea magellanica* Röding, 1798, *Triton rudis* Broderip, 1833, *Tritonium gemmiferum* Euthyme, 1889, *Murex olearium* Linnaeus, 1758 (with type locality designated as Palermo, Sicily), *Ranella gigantea* Lamarck, 1816, *Triton variegatum* Lamarck, 1816, *Murex femorale* Linnaeus, 1758, *Triton lotorium* Lamarck, 1816, *Triton tigrinum* Broderip, 1833 (with type locality designated as Corinto, Nicaragua), *Triton lignarius* Broderip, 1833 (with type locality designated as Panama Bay), *Triton turtoni* E. A. Smith, 1890, *Triton gallinago* Reeve, 1844 (with type locality designated as Mauritius Island), *Triton aegrotus* Reeve, 1844 (with type locality designated as Mauritius Island), *Tritonium exiguum* Philippi, 1887, *Buccinum flammeum* Linnaeus, 1758 (with type locality designated as Grand Bahama Island), *Cassis madagascariensis* Lamarck, 1822 (with type locality designated as Beaufort, North Carolina), *Buccinum tuberosum* Linnaeus, 1758 (with type locality restricted to Puerto Plata, Dominican Republic), *Buccinum plicatum* Linnaeus, 1758, *Cassis labiata* Conrad, 1849, *Buccinum testiculus* Linnaeus, 1758, *Cassidaria striata* Lamarck, 1816 (with type locality designated as Punta Alegre, Cuba), *Cassidaria sublaevigata* Guppy, 1866, *Cassidea granulosa* Bruguière, 1792, *Cassis abbreviata* Lamarck, 1822 (with type locality designated as Barbados), *Cassis monilifera* Guppy, 1866, *Malea camura* Guppy, 1866, *Cassis ringens* Swainson, 1822 (with type locality designated as Acapulco, Mexico), and *Ficus pilsbryi* B. Smith, 1907. The lectotype designation of *B. grayana* (incorrectly cited by Beu, 1987) is corrected. Neotype designations are made for *Biplex corrugata* Perry, 1811, *Bufonaria pesleonis* Schumacher, 1817, *Apollon quercina* Mörch, 1853, *Buccinum marginatum* Gmelin, 1791, *Ranella laevigata* Lamarck, 1822, *Eione inflata* Risso, 1826, *R. tenuis* Potiez & Michaud, 1838, *R. californica* Hinds, 1843, *Murex bufo* Bruguière, 1792, *Bursa gibbosa* Röding, 1798, *Buffo spadiceus* Montfort, 1810, *Murex crassus* Dillwyn, 1817, *Buccinum pustulosum* Lightfoot, 1786, *Murex argus* Gmelin, 1791, *Tritonium argo-buccinum* Röding, 1798 (the last three with type locality designations of Jeffreys Bay, South Africa), *Triton scaber* King, 1832, *Gyrina maculata* Schumacher, 1817, *Triton atlantica* Bowditch, 1822, *Lotorium lotor* Montfort, 1810, *Septa triangularis* Perry, 1811, *Tritocurrus amphytridis* Lesson, 1842, *Triton vestitus* Hinds, 1844, *T. vestitus* var. *senior* C. B. Adams, 1852, *Triton perforatus* Conrad, 1849, *Cassis tenuis* Wood, 1828 (with type locality designated as Galápagos Islands), *Buccinum granulatum* Born, 1778, *B. gibbum* Gmelin, 1791, *B. recurvirostrum* Gmelin, 1791, *Cassis cepa* Röding, 1798, *C. malum* Röding, 1798, *C. globulus* Röding, 1798, *Buccinum inflatum* Shaw, 1811, *Cassis minuta* Menke, 1828, *C. laevigata* Menke, 1829, *Buccinum cicatricosum* Gmelin, 1791, *Cassis corrugata* Swainson, 1822, *Dolium album* Conrad, 1854, *D. tenue* Menke, 1830, *D. antillarum* Mörch, 1877, *D. a. var. brasilianum* Mörch, 1877, *D. plumatum* Green, 1830, *Cadus coturnix* Röding, 1798, *C. meleagris* Röding, 1798, *Helix sulphurea* C. B. Adams, 1849, *Perdix reticulatus* Montfort, 1810. Other first reviser decisions are made concerning the nomenclature of *Distorsio ringens* (Philippi, 1887), *Ranella gemmifera* (Euthyme, 1889), and *Cabestana cutacea* (Linnaeus, 1767). *Marsupina* Dall, 1904, is declared a *nomen protectum* under ICDN Article 23.9.1. Three previously missing holotypes are identified: *Triton tranquebaricum* Lamarck, 1816, in the collection at Muséum d'Histoire Naturelle de Genève (with type locality designated as Île Gorée, Sénégal), and *Malea crassilabris* Valenciennes, 1832, and *Cassis centiquadrata* Valenciennes, 1832, both at Muséum National d'Histoire Naturelle, Paris. *Sassia tatei* is provided as a replacement name for *Triton armatus* Tate, 1888 (not *T. armatum* Hupé, 1854). The spellings of *Cymatium* (*Ranularia*) *mohorterae* A. H. Verrill, 1952, *Simpulum carlottae* Ferreira & da Cunha, 1957, and *Triton dautzenbergi* Ihering, 1897, are corrected. *Buccinum tuberosum* Linnaeus, 1758, is selected as the senior synonym of the species named both *B. tuberosum* and *B. plicatum* by Linnaeus (1758). *Cassis centiquadrata* Valenciennes, 1832, is selected as the senior synonym of the species named both *C. centiquadrata* and *C. doliata* by Valenciennes (1832).

RESUMEN

Las 142 especies de gastropodos tonnideneos registradas de la fauna de América tropical desde el Neógeno hasta el Reciente (México, y unas taxa de Florida y California, sur hasta Ecuador y Brasil) fueron revisadas, y también las 12 especies de Personidae y Ranellidae del Neógeno hasta el Reciente que se encuentran en Chile y Argentina. Taxa incluida son: (1) BURSIDAE: *Bursa*, 11 especies, incluyendo la especie del Atlántico este *B. scrobilator* (Linnaeus, 1758) en el Plioceno y Pleistoceno de América tropical; *Aspa marginata* (Gmelin, 1791), un especie del Atlántico registrada en el Plioceno-Pleistoceno de Limón, Costa Rica; *Crossata* con una especie del Pacífico este (California a Perú); *Marsupina*, cinco especies, incluyendo *M. judensis* n. sp. (Mioceno, Punta Judas, Costa Rica). (2) PERSONIDAE: *Distorsio*, 12 especies incluyendo *D. biangulata* n. sp. y *D. jungi* n. sp. (las dos del Mioceno, Cantaure, Venezuela); *Personopsis*, una especies Reciente. (3) RANELLIDAE, RANELLINAE: *Argobuccinum*, una especie; *Fusitriton*, tres especies; *Halgyrineum*, una especie; *Priene*, una especie chilena; *Ranella*, tres especies, incluyendo *R. chilena* n. sp. (Oligoceno-Mioceno, Chile); *Ameranella*, una especie. (4) RANELLIDAE, CYMATIINAE: *Cabestana*, una especie contemporánea del Atlántico suroeste; *Charonia*, tres especies; *Crassycymatium crassicordatum* n. gen., n. sp. (Oligoceno-Mioceno, Chile); *Cymatium*, cuatro especies; *Gelagna*, una especie;

Gutturium, una especie; *Linatella*, una especie; *Monoplex*, 31 especies, incluyendo *M. gatunicus* n. sp. (Mioceno, Panamá), *M. jackwinorum* n. sp. (Mioceno, Venezuela), *M. longispira* n. sp. (Mioceno, República Dominicana), *M. panamensis* n. sp. (Mioceno-Plioceno, las dos costas de Panamá), y dos especies sin nombre; *Ranularia*, tres especies; *Reticutriton*, cinco especies, una sin nombre; *Septa*, dos especies, incluyendo *S. landaui* n. sp. (Mioceno-Plioceno, República Dominicana); *Turritriton*, cuatro especies; *Sassia*, siete especies, incluyendo *S. warreni* n. sp.; *Cymatiella*, una especie, *C. vokesorum* n. sp. (las últimas dos: Mioceno-Plioceno, República Dominicana). (5) CASSIDAE, CASSINAE: *Cassis*, 12 especies, incluyendo *C. altispira* n. sp. (Plio-Pleistoceno, República Dominicana, Costa Rica Atlántica, y Panamá) y *C. costulifera* n. sp. (Plioceno, Costa Rica Atlántica, y Panamá); *Cypraeacassis*, siete especies, incluyendo *C. cantaurana* n. sp. (Mioceno, Cantaure, Venezuela); *Galeodea*, una especie; *Sconsia*, siete especies. (6) CASSIDAE, OOCORYTHINAE: *Dalium*, dos especies; *Oocorys*, una especie. (7) CASSIDAE, PHALIINAE: *Echinophoria*, tres especies; *Semicassis*, cinco especies. (8) TONNIDAE: *Eudolium*, una especie; *Malea*, nueve especies, incluyendo dos sin nombre; *Tonna*, dos especies. Aunque *Ficus* hoy en día está incluida en la superfamilia Ficoidea, y la mayoría de Ficidae de América tropical no están incluidas en este grupo, las tres especies de *Ficus* en la República Dominicana están descritas en el Apéndice F: *F. bernardi* n. sp., *F. gibsonsmithi* n. sp., y *F. lisselongata* n. sp.

Neosconsia ecuadoriana Olsson, 1942 (Plioceno, Ecuador), es transferida a la familia Buccinidae. Las especies argentinas del Oligoceno/Mioceno: *Ocenebra* (?) *rada* (Ihering, 1907), *Xymene obliteratus* (Cossmann, 1899), y *Urosalpinx (sensu lato) dautzenbergi* (Ihering, 1897) son transferidas a la familia Muricidae. *Ipunina vladimiri* Nielsen & Frassinetti, 2008 (Litiopidae; anteriormente identificada como una especie *Oocorys*), es registrada de Cantaure, Venezuela. *Charonia seguenzae* (Aradas & Benoit, 1870) es la curata especie de *Charonia* Reciente que solo se encuentra en el este del Mar Mediterráneo.

El presencia de la especie altantifilica *Linatella caudata* (Gmelin, 1791) en la Formación Armuellos (Plesotpceno Temprano), Península Burica, Panamá Pacífica, y de la especie pacifílica *Malea ringens* (Swainson, 1822) en la Formación Moín (Plioceno más tarde-Pleistoceno más temprano), Limón, Costa Rica Atlántica, demuestran que un pasaje marítimo poco profundo permite transportación intermitente de larvas planktotrofica mollusca entre el Pacífico este y el Atlántico oeste durante la temporada del Plioceno más tarde-Pleistoceno más temprano. Por mucha de la temporada del Plioceno Tarde y el Pleistoceno Temprano, el istmo Centro-Americano hubiera sido un puente terrestre durante periodos glaciales con niveles oceánicos bajos, y un pasaje marítimo durante los periodos interglaciales con niveles de mar altos, hasta que permanentemente paso el nivel del mar hace 2 Ma.

En este artículo se presentan nuevas decisiones taxonómicas. Se han designado localidades tipo para *Bursa asperima* Dunker, 1862 (Hawái), *B. grayana* Dunker, 1862 (frente a Mucuripe, Fortaleza, Brasil), *Triton ranelloides* Reeve, 1844 (Bahía de Sagami, Japón), *Ranella rugosa* G. B. Sowerby II, 1835 (Isla de Las Perlas, Bahía de Panamá), *Ranella coriacea* Reeve, 1844 (Île Gorée, Senegal), *Ranella ampullacea* Valenciennes, 1858 (Isla Chiloé, Chile), *Buccinum caudatum* Gmelin, 1791 (Isla de Bohol, Filipinas), *Fusus cutaceus* Lamarck, 1816 (Isla de Bohol, Filipinas), *Cassidaria cingulata* Lamarck, 1822 (Isla de Bohol, Filipinas), *Triton amictum* Reeve, 1844a (frente a Isla San José, Isla de Las Perlas, Bahía de Panamá), *Triton ficoides* Reeve, 1844 (Gorée, Senegal), *Fusus wiegmanni* Anton, 1838 (Isla Venado, Panamá), *Triton cynocephalum* (Lamarck, 1816 (Bahía, Brasil), *Triton moritinctus* Reeve, 1844 (Bahía, Brasil), *Triton gibbosus* Broderip, 1833 (Bahía de Panamá), y *Cassis abbreviata* Lamarck, 1822 (Barbados). La localidad tipo de *Triton constrictus* Broderip, 1833 ha sido emendada, de Santa Elena a Manta, Ecuador. Se han designado lectotipos para *Ranella caelata* Broderip, 1833, *Murex scrobilator* Linnaeus, 1758 (con localidad tipo designada para Palermo, Sicilia), *Ranella ventricosa* Broderip, 1833, *Buffo spadiceus* Montfort, 1810, *Ranella granulata* Lamarck, 1816 (con localidad tipo frente a Cayenne, Guiana), *Ranella nana* Broderip & G. B. Sowerby I, 1829, *Ranella albofasciata* G. B. Sowerby II, 1841, *Distorsio gatunensis* Toulou, 1909, *Tritonium thersites* Philippi, 1887, *Triton cancellatus* Lamarck, 1816 (con localidad tipo designada para Maldonado, Uruguay), *Neptunea magellanica* Röding, 1798, *Triton rudis* Broderip, 1833, *Tritonium gemmiferum* Euthyme, 1889, *Murex olearium* Linnaeus, 1758 (con localidad tipo designada para Palermo, Sicilia), *Ranella gigantea* Lamarck, 1816, *Triton variegatum* Lamarck, 1816, *Murex femorale* Linnaeus, 1758, *Triton lotorium* Lamarck, 1816, *Triton tigrinum* Broderip, 1833 (con localidad tipo en Corinto, Nicaragua), *Triton lignarius* Broderip, 1833 (con localidad tipo designada para la Bahía de Panamá), *Triton turtoni* E. A. Smith, 1890, *Triton gallinago* Reeve, 1844 (con localidad tipo designada para las Islas Mauricio), *Triton aegrotus* Reeve, 1844 (con localidad tipo designada para las Islas Mauricio), *Tritonium exiguum* Philippi, 1887, *Buccinum flammeum* Linnaeus, 1758 (con localidad tipo designada para Gran Bahama), *Cassis madagascariensis* Lamarck, 1822 (con localidad tipo designada en Beaufort, Carolina del Norte), *Buccinum tuberosum* Linnaeus, 1758 (con localidad tipo en Puerto Plata, República Dominicana), *Buccinum plicatum* Linnaeus, 1758, *Cassis labiata* Conrad, 1849, *Buccinum testiculus* Linnaeus, 1758, *Cassidaria striata* Lamarck, 1816 (con localidad tipo en Punta Alegre, Cuba), *Cassidaria sublaevigata* Guppy, 1866, *Cassidea granulosa* Bruguière, 1792, *Cassis abbreviata* Lamarck, 1822 (con localidad tipo designada para Barbados), *Cassis monilifera* Guppy, 1866, *Malea camura* Guppy, 1866, *Cassis ringens* Swainson, 1822 (con localidad tipo asignada para Acapulco, México), and *Ficus pilsbryi* B. Smith, 1907. La asignación del lectotipo de *B. grayana* (incorrectamente citado por Beu, 1987) ha sido corregida. Se han designado neotipos para *Biplex corrugata* Perry, 1811, *Bufonaria pesleonis* Schumacher, 1817, *Apollon quercina* Mörch, 1853, *Buccinum marginatum* Gmelin, 1791, *Ranella laevigata* Lamarck, 1822, *Eione inflata* Risso, 1826, *R. tenuis* Potiez & Michaud, 1838, *R. californica* Hinds, 1843, *Murex bufu* Bruguière, 1792, *Bursa gibbosa* Röding, 1798, *Buffo spadiceus* Montfort, 1810, *Murex crassus* Dillwyn, 1817, *Buccinum pustulosum* Lightfoot, 1786, *Murex*

argus Gmelin, 1791, *Tritonium argo-buccinum* Röding, 1798 (las últimas tres especies con localidad tipo en Jeffreys Bay, República de Sudáfrica), *Triton scaber* King, 1832, *Gyrina maculata* Schumacher, 1817, *Triton atlantica* Bowditch, 1822, *Lotorium lotor* Montfort, 1810, *Septa triangularis* Perry, 1811, *Tritocurrus amphitridis* Lesson, 1842, *Triton vestitus* Hinds, 1844, *T. vestitus* var. *senior* C. B. Adams, 1852, *Triton perforatus* Conrad, 1849, *Cassis tenuis* Wood, 1828 (con localidad tipo designada par alas Islas Galápagos), *Buccinum granulatum* Born, 1778, *B. gibbum* Gmelin, 1791, *B. recurvirostrum* Gmelin, 1791, *Cassis cepa* Röding, 1798, *C. malum* Röding, 1798, *C. globulus* Röding, 1798, *Buccinum inflatum* Shaw, 1811, *Cassis minuta* Menke, 1828, *C. laevigata* Menke, 1829, *Buccinum cicatricosum* Gmelin, 1791, *Cassis corrugata* Swainson, 1822, *Dolium album* Conrad, 1854, *D. tenue* Menke, 1830, *D. antillarum* Mörch, 1877, *D. a.* var. *brasilianum* Mörch, 1877, *D. plumatum* Green, 1830, *Cadus coturnix* Röding, 1798, *C. meleagris* Röding, 1798, *Helix sulphurea* C. B. Adams, 1849, *Perdix reticulatus* Montfort, 1810. Además se toman decisiones nomenclatorias para *Distorsio ringens* (Philippi, 1887), *Ranella gemmifera* (Euthyme, 1889), y *Cabestana cutacea* (Linnaeus, 1767). *Marsupina* Dall, 1904 es designada *nomen protectum* baco el CINZ Artículo 23.9.1. Tres holotipos previamente desaparecidos han sido identificados: *Triton tranquebaricum* Lamarck, 1816, en la colección del Muséum d'histoire naturelle de Ginebra (con localidad tipo designada para Île Gorée, Senegal) y *Malea crassilabris* Valenciennes, 1832, y *Cassis centiquadrata* Valenciennes, 1832, las dos en el Muséum National d'Histoire Naturelle, París. *Sassia tatei* es el reemplaza a *Triton armatus* Tate, 1888 como nombre válido (no *T. armatum* Hupé, 1854). Los nombres *Cymatium* (*Ranularia*) *mohorterae* A. H. Verrill, 1952, *Simpulum carlottae* Ferreira & da Cunha, 1957, and *Triton dautzenbergi* Ihering, 1897, han sido corregidos. *Buccinum tuberosum* Linnaeus, 1758, ha sido seleccionado como el sinónimo senior de ambas especies *B. tuberosum* y *B. plicatum* de Linnaeus (1758). *Cassis centiquadrata* Valenciennes, 1832, ha sido seleccionado como el sinónimo senior de ambas especies *C. centiquadrata* y *C. doliata* de Valenciennes (1832).

INTRODUCTION

This monograph is part of a long-continued research program, the aim of which is to understand as much as possible of the composition and phylogeny of the Tonnoidea and, above all, how the extant “teleplanic” (planktotrophic) tonnoideans achieved their enormously wide geographical ranges. In this monograph, my aims are: (1) to provide a tropical American input to understanding the biogeographical history of the very widely distributed species that now are large, prominent, ecologically important carnivores around the Southern Ocean, but have a fossil record largely in the northern hemisphere – such species as *Argobuccinum pustulosum* (Solander in Lightfoot, 1786), *Charonia lampas* (Linnaeus, 1758), *Monoplex parthenopeus* (von Salis Marschlin, 1793), *Ranella olearium* (Linnaeus, 1758), *Ranella australasia* (Perry, 1811), and the *Fusitriton magellanicus* (Röding, 1798) species complex; (2) to provide a tonnoidean contribution to understanding the closure of the Central American Isthmus, because of the well-known wide dispersal of (at least some) tonnoideans resulting from their long-lived planktotrophic larval stages, and (3) to revise the Neogene tonnoidean fauna of tropical America as a contribution to paleontological studies of the Panama region and the northern Dominican Republic. I am interested to understand the biogeographical history of all of these species. How did they come to live where they do? Where and when did they evolve? How did they spread so widely? Why do some of the very widely distributed species live now around the Southern Ocean and in southern Japan to Taiwan, but *not in the tropical realm* between [e.g., *Charonia lampas*, *Monoplex parthenopeum*, and *Monoplex exaratus* (Reeve, 1844); Beu, 1998b, 1999]. The overall aim, then, is to understand the wider taxonomy; how are the species related

to each other, and why do they live where they do?

It should be stated at the start that the Ficidae species included in this work are only the three fossil species occurring in the Dominican Republic, as Riedel (1994) has removed them to a separate superfamily Ficoidea. Many other *Ficus* species occur in Neogene rocks of tropical America, but are not studied here. I also have not included South American Neogene Cassidae [the single species, *Echinophoria monilifera* (G. B. Sowerby I, 1846), was revised by Nielsen (2003: 89, pl. 16, figs 11-16) and Griffin & Nielsen (2008: 300, pl. 21, figs 15-20)] or the Recent tropical American Cassidae or Tonnidae, except where they occur as fossils or a few new records are required, because these species are well-known taxonomically.

A work of this scope builds largely on the works that have been published previously. It is worth listing here, then, the published catalogs and revisions of tonnoideans that have preceded the present one. For the Bursidae, Personidae, and Ranellidae, my long-term interest in the family means that this catalog is reasonably complete, but for other families it will be less so, and merely lists significant revisions that I used while compiling the present monograph. The list below does not include the early, primary works, in which many of the species were named; the most important of these are Linnaeus (1758, 1767), Gmelin (1791), Röding (1798), and Lamarck (1816, 1822). In date order, the catalogs and revisions of tonnoideans of which I am aware are: Kiener (1835a, b), Cassidae; Kiener (1835c), Tonnidae; G. B. Sowerby II (1835-1836, 1841), Bursidae; Kiener (1841), Bursidae; Kiener (1842), Ranellidae; Pfeiffer (1843), Ranellidae; Reeve (1844a), Ranellidae; Reeve (1844b), Bursidae; Reeve (1848b), *Cassis*; Reeve (1849b), *Galeodea* and *Sconsia*; Reeve (1848c-

1849a), *Tonna*; Kobelt (1875; 1876a, b; 1878a, b), catalogs of all the tonnoidean families, prepared for the following works: Küster (1857), Cassidae and Tonnidae, and Küster & Kobelt (1839-1878), Bursidae, Personidae, and Ranellidae (among other families); Paetel (1888), a large collection catalog; Tryon (1880-1881, 1885), a very conservative but illustrated catalog of all tonnoideans; Cossmann (1903, 1904), important critical revisions of all tonnoidean families; Dall (1904), the most important critical review of the genera of Ranellidae and Bursidae; Dall (1909a), an important critical review of the genera of Cassidae; Bayer (1932, 1933, 1935, 1937), catalogs of Recent tonnoideans in what is now the Netherlands National Museum of Natural History, Leiden; Coulon (1933, 1936), catalogs of Recent tonnoideans in the Musée d'Elbeuf, France; Clench & Abbott (1943) and Clench (1944), western Atlantic Cassidae; Turner (1948), western Atlantic Tonnidae; Bellatante (1954), a catalog of Recent Ranellidae in the Muséum National d'Histoire Naturelle, Paris; Clench & Turner (1957), the most influential modern work on western Atlantic Ranellidae; Kilius (1962), catalog of Tonnidae; Abbott (1968), a monograph of most worldwide Cassidae (but not including taxa related to *Galeodea* and *Sconsia*); Kilius (1973), catalog of Ranellidae ("Ranellidae" in all the works listed above included what is now the separate family Personidae). More recently, (a) critical lists of the species of living Ranellidae, Personidae, and/or Bursidae have been published by me (Beu, 1985) and Piech (1995), (b) Warén & Bouchet (1990) reviewed the tonnoidean families and proposed new family-level taxa, (c) Marshall (1992) revised the living species of the tonnid genus *Eudolium*, (d) Riedel (1995) proposed a phylogeny of the Tonnoidea (largely not accepted here), (e) Henning & Hemmen (1993) published an illustrated catalog of living Ranellidae and Personidae, (f) Cossignani (1994) published an excellent, richly illustrated catalog of living Bursidae, (g) Kreipl (1997) published a similar, excellent catalog of living Cassidae, (h) I provided (Beu, 1998a) a brief overview of the anatomy, classification, and what little is known of the biology of the tonnoidean families, (i) I monographed (Beu, 1998b) the species living in the New Caledonian region, (j) I recorded (Beu, 1999) those living in Yamaguchi Prefecture, southwestern Honshu, Japan, and (k) Vos (2007) revised the living species of Tonnidae.

The seminal work on the living ranellid fauna of the western Atlantic is that of Clench & Turner (1957). Their revision set a new standard for the high quality of its illustrations, as well as for its attempts to base taxonomic decisions firmly on type material, and on large suites of specimens examined personally by the authors. Therefore, it was able to sweep away much of the miasma of misidentified species and confused ranges that had dogged earlier work on ranellids. It began the modern realisation that many species of ranellids (as well

as many other tonnoideans) really do have enormously wide geographical ranges. However, Clench & Turner were not able to see the type material of such important early workers as Linnaeus (most housed by the Linnean Society of London, in Burlington House) or, more importantly, that of Lamarck (tonnoideans all in the Muséum d'Histoire Naturelle de Genève). [The location of much of the remaining early type material was discussed by me (Beu, 1998b: 15-16) and is listed and amplified below.] More significantly, Clench & Turner's (1957) approach was still colored by the extremely conservative species-level taxonomy in the catalogs by Tryon (1880-1881) and, indeed, it has been a struggle for much of the succeeding years to recognise the true biospecies occurring in the western Atlantic. [Philippe Bouchet, MNHN, informed me that DNA studies indicate that still further species await recognition, *e.g.*, in the species here identified as *Bursa granulularis* (Röding, 1798)]. Later authors have realised, also, that a surprising variety of further species occurs in small numbers in the western Atlantic, particularly in Brazil, in addition to those of which Clench & Turner (1957) were aware. That still more await discovery is indicated by the presence of a specimen in a Brazilian private collection of *Lotoria lotoria* (Linnaeus, 1758) found alive in Brazil, but not otherwise mentioned here (Marcus Coltro, São Paulo, pers. comm., 2006). The present work has been able to draw on many different lines of new evidence, on many private collections, and on the much larger museum collections available now, 50 years later, to amplify the brilliant foundation laid by Clench & Turner. All subsequent work on Ranellidae indeed "stands on the shoulders of these giants" of malacology.

The other aspect of recent research that has improved the understanding of tonnoidean geographical ranges vastly since 1957 is the large body of work on their planktotrophic larvae, principally by Scheltema (*e.g.*, 1966, 1968, 1971, 1972a, b, 1977, 1983, 1986a, b, 1989; Pechenik *et al.*, 1984) but also, importantly, by Laursen (1981). Woodring (1928: 103) commented on the difficulty of reaching biogeographical conclusions about mollusks without knowing "the length of pelagic larval stages, and the distances larvae can be carried by currents." Other early workers such as Powell (1933) assumed that the wide geographical ranges of ranellids, in particular, resulted from long-lived larvae, transported widely in ocean currents. The importance of Scheltema's research is that it has placed this assumption on a sound footing, demonstrating the means by which the enormous ranges of many tonnoidean species have been achieved, and establishing a larval life of more than a year for *Monoplex nicobaricus* (Röding, 1798), and probably *M. parthenopeus*, and for up to 4.5 years for *Fusitriton oregonensis* (Redfield, 1846) (Strathman & Strathman, 2007). This suggests that Scheltema's estimates, based on surviving captured veligers, significantly underestimate the length of

larval life. It is now clear that some tonnoideans – particularly *Bursa*, *Cypraeacassis*, Tonnidae, and many species of Ranellidae – along with most species of Architectonicidae and a few taxa in other families, such as the cerithioid *Litiopa melanostoma* Rang, 1829, have particularly long-lived planktotrophic larvae, able to feed in the plankton and to postpone metamorphosis indefinitely, until a substratum suitable for settling is reached. These taxa have achieved the widest recorded distributions of benthic mollusks, because their long larval lives enable them to be dispersed widely but passively by currents. The particularly widely distributed Tonnoidea are *Charonia lampas*, *Ranella olearium*, *Linatella caudata* (Gmelin, 1791), *Monoplex parthenopeus*, *M. exaratus*, *Turritriton labiosus* (Wood, 1828), the Recent *Sassia* species related to *S. apenninica* (Sassi, 1827), *Eudolium bairdii* (Verrill & Smith in Verrill, 1881) and *E. crosseanum* (Monterosato, 1869), *Malea pomum* (Linnaeus, 1758), and the circum-Southern Ocean taxa (species complexes?) *Semicassis labiata* (Perry, 1811), *Argobuccinum pustulosum*, *Fusitriton magellanicus*, and *Sassia kampyla* (Watson, 1885). They can all be considered to have two very distinct phases in their life cycles, their widely distributed but disjunct breeding populations of large, obvious shells being kept in genetic continuity by their continuously dispersed but almost invisible larval populations. The significance of larval type for understanding biogeography is displayed particularly clearly by those West African tonnoideans that made brief appearances in the tropical western Atlantic during Pliocene and Pliocene times and then disappeared again, notably *Bursa scrobilator* (Linnaeus, 1758) and *Aspa marginata* (Gmelin, 1791) at Limón, Costa Rica. Equally clear examples are provided by those that continue to appear occasionally in small numbers in the western Atlantic at present, such as *Monoplex trigonus* (J., W. & F. Gibson-Smith, 1971) and *M. tranquebaricus* (Lamarck, 1816).

MUSEUMS AND COLLECTIONS EXAMINED

Collections of the richly diverse, beautifully preserved Neogene molluscan faunas of the tropical American region have been accumulated over the past century by a number of major institutions. I have not been able to visit all of them, so it is worthwhile listing the collections that have been studied for the present project.

1. The Natural History Museum, London: The original “Santo Domingo” collections made ca. 1848 by Colonel T. S. Heneken (misspelled J. S. Heniker in the original publication) and described by G. B. Sowerby I (1850). This collection also includes material added from several later collections, including a selection from the Weyl collection, reported on by Pflug (1961). As well, much of the fossil material collected and described by Guppy (1866-1911) and Trechman (1930-1937) from the West Indian islands is in this museum, along with

more recent additions from throughout the tropical American region. The other critically important, historically valuable fossil material for the present work that is held in this museum is that collected from South America by Charles Darwin, described by G. B. Sowerby I (1846; Griffin & Nielsen, 2008). Of course, The Natural History Museum also holds Recent type specimens of a high proportion of ranellid and bursid species, described by Reeve, the Sowerbys, and others such as Gray, Broderip, King, d’Orbigny, and Dunker (mostly material from the collection of Hugh Cuming).

2. Naturhistorisches Museum Basel: This museum has had a history for nearly a century of oil geologists from this area of Switzerland spending their working careers in tropical America, returning to Basel with large collections that have gradually accumulated to make this (at least, until the recent retirement of Peter Jung) the main center for the study of tropical American Neogene molluscan Paleontology. Collections have been contributed by (among others) Hans Kugler, R. Rutsch, and Peter Jung, as well as from many oil companies, and recently this has been the repository of the large collections for the Dominican Republic and Panama Paleontology projects. The enormous, highly diverse collections gathered from Neogene rocks of northern Venezuela by Jack and Win Gibson-Smith have also been incorporated into this museum’s collection. A large collection of Recent mollusks from Venezuela also has been contributed by the Gibson-Smiths. The museum also has the great advantage of having Mayer-Eymar’s huge collection of European Cenozoic mollusks available for comparison with the American ones, along with many other collections from Europe and further afield.

3. United States National Museum of Natural History, Smithsonian Institution, Washington DC: This huge museum holds the collections of many U. S. Geological Survey staff who contributed to geological surveys throughout the tropical American region, and to such international projects as construction of the Panama Canal. Most importantly, it holds the collections described by W. P. Woodring in his classic monographs of the Bowden fauna (Woodring, 1928) and the Gatun fauna of Panama (Woodring, 1959). It also holds the large private collection of A. A. Olsson (other than most of his type material, which is at the Paleontological Research Institution), and many other uniquely important collections. This museum also has extensive collections of Recent western Atlantic mollusks that have contributed significantly to the present work.

4. Paleontological Research Institution, Ithaca, New York: This independent research institute holds, primarily, the collections from the Dominican Republic reported on by Maury (1917a), as well as much of Maury’s other type material. It also holds the types of species from the late Pliocene of northern Venezuela reported on by Weisbord (1962), as well as G. D.

Harris' important collections from the U. S. Tertiary (because Harris was the founder of PRI), the type material of most species described by A. A. Olsson, and many oil company and other collections.

5. Academy of Natural Sciences of Philadelphia: This major museum holds, among many other things, much of W. M. Gabb's collections of fossils from both the Dominican Republic and Limón, Costa Rica. Pilsbry (1922) revised the Dominican Republic collections, and Pilsbry & Johnson (1917) made a significant contribution to knowledge of the Gatun fauna of Panama, based on material at the Academy. Again, this large museum also has extensive collections of Recent western Atlantic mollusks that have contributed greatly to the present work.

6. Museum of Paleontology, University of California, Berkeley: This large paleontological collection includes the largest suite of Californian fossils. It is not generally realized that it also holds large collections of Cenozoic mollusks made throughout the world by oil companies, including from the tropical American region and India-Pakistan; particularly important for the present study are unique collections from the Atlantic coastal area of Colombia.

7. Department of Geology, Tulane University, New Orleans: The large collections from the southern U. S., particularly Florida, and from tropical America gathered during many expeditions by Professors Emily H. and (the late) Harold E. Vokes have provided one of the richest sources for the present work. All taxonomists and many "amateur" collectors of fossils from the tropical American region also have benefited hugely over many years from the Vokes' generosity and kindness. These collections now have been dispersed among the Paleontological Research Institution (Dominican Republic collections), the U. S. National Museum of Natural History (tropical American collections, other than the Dominican Republic), and the Florida Museum of Natural History (collections from Florida, most importantly from the Chipola Fm) (Vokes, 1973, 1986). Early collections from the Dominican Republic that were on loan to me at the time of Professor Emily Vokes' retirement now are largely housed by the Naturhistorisches Museum Basel, with some in GNS Science, Lower Hutt, New Zealand.

As well as all of the above, it has been an extremely valuable help to the present project to be able to use the private collection of Bernard Landau (Albufeira, Portugal), who has collected fossils at most tropical American localities. Also, visiting the Museo de La Plata and Museo Nacional de Historia Natural, Argentina, and the Museo Nacional de Historia Natural, Santiago, Chile, made it possible to include the relatively few South American species of ranellids and personids in this revision.

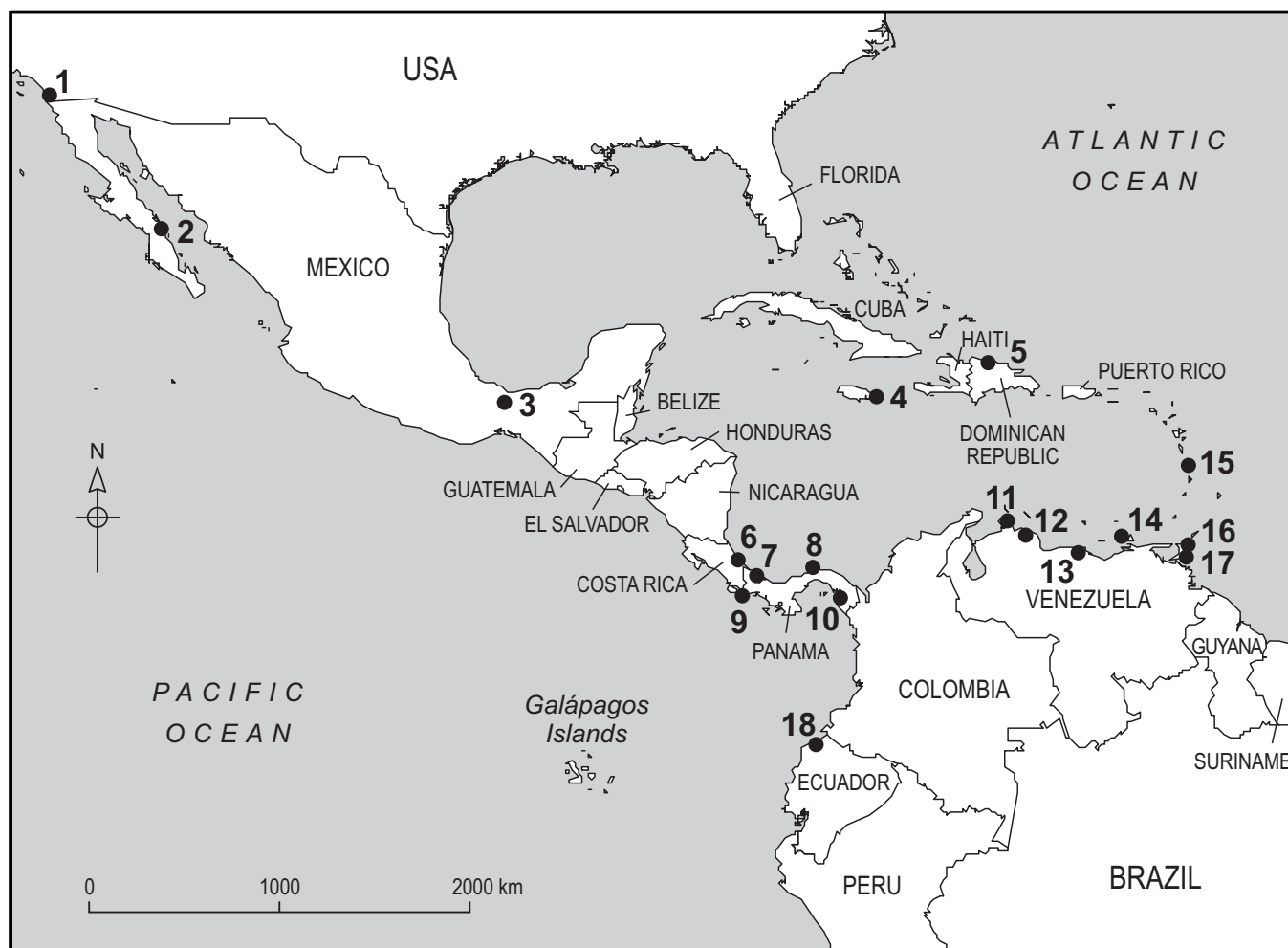
The present revision also tries to add to the usefulness of

the biogeographical analysis by including a revision of the living Ranellidae, Bursidae, and Personidae of both the western Atlantic and the eastern Pacific – an update of Clench & Turner (1957). With this aim, museum collections in Britain, the U. S., and some in Europe (particularly France, The Netherlands, and Germany) have been visited as opportunities allowed over 30 years. More specific details are listed in the Acknowledgments.

THE DOMINICAN REPUBLIC AND PANAMA PALEONTOLOGY PROJECTS

The present monograph is intended as a contribution to both the Dominican Republic Project and the Panama Paleontology Project. These similar, parallel projects aim to provide a faunal survey of these two richly fossiliferous areas of the tropical American region, largely to assess (a) the time of closure of the Central American Seaway (and concomitant formation of the Central American Isthmus, CAI) and (b) biotic change, particularly evolution and extinction, resulting from this closure of the seaway between the Atlantic and Pacific Oceans. The Dominican Republic Project was started by a group at Naturhistorisches Museum Basel, Switzerland, and was introduced in the survey by Saunders *et al.* (1986). A brief summary was also provided by Saunders *et al.* (1982). The Panama Paleontology Project was started by a group from the Smithsonian Tropical Research Center in Panama, along with the Basel group, and was introduced by Collins & Coates (1999). These two introductory surveys outlined the geology of the two areas, described sections and their ages, and provided maps and detailed sections showing the precise location of fossil localities (although neither of them covered the coastal region of Pacific Costa Rica and northern Pacific Panama around the Burica Peninsula).

However, much more than the Dominican Republic and Panama is included in the present monograph. The region covered, and some of the main fossil localities within it, are shown in Text-fig. 1. I have tried to include fossil collections from the entire tropical American region, wherever I had access to them. This information is essential for understanding the biogeography of such wide-ranging taxa as tonnoideans. For Cassidae and Tonnidae (relatively few species in the Recent fauna, with little unresolved about their taxonomy in the tropical American region), the Recent fauna has not been included, apart from a very few Recent additions such as *Cassia norai* Prati Musetti, 1995, and a Recent record of *Echinophoria hadra* (Woodring & Olsson, 1957). *Sconsia* in the Recent fauna was revised by me (Beu, 2008); I concluded that there is only one common shallow-water species, *S. grayi* (A. Adams, 1855) (= *S. lindae* Petuch, 1987). For the remaining families, Bursidae, Personidae, and Ranellidae, all possible Recent taxa and records have been included in this work, as



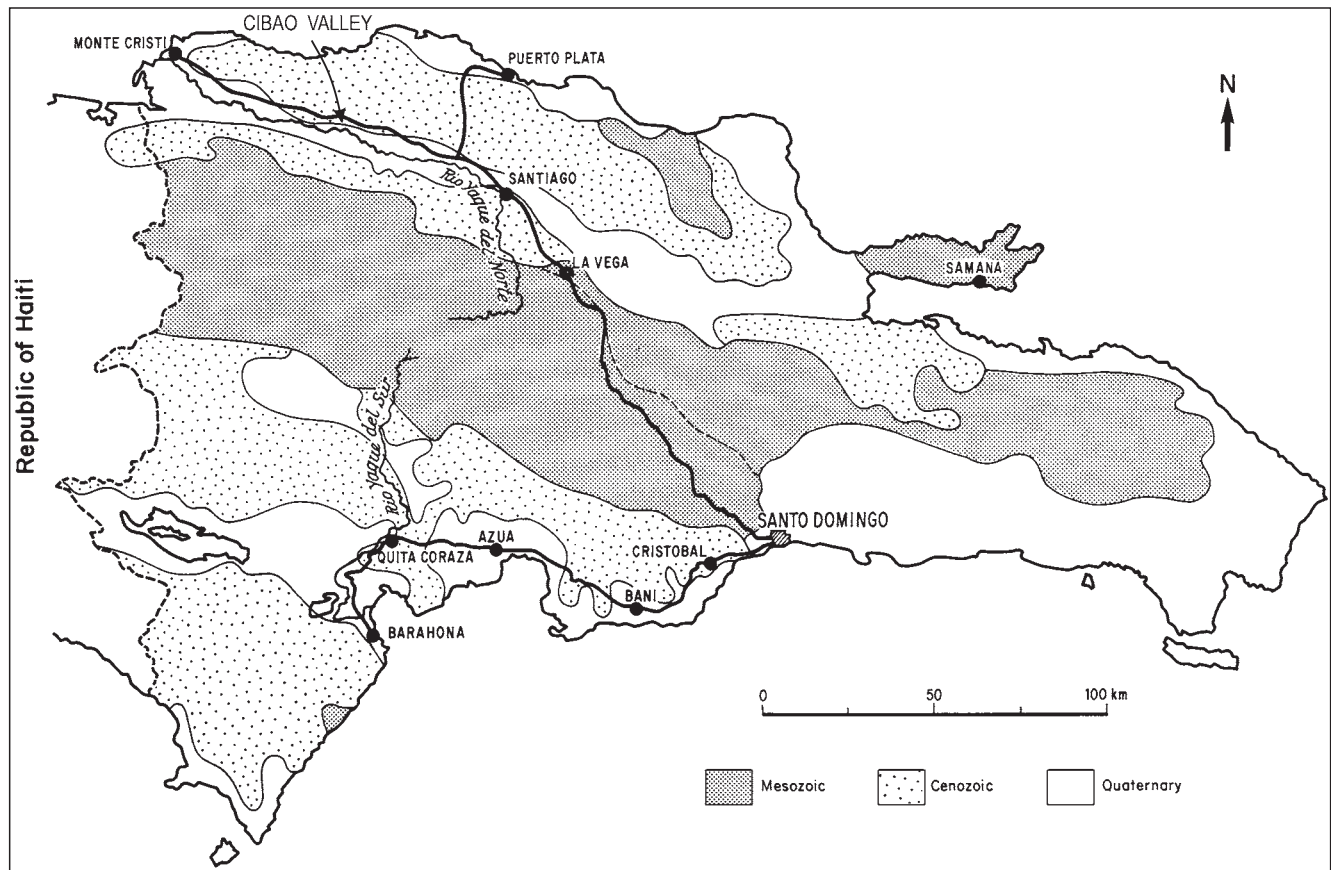
Text-fig. 1. The tropical American region, showing some of the main fossil localities included in this report. 1 – San Diego, California; 2 – Bahia Santa Inés and nearby outcrops of Mulegé Terrace (Last Interglacial), Baja California Sur, Mexico; 3 – Isthmus of Tehuantepec area, Veracruz, Mexico; 4 – Bowden, Jamaica; 5 – Cibao Valley, Dominican Republic (see Text-figs 2-3); 6 – Limón, Costa Rica; 7 – Bocas del Toro Basin, western Panama (see Text-fig. 4); 8 – Colon area, Panama Canal Basin; 9 – Burica Peninsula, border between Costa Rica and Panama; 10 – Darién, southeastern Panama; 11 – Cantaure, Paraguaná Peninsula, Venezuela; 12 – Punta Gavilán, Venezuela; 13 – Cumana, Venezuela; 14 – Isla Cubagua, Venezuela; 15 – Carriacou Island, Grenadine Islands; 16 – Melajo, Trinidad; 17 – Springvale, Trinidad; 18 – Esmeraldas area, Ecuador.

a modernization of Clench & Turner's (1957) monograph, and because a large range of further taxa is now known from the region that was not known to Clench & Turner. The inclusion of Recent material has also been important to help resolve the key questions of the evolution and extinction of taxa, and so of the effects of closure of the Central American Seaway. Therefore, although all of the Recent cassids, tonnids, and laubierinids of the region are not revised here, they are referred to in the following lists and discussion, and most have been revised recently by Marshall (1992), Kreipl (1997), Vos (2007), and me (Beu, 2008); a revision of the Laubierinidae is being prepared by me and Philippe Bouchet. Text-figs 2-3 show the location of the main sections in the Dominican

Republic, whereas Text-fig. 4 shows the main islands in the Bocas del Toro Basin, in western Atlantic Panama.

BIOGEOGRAPHY

The biogeographical history of tropical American Neogene mollusks has been a topic of interest to paleontologists since Woodring (1928, 1966, 1972, 1974, 1978) discussed Cenozoic biogeographical provinces, and classified several taxa as either paciphile or caribphile elements; the term atlantiphile is used here in preference to caribphile. (The southern South American and Southern Ocean species revised below are not included in the following discussion of biogeography). Because many tonnoidean species have very wide geographical



Text-fig. 2. Geological sketch map of the Dominican Republic (after Saunders *et al.*, 1986: text-fig. 2), showing the location of the Cibao Valley, and of Barahona and the road between Bani and San Cristobal in the southern Dominican Republic.

ranges at present, as a consequence of their long-lived planktotrophic larvae, it is particularly interesting for Panamic biogeography to examine how tonnoideans have changed their ranges and speciated with time in the tropical American region. This is aimed at providing new data for the interpretation of the closure history of the CAI.

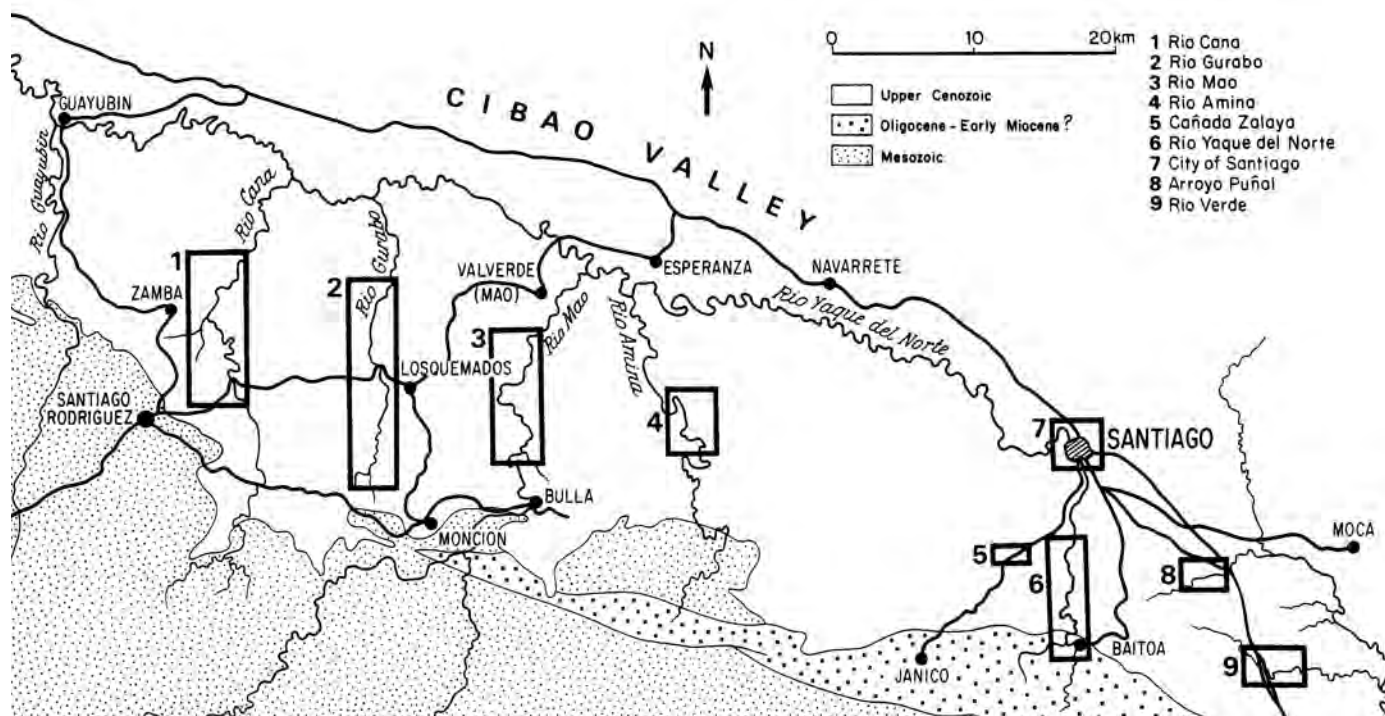
Ages of Tropical American Assemblages

The most important criterion for assessing biogeography is to compare assemblages of the same age. Because most tropical American assemblages are now considered to be significantly younger than was thought by Woodring (1928, 1966), a list is provided here of the well-known molluscan assemblages in the tropical American region that contain tonnoidean gastropods revised in this monograph, arranged by age, with references to the latest information on their age. I am grateful to Bernard Landau for providing much of the list and references from the PhD thesis that he is preparing on the Pliocene Mollusca of Cubagua Island.

(1) Late Early Miocene: Chipola Fm, Florida (Akers, 1972; Vokes, 1979, 1989; Bryant *et al.*, 1992); Baitoa Fm, Dominican Republic: 17.5-14.5 Ma (Vokes, 1979; Saunders

et al., 1986); Cantaure Fm, Venezuela (Hunter, 1978; Gibson-Smith & Gibson-Smith, 1979); Zorritos Fm, Peru (Olsson, 1932); Pirabas Fm, Pará, northeastern Brazil (Ferreira, 1980; Távora & Fernandes, 1999). An important discussion of the main mollusk-rich fossil localities of northern Venezuela was provided by Gibson-Smith & Gibson-Smith (1979). The sequence of formations is: (a) earliest, La Candelaria beds (= Agua Clara Fm?), late Early Miocene; overlain by Cantaure Fm (which contains mollusks in two discrete shellbeds); overlain by El Porvenir beds, latest Early Miocene or, more probably, early Middle Miocene; Caujarao Fm, basal member, late Middle Miocene; Caujarao Fm, Mataruca Member, early Late Miocene; Cubagua and Punta Gavilán formations, Early to middle Pliocene; and finally, Mare Fm, Late Pliocene at the base and Early Pleistocene above.

(2) Middle Miocene: Shoal River Fm, Florida (E. & H. Vokes, 1989; Jones *et al.*, 1993); Ferrotepec Fm, Mexico (Perrilliat, 1987); Valiente Fm, Bocas del Toro Basin, Atlantic Panama (16.4-12.0 Ma; Coates *et al.*, 2003); lower Gatun Fm, Atlantic Panama (Cotton, 1999); Manzanilla, Cipero and Brasso formations, Trinidad (Bolli & Primoli Silva, 1973; Bolli & Saunders, 1985; Maurasse, 1990); Grand Bay Fm,



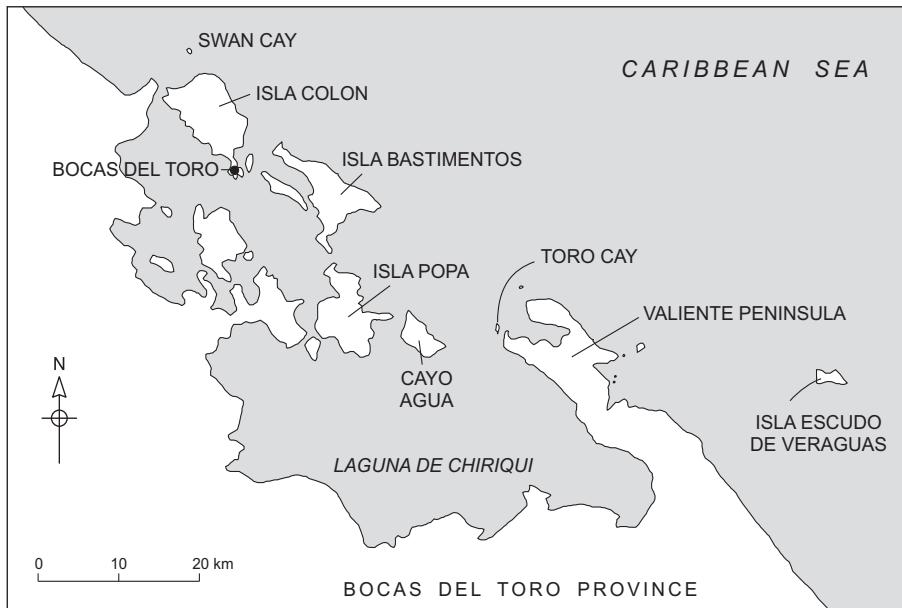
Text-fig. 3. Geological sketch map of the Cibao Valley, northern Dominican Republic, showing the main fossiliferous sections (Saunders *et al.*, 1986: text-fig. 3). Numbered sections refer to text-figures (large numbered folding maps, in pocket at rear of Saunders *et al.*, 1986), on which NMB, TU, and USGS fossil localities are mapped in detail.

Carriacou Island (Robinson & Jung, 1972; Donovan *et al.*, 2003); isolated road cut 8.6 km west of plaza at San Cristobal, on road to Bani, southern Dominican Republic, unnamed Middle Miocene formation, planktic foram zone N.11, discussed by E. Vokes (in E. & H. Vokes, 1989: 66-67).

(3) Late Miocene: Cercado Fm and basal part of Gurabo Fm, Dominican Republic (7.5-5.7 Ma: Saunders *et al.*, 1986); Punta Judas, Pacific Costa Rica (Seyfried *et al.*, 1985; Jung, 1995); middle and upper Gatun Fm, Atlantic Panama (Cotton, 1999); Nancy Point Fm, Bocas del Toro Basin, Atlantic Panama (6.5-5.6 Ma; Coates in Collins & Coates, 1999: text-fig. 5); Tuirá and Chucunaque Formations, Darien, Pacific Panama (Coates *et al.*, 2004, published a new map and description of Darien geology and concluded that all fossiliferous units are Middle to Late Miocene in age); Caujarao and El Veral Formations, Venezuela (Bolli, 1970; Hunter, 1978); Angostura Fm, Ecuador (Jung, 1989).

(4) Pliocene: Jackson Bluff Fm (= Choctawhatchee Group, in part), Florida (Ward, 1992: fig. 1; Cotton, 1999); lower Pinecrest beds, Florida (units 10-5), middle Pliocene (Lyons, 1991), also middle Pliocene (Pinecrest member, Tamiami Fm) according to Vermeij (2005: 628); upper Pinecrest (units 4-2) Late Pliocene (Lyons, 1991), equivalent to Fruitville member, Tamiami Fm, Late Pliocene (Vermeij, 2005: 628); Caloosahatchee Fm, Florida (latest Pliocene: Lyons, 1991;

Zullo, 1992: fig. 1; upper part probably Pleistocene: Ward, 1992: fig. 1; latest Pliocene according to Vermeij, 2005: 628); Agueguexquite Fm, Veracruz, Mexico (zone N20: Akers, 1981; 2.9-2.5 Ma: Cotton, 1999); Banáño Fm, Atlantic Costa Rica (3.6-2.4 Ma: Cotton, 1999); Cayo Agua Fm, Atlantic Panama (5.0-3.5 Ma: Cotton, 1999); Fish Hole Member of Shark Hole Point Fm, Atlantic Panama [3.0-2.2 Ma: Panama Paleontology Project (PPP) web locality database; "unnamed" by Coates in Collins & Coates, 1999: text-fig. 5]; Shark Hole Point Fm, Atlantic Panama (5.2-2.3 Ma: PPP locality database; Coates in Collins & Coates, 1999: text-fig. 5); Escudo de Veraguas Fm, Atlantic Panama (3.6-1.8 Ma; Cotton, 1999; Coates in Collins & Coates, 1999: text-fig. 5); Penita Fm, Charco Azul Group, Pacific Panama (3.5-2.2 Ma: Cotton, 1999); Gurabo Fm, Dominican Republic (5.6-4.0 Ma: Saunders *et al.*, 1986); Mao Fm, Dominican Republic (Saunders *et al.*, 1986; 4.0-3.5 Ma: Cotton, 1999); Bowden Shellbed, Jamaica (early Late Pliocene, zone NN16: Aubry, 1993; Early Pliocene: Jung & Heitz, 2001; Late Pliocene: Kohl & Robinson, 1999; 2.8-1.6 Ma, *i.e.*, spanning the Pliocene-Pleistocene boundary: Cotton, 1999; olistostrome with reworked "middle" Pliocene fossils: Macsotay, pers. comm. to Bernard Landau, 2007); Usiacuri Fm, Colombia (Early Pliocene: Jung, 1989); Tubará Fm, Colombia (Hunter, 1978); Springvale Fm, Trinidad (Hunter, 1978; Donovan,



Text-fig. 4. The Bocas del Toro region in western Atlantic Panama, showing the main islands with Neogene sedimentary sections mentioned in the text. Localities were mapped in detail (by PPP number), as well as for the Colon area, Panama Canal Basin, and for Limón, Atlantic Costa Rica, by Coates (in Collins & Coates, 1999: appendix 1).

1994); Punta Gavilán Fm, Venezuela (Bolli & Premoli Silva, 1973; Hunter, 1978); Cubagua Fm, Venezuela (Early Pliocene: Macsotay *et al.*, 1995); lowest part of Mare Fm, Venezuela (Gibson-Smith & Gibson-Smith, 1979; Macsotay, pers. comm. to Bernard Landau, 2007); Esmeraldas and Jama Formations, Ecuador (Jung, 1989); Canoa Fm, Ecuador (Late Pliocene: Landini *et al.*, 2002).

(5) Plio-Pleistocene boundary: Moín Fm, Limón, Atlantic Costa Rica (1.9-1.5 Ma: Cotton, 1999; McNeill *et al.*, 2000).

(6) Pleistocene: Bermont Fm, Florida (Lyons, 1991: 159; Zullo, 1992: fig. 1; including Loxahatchee member: Vermeij, 2005: 628); Mulegé Terrace cover beds, Bahia de Santa Inés, Turtle Bay, Mulegé, and nearby areas, Baja California Sur, Mexico (Last Interglacial, oxygen isotope stage 5e: Emerson *et al.*, 1981; Ashby & Minch, 1987; Ashby *et al.*, 1987; Jung, 1989; Ortlieb, 1991; Careño & Smith, 2007: 85-86); Montezuma Fm, Pacific Costa Rica (Baumgartner *et al.*, 1984); Burica Fm, Charco Azul Group, Pacific Panama (1.8-1.5 Ma: Cotton, 1999); Armuelles Fm, Charco Azul Group, Pacific Panama (1.7-0.5 Ma: Cotton, 1999); Swan Cay Fm, Atlantic Panama (1.8-0.9 Ma: Coates in Collins & Coates, 1999: text-fig. 5); La Isabela Fm, Dominican Republic (Marcano & Tavares, 1982); Matura shellbed, Talparo Fm, Trinidad (Jung, 1989); Mare Fm, Venezuela, apart from the lowest part (Gibson-Smith & Gibson-Smith, 1979; Macsotay, pers. comm. to Bernard Landau, 2007); Cumaná Fm, Venezuela

(Bolli, 1972); El Manglillo Fm, Araya Peninsula, Venezuela (Macsotay, 2005; Macsotay & Hernandez, 2005); Playa Grande Fm, Venezuela (Jung, 1989).

TONNOIDEA IN DOMINICAN REPUBLIC NEOGENE FAUNAS

Maury (1917a-b), Saunders *et al.* (1986), and E. Vokes (in E. & H. Vokes, 1989) have provided overviews of the stratigraphy and the history of study of the Neogene rocks and fossils of the Cibao Valley, northern Dominican Republic. Maury (1917a) described the route followed and the difficulties of her expedition, during which K. P. Schmidt and A. A. Olsson collected all the fossils. E. Vokes (in E. & H. Vokes, 1989: 6-22) gave helpful background information on the history of study and the stratigraphy of the sections in the Cibao Valley, with very useful outcrop photographs of critical intervals, one of them a better

view of an outcrop, Río Gurabo at Los Quemados, illustrated earlier by Maury (1917b: pl. 68B; E. Vokes in E. & H. Vokes, 1989: text-fig. 9). This was augmented by the further outcrop photographs and detailed stratigraphy, with detailed fossil locality maps, provided by Saunders *et al.* (1986). The latter authors, based at Naturhistorisches Museum Basel, set out to describe the stratigraphy based on much the longest section, in the Río Gurabo, relating sections in the Río Mao, Río Cana, and Río Amina to it laterally, with an additional description of the Baitoa Fm section (Saunders *et al.*, 1986: pl. 9) on the Río Yaque del Norte at Baitoa, near Santiago. E. & H. Vokes (1989), in contrast, set out simply to collect muricids, along with all other possible mollusks, from as many localities as possible in the region, as part of a program to revise the Cenozoic fossil Muricidae of tropical America. They amplified Maury's (1917a) and earlier poorly localized collections as they went. Consequently, they visited a number of other sections besides the main river ones sampled in detail by the Basel group. Such localities as Arroyo Puñal, Río Verde, and road cuts along highways traversed to reach the river sections have been collected only by the Vokes, later augmented by Bernard Landau's excellent collecting. Both groups concluded that the main fossiliferous formations, the Cercado, Gurabo, and Mao Formations, are at least partly laterally equivalent, diachronous facies of similar age, separable in the Río Gurabo but apparently laterally equivalent in the other main river sections. Foraminiferal and calcareous nan-

nofossil biostratigraphy has established that the Baitoa Fm is Burdigalian (mainly) to Langhian in age (late Early to early Middle Miocene), and is separated by a clear break (E. Vokes in E. & H. Vokes, 1989: text-fig. 16) from younger units. The Cercado Fm is late Serravallian to (mostly) Tortonian in age (Late Miocene). It consists of shallow-water sandstone and conglomerate, with subordinate siltstone and claystone. The highest level is siltstone packed with coral and algal debris (Saunders *et al.*, 1986: 12). The sandstone is cross-bedded in many horizons, with concentrations of the abundant large foraminiferan *Amphistegina* emphasizing the cross-bedding. E. Vokes (in E. & H. Vokes, 1989: 21) suggested a depth of deposition of 0-20 m. The Gurabo Fm is late Tortonian to Zanclean and possibly in part early Piacenzian in age (late Late Miocene to Early Pliocene). It consists of a basal conglomerate in some sections along the Río Gurabo (Saunders *et al.*, 1986: pl. 1, figs 1-2), but cut out in others, and not present in the other river sections, overlain by calcareous, fossiliferous siltstone with bedding emphasized by lines of concretions. This passes up into cross-bedded, burrowed sandstone similar to the Cercado Fm, overlain in turn by calcareous siltstone and sandy siltstone rich in corals. Corals occur in beds, scattered separate heads, and biostromes (fossil reefs), with coralliferous siltstone toward the top of the formation. Downstream from the road bridge on the Río Gurabo at Los Quemados, the uppermost part of the succession consists of massive calcareous siltstone rich in microfossils and mollusks. E. Vokes (in E. & H. Vokes, 1989: 21) suggested that shallow-water parts of the Gurabo Fm, with abundant corals, were deposited in 20-50 m of water, and deeper parts, such as the section along the lower Río Gurabo, in 50-150 m. Some parts, with massive siltstone, such as in Arroyo Zalaya and Río Verde, were deposited in 150-350 m of water (E. Vokes in E. & H. Vokes, 1989: 21). The overlying Early to Middle Pliocene Mao Fm clays were deposited in the deepest water of all, at least 350 m, although gravity flows have brought shallow-water material downslope to mix with the deep-water sediments (E. Vokes in E. & H. Vokes, 1989: 22), and the Mao Adentro Limestone member (Saunders *et al.*, 1986: pl. 6) consists of coral debris transported down-slope into the deposition site.

Tonnoideans reflect these depositional environments perhaps as much as the muricoideans were concluded to by E. Vokes (in E. & H. Vokes, 1989). The first obvious point is that the most common and widespread bursid in tropical American Neogene faunas, *Bursa rugosa* (G. B. Sowerby II, 1835), is not represented by a single specimen from the Dominican Republic. This species lives at present abundantly on the intertidal rocky shore in Panama Bay, and its absence presumably reflects the lack of intertidal facies in the Dominican Republic localities, with the possible exception of the Cercado Fm. Several other intertidal bursids, such as

B. rhodostoma and *B. corrugata*, also have no record in the Dominican Republic, despite a Miocene-Recent time range in tropical America. Approximate counts of specimens and collection numbers (listed in the text below) in the Dominican Republic tonnoidean fauna provide a more visible means of comparison (Table 1).

Taxa in Dominican Republic collections

An important bias to keep in mind when interpreting Dominican Republic faunas is relative outcrop area. A lot of the differences between formations in recorded specimen numbers simply result from the fact that outcrops assigned to the Gurabo Fm occupy approximately three-quarters (or more) of all exposures; most of the rest, assigned to Cercado Fm, and outcrops of Baitoa Fm, Mao Fm, and the unnamed formation of E. Vokes (in E. & H. Vokes, 1989: 21), is very minor. This bias presumably also affects the Atlantic Panama results described in the following section, *e.g.*, Swan Cay Fm (Pleistocene) crops out only on the very small Swan Cay, but I have even less idea of relative outcrop area for Panama formations than I have for the Dominican Republic. Without some measure of relative outcrop area, this bias cannot be accounted for. Raw counts of specimens and collections, and their paleoecological interpretation, are discussed below.

1. *Bursa amphitrites*: only 18 specimens and frags were collected, in 11 collections, all from the Gurabo Fm. The tallest specimen is from TU1278 (large arroyo on eastern side Río Gurabo at ford on Los Quemados-Sabaneta road), where the Gurabo Fm evidently was deposited in moderately deep water. It seems feasible that this species was ancestral to the *B. latitudo*-*B. natalensis* species group, which now lives in the tropical western Atlantic and Indo-West Pacific in 150-300 m or more, but most Dominican Republic specimens evidently lived in shallower water than this.

2. *Bursa grayana*: Cercado Fm, 29 specimens in three collections; Gurabo Fm, 53 specimens in 25 collections; Mao Fm, 1 specimen. The only other recorded fossils are 1 specimen each in the Cayo Agua Fm (Pliocene) at Cayo Agua, Atlantic Panama, and in the Pliocene of Atlantic Mexico (USGS 18688). This is an offshore species at present, mostly collected by divers in Florida and from fish stomachs off of Brazil. It evidently prefers offshore hard substrata, so its occurrences in the Dominican Republic reflect this offshore hard habitat in *ca.* 30-70 m and deeper. The abundance in a few Cercado Fm collections is, therefore, surprising.

3. *Marsupina bufo*: Cercado Fm, 2 specimens; Gurabo Fm, 1 specimen. The specimen in the Gurabo Fm is from TU 1449, from gravity flows in the Río Yaque del Norte near Barranca, *i.e.*, shallow-water material carried down into deeper water. Maury (1917a: 272) recorded her material, including the fine specimen that she illustrated, as from "Río Cana,

Table 1. Numbers of specimens of tonnoidean species in Dominican Republic formations. Numbered species (left margin) are not in common with Table 2; *species extending until the present day; +, further (uncounted) specimens present; -, not present; numbers in parentheses are of uncertain stratigraphical position.

	Baitoa	Cercado	Gurabo	Mao	Unnamed
1. <i>Bursa amphitrites</i>	-	-	18	-	-
<i>Bursa grayana</i> *	-	29	53	1	-
<i>Marsupina bufo</i> *	-	2	1	-	-
<i>Distorsio clathrata</i> *	-	-	2	-	-
<i>Distorsio mcgintyi</i> *	4	3	148	-	-
<i>Distorsio simillima</i>	3	9	201	-	-
2. <i>Charonia lampas</i> *	(1)	-	(1)	-	-
<i>Charonia variegata</i> *	-	1	14	-	-
<i>Cymatium praefemorale</i>	-	14	49	1	-
<i>Monoplex cercadicus</i>	1	9	18+	-	-
3. <i>Monoplex gurabonicus</i>	1	2	49	-	1
<i>Monoplex krebsii</i> *	1	-	52	-	-
4. <i>Monoplex longispira</i>	2	-	1	-	-
<i>Monoplex parthenopeus</i> *	2	1	1	1	-
5. <i>Monoplex pilearis</i> *	1	2	3	-	-
6. <i>Septa landaui</i>	6	-	1	-	-
<i>Turritriton domingensis</i>	2	9	6	-	-
7. <i>Sassia warreni</i>	-	-	7	1	-
8. <i>Cymatiella vokesorum</i>	2	-	-	-	-
<i>Cassis altispira</i>	-	-	1	-	-
9. <i>Cassis sulcifera</i>	-	46	235+	-	6
10. <i>Cypraeacassis testiculus</i> *	6	1	48	-	2
11. <i>Galeodea cf. echinophora</i> *	-	-	(2)	-	-
12. <i>Sconsia laevigata</i>	5	5	435+	3	-
13. <i>Dalium dalli</i>	-	-	12	-	-
<i>Echinophoria hadra</i> *	-	-	1	-	-
14. <i>Semicassis reclusa</i>	2	1267	135	-	-
15. <i>Malea camura</i>	-	99	192	1	1
16. <i>Malea elliptica</i>	8	40	25	-	-
<i>Malea goliath</i>	1	-	19	-	-
17. <i>Tonna galea</i> *	-	4	2	-	-
<i>Tonna pennata</i> *	-	2	2	-	-
Species totals: 32 (14*)	16 (17?)	19	29 (31?)	6	4
Specimen totals: 3,345	48	1,545	1,734+	8	10
Specimens/species: 104.5	2.8	81.3	55.9	1.3	2.5

Guayubin to Mao road, and Cerro Gordo to Mao road,” apparently two distinct localities. *Marsupina bufo* is extremely abundantly dredged on offshore soft substrata in depths of approximately 30-200 m along the northern coast of South America at present, particularly off of Suriname and Guiana, but its occurrences as a fossil are unusually “patchy.” Its rarity in the Dominican Republic evidently results from an unusual combination of a mid- to outer continental shelf depth range with an unusual environmental requirement. Diaz (1995) pointed out the northern coasts of Colombia and Venezuela as diversity “hot spots” in the Caribbean at present because of up-welling driven by the onshore trade winds, so possibly

the high productivity of upwelling areas is necessary for *M. bufo* to be abundant.

4. *Distorsio clathrata*: 2 specimens only, in the Early Pliocene part of the Gurabo Fm. There are very few records of this species from pre-Pliocene rocks of tropical America, and it possibly evolved from the *D. decussata* species group or *D. floridana* late in Miocene time. This was possibly one of the biological results of the beginning of restriction of the CAI. Also, though, Recent specimens occur in relatively shallow water for a *Distorsio* species, so possibly by the time *D. clathrata* evolved and became common, environments represented in the Dominican Republic were too deep for it.

5. *Distorsio mcgintyi*: Baitoa Fm, 4 specimens; Cercado Fm, only 3 specimens; Gurabo Fm, 148 specimens in 42 collections. *Distorsio mcgintyi* is an offshore species on soft substrata today, and its increasing abundance with increasing depth of deposition in the Dominican Republic seems to be explained simply by this depth and substratum preference.

6. *Distorsio simillima*: Baitoa Fm, 3 specimens in one collection; Cercado Fm, 9 specimens in eight collections; Gurabo Fm, 201 specimens in 68 collections. *Distorsio simillima* is one of the most abundant and characteristic tonnoideans in the Dominican Republic faunas, exceeded in abundance only by members of Cassidae and Tonnidae, particularly *Cassis sulcifera*, *Sconsia laevigata*, *Semicassis reclusa*, and *Malea camura*. As with the previous species, this seems simply to reflect its preference for offshore soft substrata.

7. *Charonia lampas*: 1 recorded specimen is from the Gurabo Fm in the Río Gurabo in the first bluff downstream from the road bridge at Los Quemados (Early Pliocene). The other specimen is possibly from Baitoa Fm, based on its style of preservation (E. Vokes, pers. comm., April 2008), although not localized in detail. It is also possibly from the Gurabo Fm near where the other specimen was collected, as John Saunders (pers. comm., 1982) reported many years ago that the fine-grained matrix (*i.e.*, unlikely to be Cercado Fm) removed from this specimen contains *Hirsutella margaritae* (Bolli & Bermudez, 1965), a planktonic foraminiferal species that appears in low latitudes at around the Miocene-Pliocene boundary (Kennett & Srinivasan, 1983: text-fig. 15,

pl. 32, figs 4-6), and was used as the main Miocene-Pliocene boundary index species in the Dominican Republic by Saunders *et al.* (1986: 17, 19), although it is possibly slightly earlier in New Zealand and other higher latitudes. *Charonia lampas* seems to have been as rare in the western Atlantic during Miocene and Pliocene times as it is now, so probably the few fossils represent a pseudopopulation recruited from South Africa, just as are present-day Brazilian specimens.

8. *Charonia variegata*: Cercado Fm, 1 internal mold only; Gurabo Fm, 14 specimens in as many collections. This species is rare in Dominican Republic faunas, probably reflecting its shallow-water soft-substratum preference at present (*e.g.*, seagrass flats) inhabited by its echinoid prey, particularly clypeasteroids. All specimens in the Dominican Republic faunas are immature. Possibly all specimens were transported in from a shallower-water habitat.

9. *Cymatium praefermale*: Cercado Fm, 14 specimens in ten collections; Gurabo Fm, 49 specimens in 24 collections; Mao Fm, 1 frag. This large, spectacular shell is uncommon at best in the Dominican Republic faunas. The distribution of specimen numbers implies that it preferred an offshore habitat, like that of its Recent relative *C. raderi*, rather than the shallow-water soft substrata, such as seagrass flats, favored by its other Recent relative, *C. femorale*.

10. *Monoplex cercadicus*: Baitoa Fm, 1 specimen; Cercado Fm, 9 specimens in six collections; Gurabo Fm, 18 specimens in 14 collections, plus "many small" specimens in TU 1279. Again, *M. cercadicus* is uncommon at best in the Dominican Republic faunas, but it seems to have preferred an offshore soft substratum. The apparently related present-day eastern Pacific species, *M. wiegmanni*, lives in shallow, near-shore, soft and hard substrata, and is trawled offshore on soft substrata by shrimpers, so if the relationship is as close as is suggested below, the lineage possibly has changed its ecological preference relatively recently.

11. *Monoplex gurabonicus*: Baitoa Fm, 1 specimen; Cercado Fm, 2 specimen in two collections; Gurabo Fm, 49 specimens in 21 collections; unnamed formation of E. Vokes (in E. & H. Vokes, 1989: 21), 1 specimen. This species is moderately common in the Gurabo Fm, and is scarcely recorded anywhere else, although its small size possibly means that some specimens have avoided collection. It seems once again to have preferred an offshore soft substratum, like that of its present-day close relative, *M. comptus*.

12. *Monoplex krebsii*: Baitoa Fm, 1 specimen; Gurabo Fm, 52 specimens in 17 collections. This is the most commonly collected offshore *Monoplex* species in the western Atlantic at present, but is as uncommon as the extinct species *M. gurabonicus* in Dominican Republic collections. It provides one of the clearest examples of a preference for Gurabo habitats over those of the Cercado Fm (from which none has been

collected), obviously reflecting its preference for offshore soft substrata.

13. *Monoplex longispira*: Baitoa Fm, 1 frag and 1 small specimen; deep-water facies of Gurabo Fm in Río Verde, 1 specimen (holotype). There are too few records to conclude much about this species, but the occurrence of the single adult specimen in the deep-water Gurabo Fm seems to imply that *M. longispira* was a deep-water, perhaps bathyal species. However, such robust, thick-shelled *Monoplex* species are mostly shallow-water rocky reef inhabitants at present, suggesting, in contrast, that this was a transported specimen from shallower water.

14. *Monoplex parthenopeus*: Baitoa Fm, 2 specimens in two collections; Cercado Fm, 1 small specimen; Gurabo Fm, 1 specimen; and 1 specimen from the Mao Adentro Limestone member of the Mao Fm. This is the most widespread large *Monoplex* species in the present-day world fauna, but is nowhere very common today, and its sparseness is evidently reflected in the Dominican Republic faunas. However, it was not very common or widely distributed around the world by Late Miocene-Early Pliocene time, and its history is little understood. The Chipola Fm (Burdigalian) specimen identified below as "*Monoplex* n. sp. A" is approximately coeval with the earliest record of *M. parthenopeus* that I am aware of, in the Baitoa Fm, and is possibly merely an early, very coarsely sculptured specimen of *M. parthenopeus*. *Monoplex parthenopeus* is a species with mysterious origins, followed by a Pliocene-Pleistocene "blooming" that saw it spread rapidly throughout much of the temperate and tropical world ocean. This presumably implies that it evolved a particularly long-lived planktotrophic larval stage at about the end of Miocene time, perhaps in response to cooling sea temperatures.

15. *Monoplex pilearis*: Baitoa Fm, 1 small specimen; Cercado Fm, 2 specimens; Gurabo Fm, 3 specimens. *Monoplex pilearis* is mostly a shallow-water species on hard substrata at present, and is commonly collected on rock (rather than coral) reefs, in the tropical Atlantic just as in the Indo-West Pacific province. Most of the few Dominican Republic records seem likely to represent transport of empty shells into deeper environments than those in which it lived.

16. *Septa landaui*: Baitoa Fm, 6 small paratypes at one locality; holotype only, from the Pliocene part of the Gurabo Fm in the Río Gurabo. Too few records of this rare species are available to be able to interpret its preferred environment, but most specimens of this genus seem to be associated with shallow-water coral reefs at present, and it is possible that all specimens were transported into deeper water than it inhabited.

17. *Turritriton domingensis*: Baitoa Fm, 2 specimens; Cercado Fm, 9 specimens in four collections; Gurabo Fm, 6 specimens in six collections. This species is closely related to

the very widespread species *T. labiosus*, which occupies a wide range of depths and hard substrata at present. Its rarity in the Dominican Republic, but greater commonness in the Cercado than in the Gurabo Formations, implies that it preferred shallow water. Possibly, again, some specimens were transported into the Gurabo Fm from a near-shore environment.

18. *Sassia warreni*: Gurabo Fm, 7 specimens from one locality; Mao Fm, 1 specimen. Again, this species is too rare to be able to reach a conclusion about its ecology, but it seems likely to have been an offshore species. Like most of the Recent species resembling the type species of *Sassia*, *S. apenninica* (Sassi, 1827), *S. warreni* might well have been a bathyal soft-substratum species whose environment is scarcely represented in the Dominican Republic. Its classic tonnoidean planktotrophic protoconch (Warén & Bouchet, 1990: fig. 163), with reticulate sculpture of thin, widely spaced axial and spiral ridges, implies that *S. warreni* would have been widespread in tropical America (and perhaps throughout the Atlantic) during Early Pliocene time, but localities where the depositional environment was deep enough to preserve it seem to have been sparse.

19. *Cymatiella vokesorum*: Baitoa Fm, 2 specimens; other material is from Trinidad, and the cutting on the road to Bani in the southern Dominican Republic. Again, there is too little material available to be able to interpret the environment preferred by this species, but it possibly occupied a similar intertidal, rocky-shore habitat to that of the southern Australian living species. This is the one Dominican Republic tonnoidean that is not recorded from the Gurabo Fm.

20. *Cassis altispira*: 1 specimen from the Gurabo Fm in the Río Cana. Possibly most of the Dominican Republic rocks were deposited in too deep water for this species. It is possible that the large specimen illustrated by Maury (1917a: pl. 44, fig. 1) as *C. sulcifera* is actually another specimen of *C. altispira*, as suggested by the narrow callus shield, tall spire, prominent spiral sculpture, and three rows of large nodules, but it is impossible to be sure from her dorsal view. Maury (1917a: 274) also commented on her material appearing at first to be two distinct species.

21. *Cassis sulcifera*: Cercado Fm, 46 specimens in 23 collections; Gurabo Fm, 235 specimens in 81 collections, plus "many small" ones in TU 1215; unnamed formation of E. Vokes (in E. & H. Vokes, 1989: 21), 6 specimens in two collections. This is one of the most common and characteristic large fossils of the Gurabo Fm, and apparently preferred a more offshore habitat than the later Pliocene-Recent western Atlantic *Cassis* species. This and its relatively small adult size indicate that it preyed upon much smaller, more offshore echinoids than the large clypeasteroids and *Diadema*, etc., preyed upon by Recent *Cassis* species (see below, under *C. tuberosa*). Perhaps the widely expanded ventral callous shield

is an adaptation to feeding on long-spined echinoids, allowing the wide range of prey recorded below for *C. tuberosa*. The similar callous shield then possibly reflects a similar range of smaller, but long-spined, prey for *C. sulcifera* rather than a close phylogenetic relationship to *C. tuberosa*.

22. *Cypraeacassis testiculus*: Baitoa Fm, 6 specimens in one collection; Cercado Fm, 1 specimen; Gurabo Fm, 48 specimens in 21 collections; unnamed formation of E. Vokes (in E. & H. Vokes, 1998: 21), 2 specimens in one collection. Again, this is an uncommon species that is best represented in the Gurabo Fm, and evidently preferred (and still prefers) offshore soft substrata, and so evidently preys upon small offshore echinoids.

23. *Galeodea* cf. *echinophora*: 2 specimens, probably both from deep-water facies of the Gurabo Fm, although one is unlocalized. *Galeodea echinophora* is a bathyal species in the Mediterranean Sea at present, and this is apparently another bathyal species whose environment is scarcely represented in the Dominican Republic.

24. *Sconsia laevigata*: Baitoa Fm, 5 specimens in two collections; Cercado Fm, 5 specimens in four collections; Gurabo Fm, 435 specimens in 102 collections, plus uncounted specimens at 12 localities; Mao Fm, 3 specimens in two collections. *Sconsia laevigata* is one of the most abundant, characteristic Gurabo Fm species, and evidently occupied the same offshore, soft-substratum habitat as *S. grayi* occupies at present along the northern coast of South America. The abundance of this species, and yet rarity of *Marsupina bufo*, indicates that the Gurabo Fm was deposited in conditions similar to those along the Colombian Caribbean coast at present, rather than the coast of eastern Venezuela and Guiana, although it is not obvious what the distinction is caused by at present.

25. *Dalium dalli*: 12 specimens in six collections, all from deep-water facies of the Gurabo Fm. This and the following species are further bathyal species whose habitat is scarcely represented in the Dominican Republic. Most of the recently collected material of *D. solidum* is from off of the coasts of Venezuela and Guiana.

26. *Echinophoria hadra*: 1 specimen from the deep-water facies of the Gurabo Fm in Arroyo Zalaya. Again, the few known Recent specimens are from off of the coast of Guiana.

27. *Semicassis reclusa*: Baitoa Fm, 2 specimens; Cercado Fm, 1,267 specimens in 32 collections, many of them small juveniles; Gurabo Fm, 135 specimens in 46 collections, many of them larger than the specimens in the Cercado Fm. This is one of only two tonnoideans that are more abundant in the Cercado than in the Gurabo Fm, and is represented by huge numbers of juvenile specimens in the Cercado shell lenses. Evidently *S. reclusa* preferred the same near-shore sandy substratum, just off of ocean beaches, as is occupied by its close relative *S. granulata* at present, and preyed on similar sandy

beach "sand dollar" clypeasteroid echinoids.

28. *Malea camura*: Cercado Fm, 99 specimens in 14 collections; Gurabo Fm, 192 specimens in 47 collections; Mao Fm, 1 specimen; unnamed formation of E. Vokes (in E. & H. Vokes, 1989: 21), 1 specimen. This *Malea* species is more abundant in the more offshore Gurabo Fm than in the shallow-water Cercado Fm, the opposite of *M. elliptica* (below). This suggests two possible explanations of their occurrences: (a) they are ecophenotypic forms of one species, or (b) they are distinct species that largely occupied different habitats and so apparently preyed upon distinct echinoderms. At present the second possibility seems the more likely, and so is adopted here, but further research is required to finalize their interpretation.

29. *Malea elliptica*: Baitoa Fm, 8 specimens in four collections; Cercado Fm, 40 specimens in nine collections; Gurabo Fm, 25 specimens in 11 collections. This is the one other tonnoidean (besides *Semicassis reclusa*) that is more common in the Cercado than in the Gurabo Fm, particularly keeping in mind that Gurabo Fm outcrops are much more extensive; this is discussed under *M. camura*.

30. *Malea goliath*: Baitoa Fm, 1 specimen; Gurabo Fm, 19 specimens (mostly frags) in six collections. Again, there is too little material to be able to interpret this species, taxonomically or ecologically; several possible taxonomic interpretations are discussed in the systematic section.

31. *Tonna galea*: Cercado Fm, 4 specimens in three collections; Gurabo Fm, 2 specimens in two collections. See following.

32. *Tonna pennata*: Cercado Fm, 2 specimens in two collections; Gurabo Fm, 2 specimens in two collections. Both *Tonna* species are so rare in the Dominican Republic that their ecological preferences are not interpretable, but it seems possible that they preyed on sparse, large, offshore, soft-substratum holothurians, whose distributions control those of their predators.

TONNOIDEA IN ATLANTIC PANAMA NEOGENE FAUNAS

An account of marine fossiliferous Neogene formations and their ages in Atlantic Panama was provided by Collins & Coates (1999), and the formations used here follow them and the PPP web database, modified by the addition of Valiente Fm by Coates *et al.* (2003). These represent the first modern studies of the stratigraphy of the region, with accurate microfossil biostratigraphy. Taxa present in Atlantic Panama formations, with approximate counts of specimens to show relative numbers, are listed in Table 2.

The most obvious difference between this fauna and the Dominican Republic faunas described above is the striking rarity and low diversity of Bursidae and Ranellidae in all formations other than the Gatun Fm, shown by the much lower

total counts of specimens and ratios of specimens to species for Atlantic Panama Basin tonnoideans than for the most diverse Dominican Republic ones, the Cercado and Gurabo Formations. The average specimen number per species overall is 34.6 in Table 2, but just over three times that (104.5) in Table 1. By coincidence, Tables 1 and 2 each list 32 species of tonnoideans and, although 15 species are in common to both faunas (*Bursa grayana*, *Marsupina bufo*, *Distorsio clathrata*, *D. mcgintyi*, *D. simillima*, *Charonia variegata*, *Cymatium prae-femorale*, *Monoplex cercadicus*, *M. krebsii*, *M. parthenopeus*, *Turritriton dominicensis*, *Cassis altispira*, *Echinophoria hadra*, *Malea goliath*, *Tonna pennata*), all of them are rare in one or both faunas. All except *M. krebsii* are represented by fewer than five specimens in one fauna or the other, and even *M. krebsii* is represented by only eight specimens in the Panama faunas. Even in the Gatun Fm, where the diversity is highest and numbers of specimens per species are comparable with those in some Dominican Republic faunas, only one or two specimens represent most species. The great exception is the abundance of *B. rugosa* in the Gatun Fm near the oil refinery gates at Isla Payardi, Colon. Two cassids in Tables 1-2 are members of closely similar, partly coeval species pairs (*Sconsia grayi* and *S. laevigata*, *Semicassis granulata* and *S. reclusa*), indicating a significant biogeographical distinction between the faunas. These faunas, therefore, possibly lived in distinct, segregated basins within the proto-Caribbean Sea. The only common *Distorsio* species in the Panama Canal Basin is *D. decussata* which, under the synonym *D. gatunensis*, has long been one of the classic fossils of the Gatun Fm (Woodring, 1959). It occurs also in reasonable numbers in the slightly older Valiente Fm (Middle Miocene; 16.4-12 Ma) in the Bocas del Toro Basin. The one other occurrence of a common *Distorsio* species is *D. clathrata*, in the Late Pliocene Escudo de Veraguas Fm (3.6-1.8 Ma) of the Bocas del Toro Basin. The other common tonnoideans in these faunas are *S. grayi* – surprisingly well represented in all formations, even the Pleistocene Swan Cay Fm (1.8-0.9 Ma), which has a very small outcrop area on Swan Cay (and so a correspondingly low diversity of tonnoideans) – and *Echinophoria hadra*. *Echinophoria hadra* is common in the Chagres Fm in the Panama Canal Basin, but there seem to be no records from the Gatun Fm, whereas it occurs in small numbers in all Bocas del Toro Group formations, other than the Swan Cay Fm, and is moderately common in the Nancy Point Fm (Late Miocene, 6.5-5.6 Ma) and the Shark Hole Point Fm (Pliocene, 5.2-2.3 Ma). In the Dominican Republic, the single record of *E. hadra* is a specimen collected by Bernard Landau from a deep-water facies of the Gurabo Fm in Arroyo Zalaya, estimated by E. Vokes (in E. & H. Vokes, 1989: 21) to have been deposited in 150-350 m of water. The difference between the depositional environments of the Gatun and Chagres Formations was described by

Table 2. Numbers of specimens of tonnoidean species in Atlantic Panama formations (Panama Canal Basin, left column; and Bocas del Toro Basin, all other columns). Numbered species (left margin) are not in common with Table 1; *, species extending until the present day; -, not present; Ch, records entirely from Chagres Fm (rather than Gatun Fm; all other Panama Canal Basin records are from the Gatun Fm).

	Gatun/Chagres	Valiente	Nancy Pt	Cayo Agua	Shark Hole Pt	Escudo de Veraguas	Swan Cay
<i>Bursa grayana</i> *	-	-	-	-	-	-	2
1. <i>Bursa ranelloides</i> *	-	-	-	1	-	-	-
2. <i>Bursa rugosa</i> *	193	7	-	-	1	-	-
3. <i>Bursa scrobilator</i> *	-	-	-	-	-	-	1
4. <i>Crossata ventricosa</i> *	-	-	-	-	1	-	-
<i>Marsupina bufo</i> *	-	-	-	7	1	3	-
<i>Distorsio clathrata</i> *	2	4	-	-	5	34	-
5. <i>Distorsio decussata</i> *	160	21	-	8	7	6	-
<i>Distorsio mcgintyi</i> *	1	-	-	1	1	-	1
<i>Distorsio simillima</i>	-	-	-	-	-	3	-
<i>Charonia variegata</i> *	-	-	-	-	-	-	1
<i>Cymatium praeefemorale</i>	-	-	-	-	1	-	-
6. <i>Linatella caudata</i> *	-	1	-	1	1	-	-
7. <i>Monoplex aquatilis</i> *	1	-	-	-	-	-	-
<i>Monoplex cercadicus</i>	1	-	-	-	-	-	-
8. <i>Monoplex gatunicus</i>	11	-	-	-	-	-	-
<i>Monoplex krebsii</i> *	1	-	-	-	2	2	3
9. <i>Monoplex panamensis</i>	1	-	-	-	-	2	-
<i>Monoplex parthenopeus</i> *	4	-	-	-	-	-	-
10. <i>Monoplex</i> n. sp. A	1	-	-	-	-	-	-
<i>Turritriton domingensis</i>	1	-	-	-	-	-	-
11. <i>Turritriton gibbosus</i> *	2	-	-	-	-	-	-
<i>Cassis altispina</i>	-	-	-	7	4	-	-
12. <i>Cassis costulifera</i>	-	-	-	-	-	5	-
13. <i>Sconsia grayi</i> *	13	87	13	109	60	74	5
14. <i>Oocorys cf. clericus</i> *	-	-	-	-	1	-	-
<i>Echinophoria hadra</i> *	36 (Ch)	2	13	1	23	5	-
15. <i>Semicassis granulata</i> *	2	1	-	8	7	1	-
16. <i>Malea</i> n. sp. aff. <i>elliptica</i>	1	-	-	-	-	-	-
<i>Malea goliath</i>	-	-	-	-	-	4	-
17. <i>Malea ringens</i> *	86	2	-	22	3	1	-
<i>Tonna pennata</i> *	-	-	-	3	-	-	-
Species totals: 32 (21*)	18	8	2	11	15	12	6
Specimen totals: 1107	517	125	26	168	118	140	13
Specimens/species: 34.6	28.7	15.6	13.0	15.3	7.9	11.7	2.2

Coates *et al.* (2003: 286): "In the Bocas del Toro region, inner neritic paleodepths, represented by the Tobabe Sandstone, prevailed until the Messinian (7.26-5.32 Ma), when widespread deepening to upper bathyal depths is recorded by the overlying Nancy Point Fm. This event was paralleled in the Panama Canal Basin by the transition from the Gatun Fm (*ca.* 8 Ma, 20-40 m paleodepth) to the overlying Chagres Fm (*ca.* 6 Ma, 200-600 m paleodepth)." Therefore, the few ranellids and bursids recorded from the Panama Canal Basin occur in the shallow-water (but apparently rapidly deposited) Gatun Fm, whereas the more common *E. hadra* occurs in the upper bathyal Chagres Fm, and is virtually the sole tonnoidean recorded from this unit. The one other tonnoidean occurring in significant numbers in Atlantic Panama basins is *Malea rin-*

gens, which is moderately abundant in the Gatun Fm, moderately common in the Cayo Agua Fm (Early Pliocene, 5.0-3.5 Ma), and occurs in small numbers in the Valiente, Shark Hole Point, and Escudo de Veraguas (Pliocene, 3.6-1.8 Ma) Formations. Occurrences of this eastern Pacific species in the Bocas del Toro Basin therefore require the CAI still to be open well after 3.6 Ma. Coates (1999: 29) pointed out evidence for a relatively shallow depth of deposition for Cayo Agua Fm: the lithology is predominantly gray-blue, muddy, lithic sandstone with horizons of pebble conglomerate and coarse-grained volcanoclastic sandstone, and with beds of thick-shelled mollusks. "In addition the mollusks and corals in Cayo Agua Fm are larger and more heavily calcified than those in the Shark Hole and Escudo de Veraguas formations." He concluded that

the Cayo Agua Fm is equivalent in age to the upper part of the Shark Hole Point and the lower part of the Escudo de Veraguas formations, and represents a shallower-water facies than either. Coates *et al.* (2003: 286) further adopted “inner neritic depths” of deposition for the Shark Hole Point and Cayo Agua Formations. The greater abundance of *Sconsia grayi* and *Malea ringens* in the Cayo Agua than in the Shark Hole Point and Escudo de Veraguas Formations possibly reflects this depositional difference, but other differences dependent on depth are not obvious from tonnoideans. The offshore species *Bursa ranelloides* occurring in the Cayo Agua Fm, compared with the intertidal rocky-shore species *B. rugosa* occurring in the Shark Hole Point Fm, seems to indicate the opposite, although, as usual, only one specimen of each is present. Most other species are simply too uncommon in these formations for their interpretation to have any meaning. Many of the taxa present in the Bocas del Toro Basin seem to represent occasional down-slope transport of shallower-water specimens into deeper-water deposition sites, perhaps reflecting rapid tectonic movements and the proximity of relatively deep water to the shore. The dominance of soft-substratum cassids, tonnids, and *Distorsio* in Atlantic Panama basins certainly seems to reflect a dominance of rapidly deposited fine sediment. A large number of species is represented by only 1-8 specimens in any formation, indicating that these basins did not preserve the preferred habitat of these species (all taxa listed in Table 2 other than *Bursa rugosa*, *Distorsio clathrata*, *D. decussata*, *Sconsia grayi*, *Echinophoria hadra*, and *Malea ringens*; 26 out of the 32 recorded taxa are rare in *all* formations). A higher rate of sedimentation than in the Dominican Republic formations, probably reflecting much greater proximity to a plate boundary, seems to have swamped the tonnoideans in sediment in the Panama Canal and Bocas del Toro basins. In contrast, slower deposition in what is now the Dominican Republic seems to have allowed a much higher diversity and abundance of tonnoideans.

FAUNAL LISTS FOR THE OTHER MAIN FOSSIL LOCALITIES

The tonnoidean faunas of the main, well-known, Neogene fossil localities in tropical America are listed here (Table 3) in order from older to younger, other than those in the Dominican Republic (Table 1) and Atlantic Panama (Table 2), which are treated above. The obvious conclusion from Table 1-3 is that there is surprisingly little similarity between faunas of the same age throughout the tropical American region, even for tonnoideans with their famously long-lived planktotrophic larvae. Evidently geographical and other barriers to dispersal were already forming distinct faunal provinces during late Early Miocene time, providing further evidence of the beginning of uplift of the CAI. Species restricted to one to three faunas are more commonly found among the Cassidae and

Tonnidae rather than other families. Species that occur in four or more faunas are *Bursa rhodostoma*, *B. rugosa* (the greatest number of faunas, nine), *Marsupina bufo*, *Distorsio clathrata*, *D. mcgintyi*, *Monoplex krebsii*, *M. parthenopeus*, and *Malea ringens*. *Cassis altispira* might well be another member of this group, but most material is too poor for certain identification. In the faunas of Atlantic Panama basins (Table 3), common species are again *Bursa rugosa*, *D. clathrata*, *M. krebsii*, and *M. ringens*, with the addition of *Distorsio decussata*, *Sconsia grayi*, and *Echinophoria hadra*. However, in the Dominican Republic faunas (Table 1), few of these are common or widespread; the only species occurring in reasonable numbers in most faunas is *Monoplex krebsii*, although *M. parthenopeus* occurs in small numbers in most. Species of *Cassis* and *Malea* have undergone the most rapid extinction and speciation of the tonnoideans studied here. This is indicated by, among other things, the lower percentages of Recent species within families Cassidae and Tonnidae than in the other families in Tables 1-3. Bursidae + Personidae + Ranellidae (BPR) includes 53% of species extending to the present day in the Dominican Republic faunas (Table 1), whereas Cassidae + Tonnidae (CT) includes 42%; BPR = 68% of species extending to the present day in the Panama faunas (Table 2), whereas CT = 60%; BPR = 69% of species extending to the present day in the other listed faunas (Table 3), whereas CT = 35%. Clearly, depositional environment has also played a part in the distinctiveness of several faunas. In particular, the Dominican Republic faunas seem to have relatively little in common with coeval faunas elsewhere in the region, partly because they were deposited in slightly to markedly deeper water than many others, and shallow-water, rocky shore species such as *Bursa rugosa* do not occur there, but also partly because they were further from active tectonic areas and so were not so swamped with fine sediment.

Similarity Indices

Three similarity indices (Hammer & Harper, 2006: 212-213) were used to calculate similarities between some of the main obviously comparable faunas listed in Tables 1-3, based on presence/absence counts of species. Jaccard's index is calculated as M/N (M = the number of species common to both samples; N = the number of unshared species in both, *i.e.*, $M+N$ = the total number of species in both samples). Simpson's index is calculated as M/S (S = the total number of species in the smaller of the two samples). Dice's index (also known as Sørensen's) is calculated as $2M/(2M+N)$. All indices give results between 0 (no similarity) and 1 (identical). The results are shown in Table 4.

Dice's index was considered by Hammer & Harper (2006: 212) to be similar to Jaccard's, but normalizes with respect to the average rather than the total number of species in the two samples. It is therefore less sensitive than Jaccard's to dif-

Table 3. Presences and absences of tonnoideans in the faunas of some of the main fossil localities in tropical America, other than the Dominican Republic (Table 1) and Atlantic Panama (Table 2). x, species present; -, species absent; ?, species identity in doubt. Locality columns: Chipola Fm, Florida (late Early Miocene); Cantaure, Paraguaná Peninsula, Venezuela (late Early Miocene); Carriacou, Grenadine Islands (Middle Miocene); Caujarao Fm, Carrizal, Venezuela (Middle Miocene); Darien, Pacific Panama (Middle Miocene); Punta Gavilán, northern Venezuela (Early Pliocene); Springvale Quarry, Trinidad (Early Pliocene); Cubagua Fm, Cubagua Island, Venezuela (Early Pliocene); Onzole Fm, Ecuador (Early Pliocene); Agueguexquite Fm, Isthmus of Tehuantepec, Mexico (Pliocene) [Note: blank column indicates cassids and tonnids not listed]; Moín Fm, Limón, Atlantic Costa Rica (Late Pliocene-earliest Pleistocene); Bowden shellbed, Jamaica (Late Pliocene); lower Mare Fm, Cabo Blanco, Venezuela (Late Pliocene); Armuelles Fm, Burica Peninsula, Pacific Panama (Early Pleistocene); Recent (including only those fossil species that extend to the present day); parentheses indicate Recent occurrences in Mediterranean-West Africa only.

[illegible]

Table 3 (continued).

	Chipola Fm	Cantaure Fm	Carriacou Island	Caujarao Fm	Darien	Punta Gavilán	Springvale Fm	Cugabua Island	Onzole Fm	Agueguexquite	Limón	Bowden	Lower Mare Fm	Armuelles Fm	Recent
<i>Septa occidentalis</i>	-	-	-	-	-	-	-	-	-	-	x	-	-	-	x
<i>Turritrit. domingensis</i>	-	x	-	x	-	-	-	x	-	-	-	-	-	-	-
<i>Turritriton labiosus</i>	-	-	-	-	-	-	-	-	-	-	x	x	-	-	x
<i>Sassia</i> cf. <i>apenninica</i>	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cassis altispira</i>	-	-	-	-	?	-	-	-	?		?	?	x	-	-
<i>Cassis costulifera</i>	-	-	-	-	-	-	-	-	-		-	?	-	-	-
<i>Cassis delta</i>	x	-	-	-	-	-	-	-	-		-	-	-	-	-
<i>Cassis flammea</i>	-	-	-	-	x	-	-	-	-		-	-	x	-	x
<i>C. madagascariensis</i>	-	-	-	-	-	-	-	-	-		-	-	x	-	x
<i>Cassis sulcifera</i>	-	-	-	x	-	-	-	-	-		-	-	-	-	-
<i>Cassis tuberosa</i>	-	-	-	-	-	-	-	-	-		-	-	x	-	x
<i>Cypraecassis cantaurana</i>	-	x	-	-	-	-	-	-	-		-	-	-	-	-
<i>Cypraec. chipolana</i>	x	-	-	-	-	-	-	-	-		-	-	-	-	-
<i>Cypraec. testiculus</i>	-	x	-	x	-	-	-	-	-		-	-	-	-	x
<i>Cypraecassis wilmae</i>	-	-	-	-	-	-	-	-	-		-	-	-	x	x
<i>Dalium ecuadorianum</i>	-	-	-	-	-	-	-	-	x		-	-	-	-	-
<i>Sconsia grayi</i>	-	-	-	-	x	-	-	-	-		x	x	-	-	x
<i>Sconsia laevigata</i>	-	x	-	-	-	cf.	-	-	-		-	-	-	-	-
<i>Sconsia paralaevigata</i>	x	-	-	-	-	-	-	-	-		-	-	-	-	-
<i>Echinophoria famulans</i>	-	-	x	-	-	-	-	-	-		-	-	-	-	-
<i>Echinophoria hadra</i>	-	x	-	-	-	x	-	-	-		-	-	-	-	x
<i>Echinophor. woodringi</i>	-	-	-	-	-	-	-	-	-		-	-	-	-	-
<i>Semicassis aldrichi</i>	x	x	-	-	-	-	-	-	-		-	-	-	-	-
<i>Semi. centiquadrata</i>	-	-	-	-	x	-	-	-	?		-	-	-	x	x
<i>Semicassis granulata</i>	-	-	-	-	-	-	-	-	-		x	-	x	-	x
<i>Semi. maleaformis</i>	-	-	-	-	-	-	x	-	-		-	-	-	-	-
<i>Semicassis reclusa</i>	-	-	-	x	-	-	-	-	-		-	x	-	-	-
<i>Semicassis senni</i>	-	-	-	-	-	x	-	-	-		-	-	-	-	-
<i>Eudol. subfasciatum</i>	x	x	-	-	-	-	-	-	-		-	-	-	-	-
<i>Malea camura</i>	-	-	-	x	-	-	-	-	-		-	x	-	-	-
<i>Malea densecostata</i>	-	-	-	-	-	x	-	-	-		-	-	-	-	-
<i>Malea mareana</i>	-	-	-	-	-	-	-	-	-		-	-	x	-	-
<i>Malea ringens</i>	-	-	-	-	x	-	-	-	x		?	-	-	x	x
<i>Malea</i> n. sp. A	-	x	-	-	-	-	-	-	-		-	-	-	-	-
<i>Malea</i> n. sp. B	-	-	-	-	-	-	-	x	-		-	-	-	-	-
<i>Tonna galea</i>	-	-	-	-	-	-	-	-	-		x	-	x	-	x
<i>Tonna pennata</i>	-	-	-	-	-	-	-	-	-		-	-	x	-	x
Species numbers: 80	12	18	4	11	10	10	5	13	11	[5]	21	14	14	13	45

ferences in sample size. It also puts more weight on matches rather than mismatches, because of the multiplication of M by two. In contrast, Simpson's index was considered by Hammer & Harper (2006: 212) to be insensitive to the size of the larger sample. In effect, it disregards absences in the smaller sample. They considered that this might make Simpson's index more appropriate when sampling is thought to be incomplete, as probably applies here to eastern Pacific Neogene faunas. Both Jaccard's and Dice's indices decrease regularly down Table 4

in a manner that seems reasonable, in view of distances between samples and their positions within depositional basins, despite Dice's values being consistently higher than Jaccard's. However, Simpson's index does not parallel the others. It appears that the samples in the middle of the table with fewer species give higher values using Simpson's index, so the results using the other two indices seem to be more reliable than Simpson's.

The two Late Pliocene faunas compared in the tropical

western Atlantic, the Moín Fm and Bowden shellbed, have the highest similarity. The similarity between the faunas of Darien and the Onzole Fm of Ecuador, both on the eastern coast of tropical America, is the next highest, despite the older age of the Darien fauna (Middle-Late Miocene) than of the Onzole Fm (Early Pliocene). The Dominican Republic and Atlantic Panama faunas (Tables 1-2) are moderately similar judged by all indices, whereas the similarity of the Chipola Fm and Cantaure shellbed faunas is lower, and all other Atlantic faunas compared have low similarity indices. This again points to the existence of depositional basins in the tropical Atlantic separating the taxa inhabiting the Dominican Republic, Atlantic Panama, and Venezuelan areas.

The results should be interpreted cautiously because of possible ecological differences between the faunas being compared. Nevertheless, they seem to offer some information on CAI closure. Not surprisingly, they indicate that larvae were still being transported through the CAI at the time of deposition of the faunas of Darien and Atlantic Panama (Middle-Late Miocene), as the similarity indices of these two faunas are identical to those of Punta Gavilán and Atlantic Panama. In contrast, the youngest faunas on opposite sides of the Americas, those of the Moín and Armuelles Formations (Late Pliocene-Early Pleistocene), are highly dissimilar. This implies almost complete cessation of larval transport through the CAI by this time. Even more extremely, the Armuelles Fm has no species in common with the Bowden shellbed (*Bursa corrugata* potentially could be found in both of them, but is not yet known in either). The contrast with the correspondingly high similarity between the Moín Fm and Bowden, the highest calculated by all three indices, indicates that the Atlantic fauna was strongly distinct from the eastern Pacific one by Late Pliocene-earliest Pleistocene time. This again seems to be good evidence that larval transport through the CAI had

virtually ceased. Nevertheless, the presence of the eastern Pacific species *Malea ringens* in both the Moín and Armuelles Formations indicates that minor larval transport was still possible through the CAI during earliest Pleistocene interglacial periods of high sea level. The presence of *Linatella caudata* in the Armuelles Fm is suggested below to be further indication of larval transport in the opposite direction through the CAI during Early Pleistocene time. *Linatella caudata* is common to the Armuelles, Punta Gavilán, Springvale, and Cubagua Formations, as well as the Recent Atlantic fauna and the Pliocene and Pleistocene of Florida, even though there are as yet no records from Bowden.

RECENT TONNOIDEAN FAUNAS

Recent faunas of the broad study area are listed below for comparison with the lists of fossils. Authors' names are provided for species not otherwise referred to in the taxonomic section below; E = endemic, *i.e.*, restricted to the region.

1. Eastern Pacific: *Bursa asperrima* (rare), *B. corrugata*, *B. granularis* (rare), *B. rugosa* (E), *Crossata ventricosa* (E), *Marsupina nana* (E), *Distorsio constricta* (E), *D. decussata* (E), *D. jenniernestae* (E), *D. minoruohnishii* (E), *Argobuccinum pustulosum*, *Fusitriton magellanicus*, *F. oregonensis*, *Priene scabrum* (E), *Charonia tritonis* (rare), *Cymatium tigrinum* (E), *Gelagna succincta* (rare), *Guttarium muricinum* (rare), *Monoplex amictus* (E), *M. aquatilis* (rare), *M. keenae* (E), *M. lignarius* (E), *M. macrodon* (E), *M. mundus* (rare), *M. vestitus* (E), *M. wiegmanni* (E), *Reticutriton lineatus* (E), *Turritriton gibbosus*, *T. labiosus* (rare), *Cypraecassis coarctata* (E), *C. tenuis* (E), *C. wilmae* (E), *Oocorys elevata* (E), *O. rotunda* (Dall, 1908) (E), *Casmaria vibexmexicana* (Stearns, 1893) (E), *Echinophoria pilsbryi* (Woodring & Olsson, 1957) (E), *Semicassis centiquadrata* (E), *Malea ringens* (E) (38 species, 24 endemic = 63%) ("rare" implies eastern Pacific pseudopopulations recruited across the East Pacific barrier from the western Pacific; 8 species = 21%).

2. Western Atlantic: *Bursa corrugata*, *B. granularis*, *B. grayana* (E), *B. natalensis* (E), *B. ranelloides*, *B. rhodostoma*, *Marsupina bufo* (E), *Distorsio clathrata* (E), *D. mcgintyi* (E), *D. perdistorta*, *Personopsis grasi*, *Fusitriton magellanicus*, *F. brasiliensis* (E), *Ranella gemmifera* (rare), *R. olearium* (rare), *Charonia lampas* (rare), *C. tritonis* (rare), *C. variegata* (E), *Cabestana felipponei* (E), *Cymatium femorale* (E), *C. raderi* (E), *Gelagna succincta* (rare), *Guttarium muricinum*, *Linatella caudata*, [*Lotoria lotoria* (Linnaeus, 1758), one unconfirmed record; not included in species count], *Monoplex aquatilis*, *M. comptus*, *M. exaratus* (rare), *M. krebsii*, *M. pilearis*, *M. mundus*, *M. nicobaricus*, *M. parthenopeus*, *M. tranquebaricus* (rare), *M. trigonus* (rare), *M. vespaceus* (rare), *Ranularia cynocephalum*, *R. gallinago* (rare), *R. rehderi* (E), *Reticutriton pfeifferianus*, *Septa occidentalis*, *Turritriton gibbosus* (rare), *T.*

Table 4. Jaccard's, Simpson's, and Dice's similarity indices for some of the main comparable Neogene tonnoidean faunas in tropical America (listed in Tables 1-3), in order from highest to lowest similarity of Jaccard's and Dice's indices.

	Jaccard	Simpson	Dice
Moín Fm: Bowden	0.667	0.714	0.571
Darien: Onzole Fm	0.286	0.6	0.444
Dominican Republic: Atlantic Panama	0.234	0.469	0.379
Chipola Fm: Cantaure	0.2	0.5	0.333
Atlantic Panama: Darien	0.167	0.7	0.286
Punta Gavilán: Atlantic Panama	0.167	0.7	0.286
Punta Gavilán: Dominican Republic	0.143	0.6	0.25
Moín Fm: Armuelles Fm	0.031	0.077	0.059
Bowden: Armuelles Fm	0	0	0

labiosus, *T. tenuiliratus*, *Sassia lewisi*, *Cassis flammea* (E), *C. madagascariensis* (E), *C. norai* (rare), *C. tuberosa*, *Cypraecassis testiculus* (E), *Sconsia alexarthuri* Parth, 1984 (E), *S. grayi* (E), *S. nephele* (E), *Oocorys clericus* (E), *O. sulcata* Fischer, 1884, *O. verrilli* (Dall, 1889), *Dalium solidum* Dall, 1889 (E), *Eucorys barbouri* (Clench & Aguayo, 1939) (E), *E. bartschi* (Rehder, 1943) (E), *Casmaria atlantica* Clench, 1944 (E) [= *C. pernyi* (Iredale, 1912)], *Echinophoria coronadoi* (Crosse, 1867) (E), *E. hadra* (E), *Semicassis granulata* (E), *Eudolium bairdii* (Verrill & Smith, 1881), *Eudolium crosseanum* (Monterosato, 1869), *Malea pomum* (Linnaeus, 1758) (rare), *Tonna galea*, *T. pennata*, *Akibumia* n. sp. Beu & Bouchet, in prep. (68 species, 25 endemic = 37%) ("rare" implies western Atlantic pseudo-populations recruited from West Africa or South Africa; 12 species = 18%).

3. Eastern Atlantic and Mediterranean (species occurring in, but not necessarily limited to, the latter identified by "m"): *Bursa corrugata*, *B. ranelloides*, *B. rhodostoma*, *B. scrobilator* (m, E), *Aspa marginata* (E), *Distorsio perdistorta*, *D. smithi* (E), *Personopsis grasi*, *Halgyrineum louisae*, *Ranella olearium* (m), *Charonia lampas* (m), *C. seguenzae* (m, E), *C. variegata* (rare), *Cabestana cutacea* (m, E), *Cymatium femorale* (rare), *Gelagna succincta* (rare), *Gutturnium muricinum* (rare), *Linatella caudata*, *Monoplex aquatilis* (rare), *M. comptus*, *M. corrugatus* (m, E), *M. krebsii* (rare), *M. pilearis* (rare), *M. parthenopeus* (m), *M. tranquebaricus*, *M. trigonus*, *Ranularia cynocephalum* (rare), *Septa occidentalis* (rare), *Turritriton kobelti* (E), *T. labiosus*, *T. tenuiliratus*, *Sassia lewisi*, *Cassis norai* (E?), *C. tessellata* (Gmelin, 1791) (E), *C. tuberosa* (rare?), *Cypraecassis testiculus senegalica* (Gmelin, 1791) (E), *Galeodea echinophora* (Linnaeus, 1758) (m, E), *G. rugosa* (Linnaeus, 1771) (m, E), *Oocorys grandis* Beu, 2008, *O. sulcata* Fischer, 1884, *O. verrilli* (Dall, 1889) (rare), *Semicassis saburon* (Bruguère, 1792) (m, E), *S. undulata* (Gmelin, 1791) (m, E), *Eudolium bairdii* (Verrill & Smith, 1881), *E. crosseanum* (Monterosato, 1869) (m), *Tonna galea* (m), *T. pennata* (rare), *Akibumia orientalis* (Schepman, 1909) (rare), *A. peregrinatrix* (Waren & Bouchet, 1990), *Akibumia* n. sp. A Beu & Bouchet, in prep., *Pisanianura grimaldii* (Dautenberg, 1889) (51 species, 14 endemic = 27%) ("rare" implies West African pseudopopulations recruited from the western Atlantic; 13 species = 25%).

An interesting subgroup here consists of species that are largely restricted to West Africa and/or the Mediterranean, but that are identified in the main text, below, as having made geologically brief range extensions to the western Atlantic, with their times of western Atlantic appearance listed in parentheses: *Bursa scrobilator* (Late Pliocene-Early Pleistocene, mainly recorded from Limón), *Aspa marginata* (Late Pliocene-Early Pleistocene, Limón), *Monoplex tranquebaricus* (Miocene?; Pleistocene and Recent; most records from Isla Cubagua), *M. trigonus* (Recent), ?*Sassia apenninica* (Miocene, Carriacou

only; Miocene and Pliocene in Europe). The unidentified species of *Galeodea* in Middle Miocene-Pliocene rocks of the Dominican Republic also possibly is the European Miocene-Recent species *G. echinophora* (Linnaeus, 1758), but known specimens are not complete enough for definite identification, despite the recent collection of a similar shell from deep water off of Martinique.

4. Tropical Indo-West Pacific: The fauna is listed from Beu (1998b: 17-20), with minor amendments, a list of Cassidae added from Abbott (1968), Kreipl (1997), and Beu (2008), Laubierinidae from Beu & Bouchet (in prep.), *Eudolium* from Marshall (1992) as modified by Vos (2007), and Tonnidae from Vos (2007); only species that are NOT endemic are identified with an asterisk*.

BURSIDAE: *Bufonaria cavitensis* (Reeve, 1844), *B. cristinae* Parth, 1989, *B. crumena* (Lamarck, 1816), *B. echinata* (Link, 1807), *B. elegans* (G. B. Sowerby II, 1836), *B. foliata* (Broderip, 1826), *B. margaritula* (Deshayes, 1832), *B. perelegans* Beu, 1987, *B. rana* (Linnaeus, 1758), *B. thersites* (Redfield, 1846); *Bursa asperima*, *B. awatii* Ray, 1949, *B. bufonia* (Gmelin, 1791), *B. condita* (Gmelin, 1791), *B. cruentata* (G. B. Sowerby II, 1835), *B. davidboschi* Beu, 1987, *B. fosteri* Beu, 1987, **B. granularis*, *B. humilis* Beu, 1981, *B. lamarckii* (Deshayes, 1853), *B. latitudo* Garrard, 1961, *B. lucaensis* Parth, 1991, *B. luteostoma* (Pease, 1861), *B. quirihorai* Beu, 1987, **B. ranelloides*, **B. rhodostoma*, *B. rosa* (Perry, 1811), *B. tuberosissima* (Reeve, 1844), *B. verrucosa* (G. B. Sowerby I, 1825); *Bursina borisbeckeri* (Parth, 1996), *B. fernandesii* (Beu, 1977), *B. fijiensis* (Watson, 1881), *B. gnorima* (Melvill, 1918), *B. ignobilis* (Beu, 1987), *B. nobilis* (Reeve, 1844); *Tutufa* (*Tutufa*) *bardeyi* (Jousseume, 1894), *T. bubo* (Linnaeus, 1758), *T. bufo* (Röding, 1798), *T. tenuigranosa* (E. A. Smith, 1914), *T. (Tutufella) bobolica* Beu, 1987, *T. nigrita* Mühlhäusser & Blöcher, 1979, *T. oyamai* Habe, 1973, *T. rubeta* (Linnaeus, 1758) (43 species, 40 endemic = 93%).

RANELLIDAE, RANELLINAE: *Biplex bozzettii* Beu, 1998 [= *B. perca*?], *B. perca* (Perry, 1811), *B. pulchella* (G. B. Sowerby I, 1825), *B. aculeata* (Schepman, 1909) [see below, under *Marsupina nana*, for change of name from *Biplex pulchra* (G. B. Sowerby II, 1836)], *Fusitriton galea* Kuroda & Habe in Habe, 1961; *Gyrineum bituberculare* (Lamarck, 1816), *G. concinnum* (Dunker, 1862), *G. gyrinum* (Linnaeus, 1758), *G. hirasei* (Kuroda & Habe, 1961), *G. lacunatum* (Mighels, 1843), *G. longicaudatum* Beu, 1998, *G. natator* (Röding, 1798), *G. pusillum* (Broderip, 1833), *G. roseum* (Reeve, 1844), *G. wilmerianum* Preston, 1908; **Halgyrineum louisae*; *Ranella australasia* (Perry, 1811), **R. olearium* (18 species, 16 endemic = 89%).

RANELLIDAE, CYMATIINAE: **Charonia lampas*, *C. tritonis*, *Cymatium ranzanii* (Bianconi, 1850), *Gelagna pallida* Parth, 1996, **G. succincta*, **Gutturnium muricinum*,

**Linatella caudata*, *Lotoria armata* (G. B. Sowerby III, 1897), *L. grandimaculata* (Reeve, 1844), *L. lotoria* (Linnaeus, 1758), *L. perryi* (Emerson & Old, 1963), **Monoplex aquatilis*, **M. comptus*, **M. exaratus*, *M. gemmatus* (Reeve, 1844), *M. intermedius* (Pease, 1869), **M. mundus*, **M. nicobaricus*, *M. norai* Garcia-Talavera & de Vera, 2004, **M. parthenopeus*, *M. pen-niketi* (Beu, 1998), **M. pilearis*, *M. thersites* (Reeve, 1844), **M. vespereus*, *Ranularia andamanensis* (Beu, 1987), *R. ar-thuri* (Beu, 1987), *R. boschi* (Abbott & Lewis, 1970), *R. cau-data* (Gmelin, 1791), **R. cynocephalum*, *R. dunkeri* (Lischke, 1868), *R. encaustica* (Reeve, 1844), *R. exilis* (Reeve, 1844), **R. gallinago*, *R. gutturnia* (Röding, 1798), *R. monilifera* (A. Adams & Reeve, 1850), *R. oblita* (Lewis & Beu, 1976), *R. oboesa* (Perry, 1811), *R. parthi* (Arthur, 1991), *R. pyrula* (A. Adams & Reeve, 1850), *R. pyrum* (Linnaeus, 1758), *R. sarcos-toma* (Reeve, 1844), *R. sinensis* (Reeve, 1844), *R. springsteeni* (Beu, 1987), *R. testudinaria* (A. Adams & Reeve, 1850), *R. tri-lineata* (Reeve, 1844), *R. tripa* (Lamarck, 1822), **Reticutriton pfeifferianus*, *Septa bibbeyi* (Beu, 1987), *S. closeli* (Beu, 1987), *S. flaveola* (Röding, 1798), *S. hepatica* (Röding, 1798), *S. marerubra* (Garcia-Talavera, 1985), *S. mixta* (Arthur & Garcia-Talavera, 1990), **S. occidentalis*, *S. peasei* (Beu, 1987), *S. rubecula* (Linnaeus, 1758), *Turritriton fittkau* (Parth, 1991) [= *T. tenuiliratus*?], **T. labiosus*, **T. tenuiliratus*, *Sassia melpangi* Harasewych & Beu, 2007, *S. midwayensis* (Habe & Okutani, 1968), *S. nassariformis* (G. B. Sowerby III, 1902), *S. palmeri* (Powell, 1967), *S. remensa* (Iredale, 1936), *S. semi-torta* (Kuroda & Habe in Habe, 1961), *Cymatiella pumilio* (Hedley, 1903) (66 species, 48 endemic = 73%).

PERSONIDAE: *Distorsio anus* (Linnaeus, 1758), *D. burgessi* Lewis, 1972, *D. euconstricta* Beu, 1987, *D. graceiel-lae* Parth, 1989, *D. habe* Lewis, 1972, *D. kurzi* Petuch & Harasewych, 1980, *D. muelhhauseri* Parth, 1990, *D. parvi-mpedita* Beu, 1998, **D. perdistorta*, *D. reticularis* (Linnaeus, 1758), *D. somalica* Parth, 1990, *D. ventricosa* Kronenberg, 1994, *Distorsionella lewisi* (Beu, 1978), *D. pseudaphera* Beu, 1998, *Distorsomina pusilla* (Pease, 1861), *Personopsis purpu-rata* Beu, 1998, *P. trigonaperta* Beu, 1998 (17 species, 16 en-demic = 94%).

CASSIDAE: *Cassid abbotti* Bouchet, 1988, *C. cornuta* (Linnaeus, 1758), *C. nana* Tenison Woods, 1879, *C. fim-briata* Quoy & Gaimard, 1833, *C. torva* (Iredale, 1927), *C. kreipli* Morrison, 2003, *C. patamakanthini* Parth, 2000, *Cypraecassis rufa* (Linnaeus, 1758), *Galeodea alcocki* (E. A. Smith, 1906), *G. bituminata* (Martin, 1933), *G. hoarai* Drivas & Jay, 1989, *G. keyteri* (Kilburn, 1975), *G. leucodoma* Dall, 1907, *G. maccamleyi* Ponder, 1983, *Microconsia limpusi* Beu, 2008, **Oocorys grandis* Beu, 2008, **O. sulcata* Fischer, 1884, **O. verrillii* (Dall, 1889), *Echinophoria bituberculosa* (Martens, 1901), *E. carnosa* Kuroda & Habe in Habe, 1961, *E. wyvillei* (Watson, 1886), *Phalium areola* (Linnaeus, 1758),

P. bandatum bandatum (Perry, 1811), *P. bandatum exaratum* (Reeve, 1848), *P. decussatum* (Linnaeus, 1758), *P. fimbria* (Gmelin, 1791), *P. flammiferum* (Röding, 1798), *P. glaucum* (Linnaeus, 1758), *P. muangmani* Raybaudi & Prati Musetti, 1995, *Casmaria erinaceus* (Linnaeus, 1758), *C. kalosmodix* Melvill, 1883, *C. nipponensis* Abbott, 1968, *C. perryi* (Iredale, 1912), *C. ponderosa ponderosa* (Gmelin, 1791), *C. ponder-sosa unicolor* (Dautzenberg, 1926), *Semicassis angasi* (Iredale, 1927), *S. bisulcata* (Schubert & Wagner, 1829), *S. bondarevi* Mühlhäusser & Parth, 1993, *S. bulla* Habe, 1961, *S. canali-culata* (Bruguère, 1792), *S. craticulata* (Euthyme, 1885), *S. dorae* (Kreipl & Mühlhäusser, 1996), *S. faurotis* (Jousseume, 1888), *S. fernandesi* (Kilburn, 1975), *S. glabrata* (Dunker, 1852), *S. inornata* (Pilsbry, 1895), *S. labiata* (Perry, 1811), *S. microstoma* (Martens, 1903), *S. paucirugis* (Menke, 1843), *S. pyrum* (Lamarck, 1822), *S. royana* (Iredale, 1914), *Semicassis* n. sp. Beu & Bouchet, in prep., *S. sophia* (Brazier, 1872), *S. thomsoni* (Brazier, 1872), *S. umbilicata* (Pease, 1861), *S. wes-tralis* Kreipl, 1997 (56 species, 53 endemic = 95%).

LAUBIERINIDAE: *Akibumia flexibilis* Kuroda & Habe, 1959, *Akibumia* n. sp. B Beu & Bouchet, in prep., **A. ori-entalis* (Schepman, 1909), *Pisanianura breviaxis* (Kuroda & Habe in Habe, 1961), **P. grimaldii* (Dautzenberg, 1889) (= "*Oocorys*" *donghaiensis* Xu, 1989; Beu & Bouchet, in prep.) (5 species, 3 endemic = 60%).

TONNIDAE: **Eudolium bairdii* (Verrill & Smith in Verrill, 1881), **E. crosseanum* (Monterosato, 1869), **Malea pomum* (Linnaeus, 1758), *Tonna alanbeui* Vos, 2005, *T. al-lium* (Dillwyn, 1817), *T. ampullacea* (Philippi, 1845, in 1842-1851), *T. berthae* Vos, 2005, *T. boucheti* Vos, 2005, *T. canaliculata* (Linnaeus, 1758), *T. chinensis* (Dillwyn, 1817), *T. cumingi* (Hanley in Reeve, 1849), *T. deshayesi* (Reeve, 1849), *T. dolium* (Linnaeus, 1758), *T. dunkeri* (Hanley, 1860), *T. hawaiiensis* Vos, 2007, *T. lischkeana* (Küster, 1857), *T. luteos-toma* (Küster, 1857), *T. melanostoma* (Jay, 1839), *T. morrisoni* Vos, 2005, *T. oentoengi* Vos, 2005, *T. perdix* (Linnaeus, 1758), *T. poppei* Vos, 2005, *T. rosemaryae* Vos, 1999, *T. sulcosa* (Born, 1778), *T. tankervillii* (Hanley, 1860) (= *cerevisina* Hedley, 1919), *T. tenebrosa* (Hanley, 1860), *T. tessellata* (Lamarck, 1816), *T. tetracotula* Hedley, 1919, *T. variegata* (Lamarck, 1822), *T. zonata* (Green, 1830) (30 species, 27 endemic = 90%; total tropical IWP Tonnoidea = 235 species, 203 en-demic = 86%).

BIOGEOGRAPHICAL ELEMENTS IN THE TROPICAL AMERICAN FAUNA

A useful approach to the study of tropical American ton-noidean biogeography is to classify species by their biogeo-graphical ranges established in the taxonomic section below. Although the Recent Cassidae and Tonnidae of the region are not revised in detail in this monograph, they are listed here to

help understand the biogeographical origins of the Neogene fossils.

1. Species now extinct in the region (*i.e.*, known only as fossils): These usefully can be classified further into:

(a) Apparently ancestral to living species (with the apparent descendent listed after each): *Marsupina judensis* (*M. nana*), *Distorsio jungi* (*D. decussata*, and/or *D. simillima*), *Cymatium praefemorale* (*C. femorale* and/or *C. raderi*), *Monoplex cercadicus* (*M. wiegmanni*), *M. gurabonicus* (*M. comptus*), *Reticutriton carlottae* (? = *R. pfeifferianus*), *R. elsmerensis* (*R. lineatus*), *Turritriton domingensis* (*T. labiosus*), *Cassis altispira* (*C. norai*), *C. floridensis* (*C. madagascariensis*), *C. sulcifera* (*C. tuberosa*), *Dalium dalli*, *D. ecuadorianum* (a lineage leading up to *D. solidum*), *Semicassis reclusa* (*S. granulata*), *Malea camura* (*M. pomum*); and

(b) Completely extinct species groups: *Bursa amphitrites*, *B. chipolana*, *Marsupina freya*, *M. strongi*, *Distorsio biangulata*, *D. floridana*, *Monoplex jackwinorum*, *M. panamensis*, *M. ritteri*, *Septa landaui*, all *Sassia* and *Cymatiella* species other than *S. lewisi* and *S. kampyla*, *Cassis costulifera* (possibly ancestral to *C. flammea*, unclear), *C. ketteri*, *Galeodea* aff. *echinophora* (status unclear), *Sconsia laevigata*, *Semicassis aldrichi*, *Eudolium subfasciatum*, and all *Malea* species other than *M. ringens* and *M. pomum*. *Monoplex chlorostomoides*, *M. infelix* and *M. williamsi* are too poorly known to be interpreted.

2. Cosmopolitan, in all warm-temperate and tropical seas: The only true tonnoidean member of this class appears to be *Turritriton labiosus*, although even this species is rare in the eastern Pacific and eastern Atlantic and has not been recorded from the Mediterranean Sea.

3. Species occurring widely in the Indo-West Pacific and in both the eastern and western Atlantic; some of these (with an asterisk) occur also rarely (*i.e.*, as pseudopopulations recruited from the western Pacific) in the eastern Pacific: **Bursa granularis*, *B. rhodostoma*, *Distorsio perdistorta*, *Halgyrineum louisae*, **Gelagna succincta*, **Gutturnium muricinum*, *Linatella caudata*, **Monoplex aquatilis*, *M. comptus*, **M. mundus* (not recorded from the eastern Atlantic), *M. nicobaricus*, *M. vespa-ceus* (not recorded from the eastern Atlantic), *Reticutriton pfeifferianus*, *Septa occidentalis*, *Oocorys sulcata*, *O. verrilli*, *Eudolium bairdii*, and *E. crosseanum*. An interesting subgroup of the above is species occurring in both the eastern and western Atlantic, as well as the Mediterranean, but in the Indo-West Pacific area occurring *only in the Southern Ocean*, and only rarely straggling into the tropics: *Ranella olearium* and *Charonia lampas* (the latter occurs in Japan-Taiwan as well).

4. Species occurring in the eastern Pacific and in both the eastern and western Atlantic, but *not* in the Indo-West Pacific: *Bursa corrugata* only.

5. Species occurring in the eastern Pacific and western Atlantic, but *not* in the eastern Atlantic or Indo-West Pacific, *i.e.*,

limited to the broader tropical American region: *Echinophoria hadra*, alone, in the Recent fauna. Taking fossil records into account: *Bursa rugosa* (fossil only, in the Caribbean), *Distorsio clathrata* (fossil only, in the eastern Pacific), *Monoplex lignarius* (fossil only, in the Caribbean), *M. panamensis* (extinct), *Cassis altispira* (extinct; apparently ancestral to the living Cape Verde Islands (and southern Caribbean?) endemic species *C. norai*), and *Malea ringens* (fossil only, in the Caribbean).

6. Indo-West Pacific species that extend their ranges to the eastern Pacific, but do *not* occur in the Atlantic: *Bursa asperima* only. The collection of a single living specimen of *Charonia tritonis* in Brazil (see below) removes this species from this category.

7. Species occurring in the western Atlantic (and, in most cases, the eastern Atlantic) and in the Indian Ocean, but *not* in the western Pacific: *Bursa ranelloides* (has disjunct populations also in southern Japan and the Hawaiian Islands), *Ranularia cynocephalum*, and *R. gallinago*; a subgroup of these consists only of *Ranella gemmifera*, which occurs in the western Atlantic and South Africa, but as yet has not been recorded from the eastern Atlantic.

8. A special case of the previous class is the antitropical or "Pacific fringe" species, which occur in the Atlantic and Indian Oceans, and around the Pacific fringes, but only rarely straggle to (*i.e.*, apparently are out-competed in) the tropical western Pacific: *Charonia lampas*, *Monoplex exaratus*, and *M. parthenopeus*.

9. Eastern and western Atlantic species, not occurring in *either* the eastern Pacific or the Indo-West Pacific: *Personopsis grasi*, *Charonia variegata*, *Cymatium femorale*, *Monoplex krebsii*, *Sassia lewisi*, *Cassis tuberosa*, *Cypraecassis testiculus*, and possibly *Cassis norai*. Of this group, only *Charonia variegata*, *Sassia lewisi*, *Cassis tuberosa*, and *Cypraecassis testiculus* are common and apparently have established breeding populations in the eastern Atlantic. *Cymatium femorale* and *Monoplex krebsii* are rare in the eastern Atlantic and probably exist there only as pseudopopulations, *i.e.*, they arrive in the area as planktonic larvae that survive and grow, in some cases to adulthood, but do not breed. Taking fossils into account, *Bursa scrobilator* and *Aspa marginata* also fall into this category, having been transported in the opposite direction during Late Pliocene-earliest Pleistocene time.

10. Species restricted to Atlantic islands and seamounts: A final very minor group, but of unusual interest in view of the long larval lives of most tonnoideans, and the implication that these species must formerly have had long larval lives to enable them to reach their isolated islands, but have since changed their larval dispersal ability: *Monoplex turtoni* and *Sassia philomelae*. Note, though, that this does not refer to the eastern Atlantic islands, including the Cape Verde, Canary, and Selvagem islands and Madeira, because many western

Atlantic tonnoideans that reach the eastern Atlantic occur only at these offshore islands, and not on the West African mainland coast (Le Loeuff & Cosel, 1998): *Bursa granularis*, *B. rhodostoma*, *Cymatium femorale*, *Gutturium muricinum*, *Linatella caudata*, *Monoplex aquatilis*, *M. comptus*, *M. krebsii*, *M. nicobaricus*, *M. pilearis*, *Ranularia cynocephalum*, *Septa occidentalis*, *Turritriton labiosus*, *Sassia lewisi*, *Cassis norai*, and *C. tuberosa*.

11. Geminate species pairs, in which one species occurs on each coast of tropical America, in many (but by no means all) cases as a result of speciation following the uplift of the Isthmus of Panama (in all cases the Atlantic species is listed first):

(a) Still living pairs: *Marsupina bufo*, *M. nana*; *Distorsio mcgintyi*, *D. constricta*; *Cymatium femorale*, *C. tigrinum*; *Monoplex krebsii*, *M. amictus*; *M. pilearis*, *M. macrodon*; *M. parthenopeus*, *M. keenae*; and *Semicassis granulata*, *S. centiquadrata*. Only one cassid and no tonnids belong in this group.

Of these pairs, it is important to note that the only true geminate pairs, in the sense of having speciated as result of subdivision of their population *by the uplift of the CAI*, supported by hard evidence in the form of dates of fossils on the two coasts of tropical America, are *Monoplex parthenopeus* and *M. keenae*, and *M. pilearis* and *M. macrodon*. In both cases, the differences between the taxa on the two coasts are subtle enough that their status is debated; genetic studies are needed to be sure whether the two forms are species, subspecies, or the differences in shell characters are insignificant. Genetic studies are also required to be able to tell whether *Bursa corrugata* falls within this category; the shells from the two coasts of tropical America appear to be indistinguishable, but a genetic separation would not be surprising. The fossil record and the subtle differences between the segregated forms indicate that these examples result directly from uplift of the CAI segregating them during earliest Pleistocene time, supporting my contention that final separation of planktotrophic mollusks on the two coasts of tropical America by uplift of the CAI occurred at about 2 Ma. These are the *real* differences resulting from final separation of the oceans by the uplift of the CAI. I contend that the other, more marked differences between taxa in the western Atlantic and eastern Pacific likely result from earlier genetic separation as a result of a filter barrier operating in the seaway as constriction commenced and islands rose and fell, after about 15 Ma.

A more complex scenario for the *Monoplex parthenopeus* species group is required to explain the presence of *M. vestitus* in the eastern Pacific. This species apparently resulted from an earlier (Pliocene) segregation of the *M. parthenopeus* population to produce an eastern Pacific isolate, and subsequent allopatric speciation to produce *M. vestitus*. This complex of

species therefore seems to reflect a complex history of constriction and closure of the CAI.

(b) Pairs in which one member is extinct: *Monoplex ceradicus* (Dominican Republic, extinct), *M. wiegmanni*; *Dalium solidum*, *D. ecuadorianum* (Ecuador, extinct); possibly includes *Reticutriton pfeifferianus* (*R. carlottae*, Brazil, extinct?; possibly simply a synonym), *R. lineatus*, Galápagos; and *Cypraeccassis chipolana* (Florida, extinct), *C. wilmae*. These all result from apparently earlier speciation events before closure of the CAI.

(c) Three chains of species that appear to have originated from a single species with a formerly eastern Pacific to Mediterranean distribution (*i.e.*, a similar distribution to that of the living *Bursa corrugata*) or an Indo-West Pacific–Atlantic distribution (*i.e.*, originally Tethyan?): (a) *Monoplex corrugatus* (West Africa and Mediterranean), *M. krebsii* (eastern and western Atlantic), and *M. amictus* (eastern Pacific); (b) *Charonia sequezae* (eastern Mediterranean), *C. variegata* (common in western Atlantic, rare in eastern Atlantic), and *C. tritonis* (Indo-West Pacific); and (c) *Turritriton gibbosus* (eastern Pacific; western Atlantic – first western Atlantic record confirmed here), *T. kobelti* (West Africa and Mediterranean); apparently also includes *T. grundensis* (Miocene, north-central Europe).

12. Atlantic-Indo-West Pacific geminate pairs: Another category of geminate species pairs that provides some useful biogeographical information is those Atlantic species that have a closely similar, but apparently specifically distinct, relative in the Indo-West Pacific fauna. The only such pairs evident at present are: *Tonna pennata* (western Atlantic) and *T. perdis* (Indo-West Pacific); *Tonna galea* (Atlantic-Mediterranean) and *T. zonata* (Green, 1830) (Indo-West Pacific); and *Bursa natalensis* (western Atlantic) and *B. latitudo* (Garrad, 1961) (Indo-West Pacific). Presumably these species pairs resulted from fragmentation of an originally single species, just as do the pairs listed above. It appears, though, that most species with such a distribution have remained undivided. *Eudolium crosseanum* (Atlantic-Mediterranean) and *E. pyriforme* (Indo-West Pacific) (again, Tonnidae) formerly were considered to be another such pair (Marshall, 1992), but Vos (2007) considered these two forms to be conspecific.

Paciphile and Atlantiphile Taxa

Woodring (1928, 1966) initiated a new way of thinking about tropical American molluscan biogeography when he classified taxa as either paciphile or atlantiphile. Those species that occur *only* in the greater tropical American region usefully can reveal distributional changes through time by being classified as either paciphile or atlantiphile, where relevant – *i.e.*, this classification clearly applies only to those species that have changed their distributions with time.

(1) Paciphile taxa; those taxa that have changed from an almost entirely western Atlantic fossil distribution to an almost entirely eastern Pacific distribution at present: *Bursa rugosa*; *Monoplex lignarius*; most notably, *Malea*, which has a long, diverse record in the western Atlantic, but the only common species live in the eastern Pacific (*M. ringens*) and western Pacific (*M. pomum*); although this example is weakened by the recognition of *M. pomum* living off of northern Brazil. The species group of *Distorsio decussata* also might be classified here, because its earliest representative is *D. jungi* n. sp. in the late Early Miocene Cantaure Fm of Venezuela. The large, widespread Caribbean-Panamic fossil species *D. simillima* also belongs in this group, whereas *D. decussata*, the single living member, is limited to the eastern Pacific at present. However, this example, also, is weakened by the Oligocene-Miocene occurrence of *D. ringens*, a member of the *D. decussata* species group, along the Pacific coasts of Chile and Peru.

Other taxa were classified as paciphile by Woodring (1966) in a wider sense, *i.e.*, those with *any* former occurrence in the Atlantic that are now limited to the eastern Pacific. Several other tonnoideans (*Distorsio decussata*, *Crossata ventricosa*, and *Monoplex wiegmanni*) would then be included among paciphile taxa.

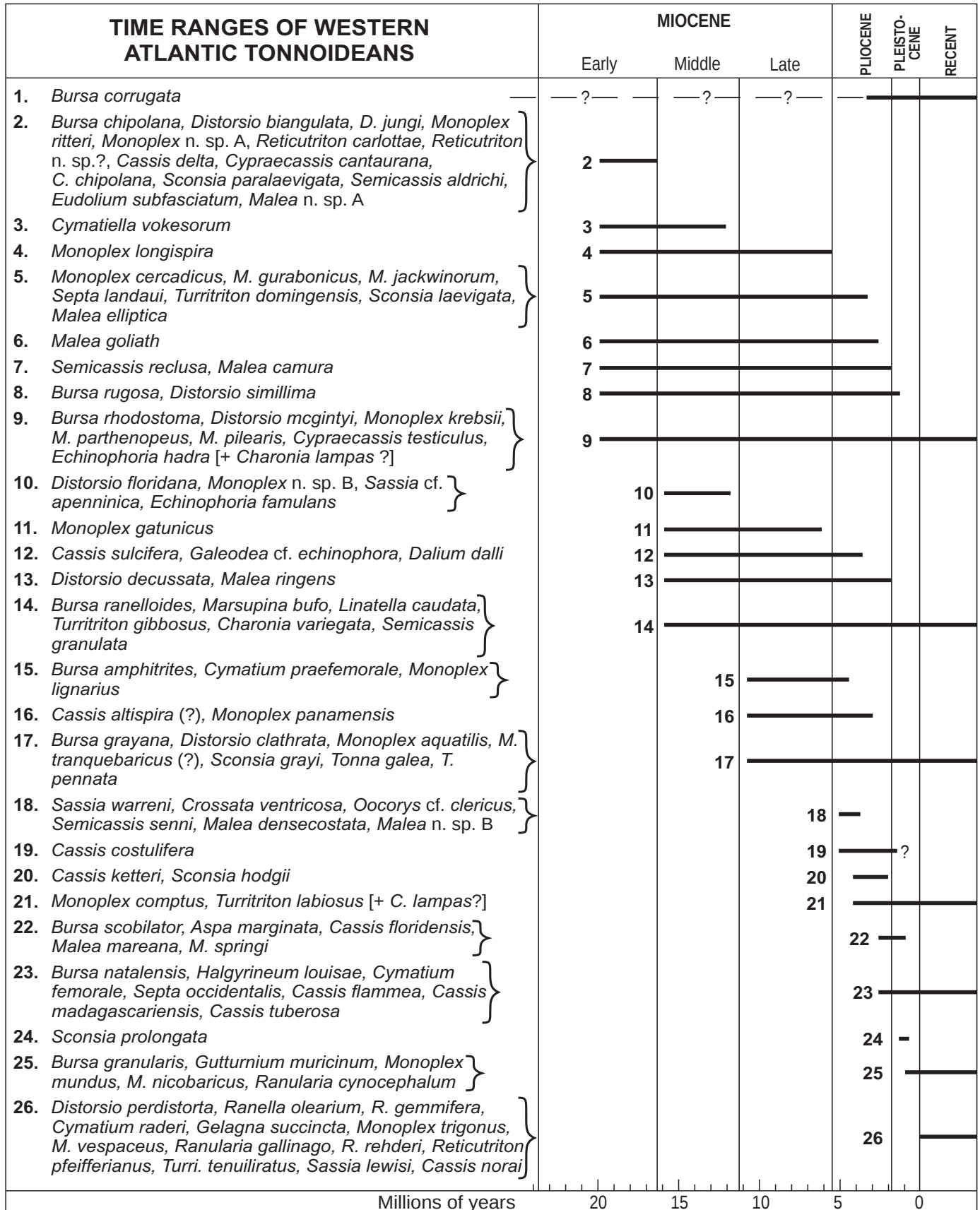
(2) Atlantiphile taxa; those taxa that have changed from an almost entirely eastern Pacific fossil distribution to an almost entirely western Atlantic distribution at present: *Dalium* appears to be the only tonnoidean example (fossil in Chile, *Dalium* n. sp.?; in Mexico and the Dominican Republic, *D. dalli*; in Ecuador, *D. ecuadorianum*; and living in the Caribbean, *D. solidum*), and this is greatly weakened by the outer shelf to bathyal habitat of *Dalium*, and its consequent rarity as a fossil. In any case, *Dalium* seems to be better understood as an example of a formerly pan-American genus that has been reduced to an Atlantic distribution as a result of extinction in the eastern Pacific. Clearly, atlantiphile taxa form a negligible group among tonnoideans, as they do among all mollusks (Woodring, 1966: table 5). In the more limited sense used by Woodring (1966), having *any* former occurrence in the eastern Pacific, this category includes *Distorsio clathrata*, *Linatella caudata*, *Cassia*, and *Sconsia*.

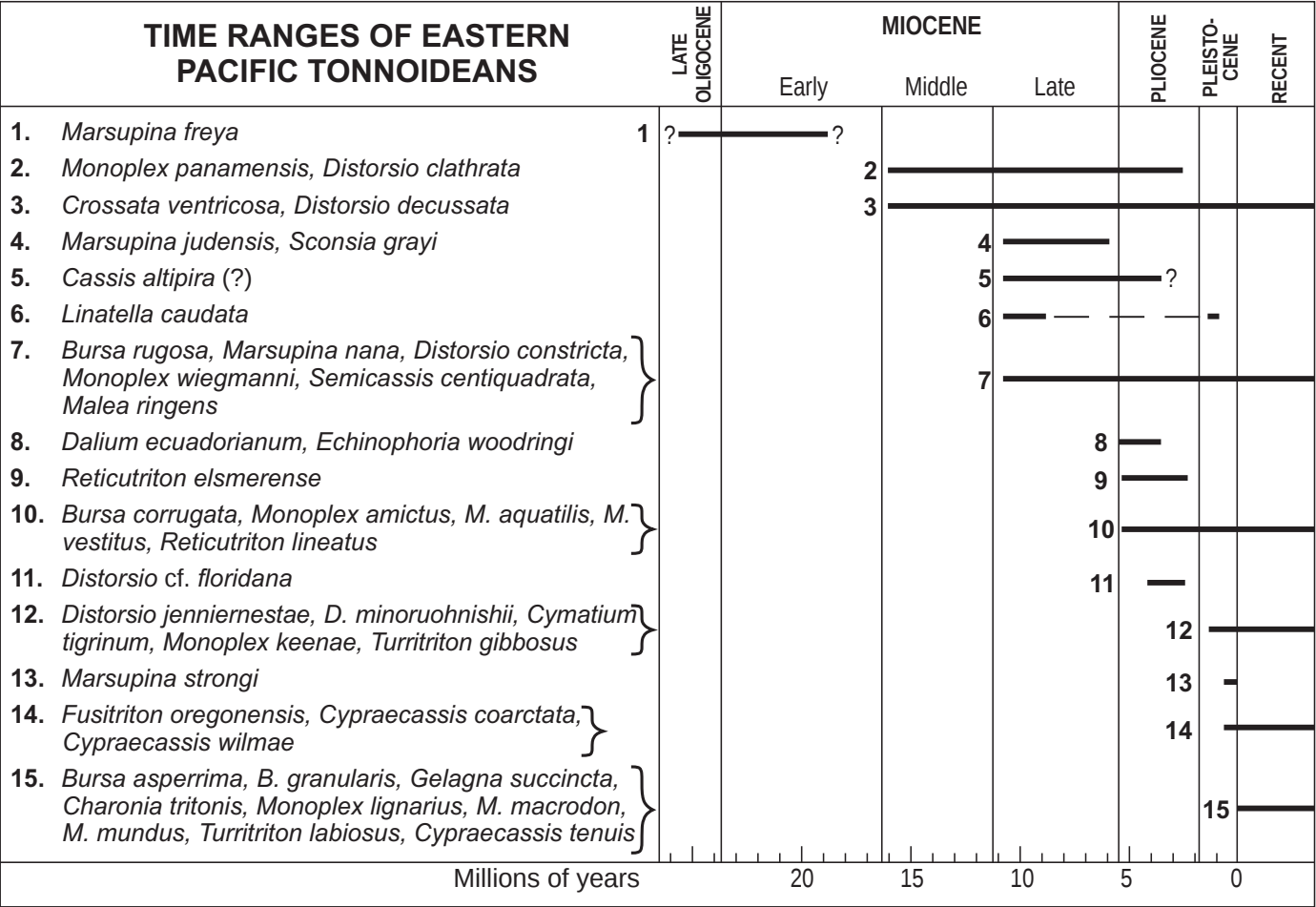
Comparison of Time Ranges on the Two Sides of Tropical America

Text-figs 5-6 show time ranges of tonnoideans on the two coasts of tropical America. Ranges have been distinguished on the two coasts for taxa that occur on both. The point made most clearly by Text-figs 5-6 is the very much poorer fossil

record in the eastern Pacific than in the western Atlantic. A simple count of taxa provides the most obvious comparison: 108 listed in the western Atlantic figure (Text-fig. 5) and 42 in the eastern Pacific (Text-fig. 6). (A few species of Recent Cassidae are not listed in both: *Echinophoria coronadoi*, *Casmaria atlantica*, three *Oocorys* species, two *Eucorys* species, and *Dalium solidum* in the western Atlantic; *Echinophoria pilsbryi*, *Casmaria vibexmexicana*, and three *Oocorys* species in the eastern Pacific; see lists above. None of these has any fossil record). The relative paucity of fossil localities and of tonnoideans at them in the eastern Pacific means that biotic change, whether caused by environmental (*e.g.*, temperature) change or by closure of the CAI, will always be much less well recorded than would be ideal. However, some time ranges that differ on the two coasts provide a little more information on the closure of the CAI. For example, *Sconsia grayi* appeared briefly in the eastern Pacific fossil record (Text-fig. 6, line 4) during Late Miocene time, when the CAI remained widely open in all reconstructions. It appeared at about the same time in the western Atlantic (Text-fig. 5, line 17), although of course lasting much longer as the eastern Pacific population rapidly was extinguished again, whereas *S. grayi* still survives in the western Atlantic. A similar history is shown in reverse by *Distorsio decussata*, which appeared during Middle Miocene time on both coasts, but this paciphile species lasted as an abundant element of the fauna of Atlantic Panama until almost the end of Pliocene time. *Distorsio clathrata* had a surprisingly contrasting history, with an earlier appearance in the eastern Pacific (Middle Miocene; Text-fig. 6, line 2) than in the Atlantic (Late Miocene; Text-fig. 5, line 17; although few specimens are known older than Early Pliocene), but it remains an abundant species in the Atlantic living fauna. A still more dramatic case of reversal of provinces is shown by *Monoplex lignarius*, which is recorded in Late Miocene and Early Pliocene rocks in the western Atlantic region (Text-fig. 5, line 15), but has no fossil record whatever in its present range, the eastern Pacific (Text-fig. 6, also line 15). However, this type of record likely results from the previously mentioned poor fossil record in the eastern Pacific, where many or perhaps all species have inaccurately recorded time ranges. The contrasting ranges of *Linatella caudata* (Text-fig. 5, line 14; Text-fig. 6, line 6) on the two coasts seem to be particularly significant for understanding closure of the CAI. As stated above, *L. caudata* is recorded in eastern Pacific rocks only during Late Miocene and Early Pleistocene time, whereas it has a continuous Middle Miocene to Recent record in the western Atlantic. This implies that at least a few planktotrophic larvae could be trans-

Text-fig. 5 (at right). Time ranges of tropical tonnoideans in the western Atlantic. Taxa are arranged in order of their first and then their last appearances, and show actual time ranges within the province regardless of later history, *i.e.*, Atlantic ranges are shown for taxa occurring coevally or at other times in the eastern Pacific.





Text-fig. 6. Time ranges of tropical tonnoideans in the eastern Pacific, compiled as in Text-fig. 5, i.e., eastern Pacific ranges are shown of taxa occurring coevally or at other times in the Atlantic.

ported through the CAI during Early Pleistocene time. If this inferred history is correct, the date of final uplift of the CAI above sea level was 1.8 Ma or later.

Despite the poorer eastern Pacific than western Atlantic fossil record, the lowest lists (Text-fig. 5, line 26; Text-fig. 6, line 15) each include three species that have no fossil record in the area. The western Atlantic record includes *Cymatium raderi*, *Ranularia rehderi*, and *Sassia lewisi*, all of which occur nowhere else and must have evolved in the western Atlantic. The eastern Pacific list also includes three species (*Monoplex lignarius*, *M. macrodon*, and *Cypraecassis tenuis*) that are limited to this fauna at present. However, in this case, all three eastern Pacific species have either a possible (*C. tenuis*) or a definite (*M. lignarius*) earlier record in the western Atlantic, or have evolved as a sister species of a western Atlantic congener after uplift of the CAI (*M. macrodon*, from *M. pilearis*). The other restricted eastern Pacific species that seems clearly to have evolved as a sister species of an Atlantic one after up-

lift of the CAI (*Monoplex keenae*, Text-fig. 6, line 12; from *M. parthenopeus*) has a Pleistocene fossil record in the eastern Pacific.

Text-figs 5-6 also display clearly the possible earlier sister species relationships, discussed above, that have developed as the CAI gradually narrowed and shallowed. *Distorsio constricta* (Text-fig. 6, line 7) must, at some level, be a sister species of the western Atlantic species *D. mcgintyi*. *Distorsio constricta* is known from Late Miocene time onward, although a rare fossil, in the eastern Pacific. *Distorsio mcgintyi* is recorded earliest in the late Early Miocene Cantaure shellbed in Venezuela (Text-fig. 5, line 9). *Monoplex wiegmanni* has an identical history in the eastern Pacific to that of *D. constricta*, and is hypothesized elsewhere here to have evolved from the western Atlantic species *M. cercadicus* (Text-fig. 5, line 5), which has a record from early Late Miocene to Early Pliocene time. *Cypraecassis chipolana* (Text-fig. 5, line 2) is similarly hypothesized to be the ancestor of the eastern Pacific species *C. wilmae* (Text-fig. 6,

line 14), and it seems feasible that *C. cantaurana* (Text-fig. 5, line 2) was ancestral to the eastern Pacific species *C. tenuis*, although there is no definite fossil record of the latter species (Text-fig. 6, line 15). Another relatively long-separated species pair consists of the eastern Pacific species *Semicassis centiquadrata* (Text-fig. 6, line 7) and the western Atlantic species *S. granulata* (Text-fig. 5, line 14), both recorded from Late Miocene (*S. centiquadrata*) or Middle Miocene time onward, and both still living on their respective coasts of tropical America. A slightly more complex history seems to be recorded by *Dalium* species, because the Atlantic species *D. dalli* (Text-fig. 5, line 12) has a Middle Miocene to Early Pliocene record. It also occurs in Miocene rocks in the Isthmus of Tehuantepec, Veracruz, Mexico, and a closely similar species occurs in Early Miocene rocks of south-central Chile. The living species, *D. solidum*, occurs only in the southern Caribbean Sea and West Indies, whereas the eastern Pacific species *D. ecuadorianum* (Text-fig. 6, line 8) is limited to Early Pliocene bathyal rocks in northern Ecuador – although this must be one of several records of bathyal taxa that are rendered particularly obscure by the exceedingly poor fossil record of bathyal mollusks in tropical America. A formerly widely distributed genus apparently has been reduced to a western Atlantic range at the present time by extinction in the eastern Pacific after closure of the CAI. The only other eastern Pacific species that seem likely to have a sister-species relationship with Atlantic species are both seen in Text-fig. 6, line 10, *i.e.*, first recorded in Early Pliocene rocks: *Monoplex amictus* and *M. vestitus*. Again as noted above, *M. amictus* seems clearly to have evolved from the western Atlantic species *M. krebsii* (Text-fig. 5, line 9) and the eastern Atlantic-Mediterranean species *M. corrugatus* (Lamarck, 1822), whereas *M. vestitus* likely evolved from an early population of *M. parthenopeus* segregated in the eastern Pacific before Early Pliocene time. All of these presumed species pairs provide evidence of a filter barrier operating in the CAI during late Early Miocene to Early Pliocene time, and disclose nothing about the time of final closure of the CAI.

SOME WIDER BIOGEOGRAPHICAL IMPLICATIONS

SPECIATION AND WIDTH OF RANGES

The first obvious conclusion from the above lists and discussion is that, even among such a supposedly wide-ranging group as the tonnoideans, no species are restricted at present to both the eastern Pacific and western Atlantic, only. The few other species that still occur in both of these provinces also occur more widely, although nearly all those that occur in the eastern Pacific are pseudopopulations recruited from the western Pacific as planktotrophic larvae. The clear implication is that disruption of their geographical ranges by the uplift of

the Isthmus of Panama caused either speciation or withdrawal to the eastern Pacific (*i.e.*, extinction in the Atlantic) in *all* of the relatively narrowly distributed tropical American tonnoideans.

The one exception to this rule is *Bursa corrugata*, which appears to have remained as one, undivided species throughout the eastern Pacific and the eastern and western Atlantic – at least, the shells of these populations do not seem to me to be separable consistently. Even in this example, though, West African and central Atlantic island specimens (form or subspecies *pustulosa* Reeve, 1844) have fewer, larger peripheral nodules than eastern Pacific and western Atlantic specimens, although, intriguingly, the European Miocene fossils referred to under *B. corrugata* are more similar to eastern Pacific and western Atlantic specimens than they are to Recent eastern Atlantic ones. It is easy to see how the western Atlantic population could remain unmodified after the closure of Panama, through the influx of West African genes as planktotrophic larvae. However, a unique situation appears to be demonstrated by the eastern Pacific population. This is the only tonnoidean taxon I am aware of that has been subdivided by the closure of the Panama seaway to leave a restricted eastern Pacific population, with no possible genetic influx from the western Pacific (because there is no fossil or Recent record of *B. corrugata* in the Indo-West Pacific), in which the eastern Pacific population apparently has not undergone genetic modification since the closure of the seaway. The only possible explanation for this situation seems to be that the eastern Pacific gene pool was large enough to prevent allopatric speciation.

Of course, the definition of “species” is critical to this concept. Here being classified in one species merely implies that specimens are morphologically indistinguishable to me; no molecular study has been carried out on these taxa as yet. The level of distinction between what are here classified as species varies through a wide spectrum, perhaps best exemplified by the *Monoplex parthenopeus* “complex.” *Monoplex parthenopeus* is the name used here for the population inhabiting the Mediterranean Sea, the eastern and western Atlantic, South Africa and perhaps all of East Africa, the Red Sea and Gulf of Arabia, New Zealand and southern Australia to the Kermadec Islands and (rarely) New Caledonia, (rarely) Hawaii, and commonly again in Taiwan to central Japan. The name *C. keenae* is used here for a weakly distinct population in the eastern Pacific, from the Galápagos Islands and the Gulf of California to Peru, with more numerous spiral cords and axial ridges – one-and-a-half times as many as in *M. parthenopeus*. Some authors prefer to regard *M. keenae* as at most a subspecies of *M. parthenopeus*, although it must be admitted that genetic exchange between the Atlantic and eastern Pacific populations is no longer possible. The presumption is that *M. keenae* has evolved through a founder event and genetic bottleneck af-

fecting the eastern Pacific population of *M. parthenopeus* (allopatric speciation) since the final closure of the CAI. A much stronger distinction is recognized by all malacologists between the widespread *M. parthenopeus* and the eastern Pacific species *M. vestitus*, although the similarities between these species are close enough to suggest that *M. vestitus* evolved from an earlier (presumably Miocene) allopatric speciation event affecting an earlier population of *M. parthenopeus* in the eastern Pacific [e.g., it is suggested below that C. B. Adams' (1852) name *M. vestitus senior* was based on specimens of *M. keenae*]. The fossils of these two species reported below support this interpretation, because the earliest fossil record of *M. keenae* is Pleistocene, whereas the earliest record of *M. vestitus* is from the Early Pliocene Onzole Fm of Ecuador.

The major biogeographical conclusion is the unsurprising one that a wide geographical range confers resistance to the type of genetic bottleneck that presumably brought about allopatric speciation in subdivided tropical American populations. Widely dispersed planktotrophic larvae of the more widely distributed species presumably continued to arrive in the populations on both sides of Panama, preventing genetic bottlenecks.

GEOLOGICALLY RECENT EXTINCTION

Some idea of Neogene extinction in the region is provided visually by Text-figs 5-6. Another is provided by the proportions of the various biogeographical elements in the living tonnoidean faunas of the four major biogeographical regions, which for the faunas listed above are shown in Table 5A. Table 5B also lists similarity indices between them, calculated in the same way as outlined above for tropical American Neogene tonnoidean faunas. "Shared" in Table 5 implies planktotrophic taxa recruited as larvae from the nearest fauna across the ocean. The area considered here that stands out, from the point of view of tonnoideans, as having a highly endemic living fauna (apart from the huge Indo-West Pacific fauna, in which many local endemics are subsumed in one list) is therefore the tropical eastern Pacific. All common mainland species in the eastern Pacific, other than the rare western Pacific stragglers (eight species; Emerson, 1991) and *Bursa corrugata*, are endemic. In contrast, nearly half (43%) of the western Atlantic fauna is shared with the tropical Indo-West Pacific – i.e., these two areas have a substantially intact mid-Cenozoic (Tethyan) fauna – with moderate endemism (37%), and most of the rest of the fauna shared with West Africa-Mediterranean (50%). The western Atlantic fauna has been affected by a moderate amount of extinction and speciation since the uplift of the CAI, although Jackson *et al.* (2003) were at pains to point out that molluscan diversity in the western Atlantic has increased markedly through late Neogene time, rather than decreased as previous studies had suggested. But the great distinction

of the eastern Pacific fauna must result from a much greater influence of both extinction and speciation (following the closure of the CAI) than in the western Atlantic, combined with the extinction of many formerly pan-tropical American taxa in the western Atlantic and their consequent restriction to the eastern Pacific, and with a lack of the type of immigration of breeding elements from the Indo-West Pacific that has occurred during Pleistocene-Recent time in the Atlantic.

Similarity indices (Table 5B) support the main conclusions arrived at from species-by-species comparisons. Again, there is some evidence of bias by small sample size in Simpson's index and the other indices are considered to be more reliable. Clearly, much the most similar Recent tonnoidean faunas, whatever index is used, are those of the eastern and western Atlantic. The western Atlantic and Indo-West Pacific faunas are also quite similar, the eastern Atlantic and Indo-West Pacific less so. Rather surprisingly, the eastern and western Atlantic faunas are almost equally similar to the eastern Pacific fauna. The lowest similarity is between the eastern Pacific and the Indo-West Pacific, highlighting the effectiveness of the eastern Pacific filter barrier, which apparently affects long-lived planktotrophic tonnoideans almost as much as other mollusks.

The eastern Pacific barrier evidently has been quite effective at preventing transport of larvae to the eastern Pacific since the CAI closed, i.e., since Early Pleistocene time, whereas the high similarity between the western Atlantic and Indo-West Pacific faunas demonstrates that the Agulhas leakage (see "Transport from the Indian to the Atlantic Ocean," below) has allowed substantial transport of larvae from the Indian Ocean to the Atlantic over this same period. The main point about the eastern Pacific barrier for biogeography is that it prevents the transport of molluscan larvae to the eastern Pacific in numbers sufficient to establish a breeding population, whereas larvae are transported around South Africa in sufficient numbers for many species to establish breeding populations in the western Atlantic. The eastern Pacific barrier evidently began to affect molluscan faunas as soon as current flow through the Central American Seaway became restricted, apparently during Middle to Late Miocene time (Collins *et al.*, 1996; Beu, 2001). It seems to have operated during much of the period of gradual seaway closure, i.e., for the last 3-8 million years, and perhaps for 12-15 million years. Therefore, species that became isolated in the eastern Pacific, through seaway constriction and eventual closure, mostly remain as remnants of their original pan-tropical American population, although others (e.g., *Monoplex vestitus*) have evolved into eastern Pacific daughter species. In contrast, western Atlantic populations of the same species mostly became extinct. As noted above, the single exception evident in the present work, other than rare stragglers (non-breeding pseudopopulations) from the tropical western Pacific, is *Bursa corrugata*.

Table 5. (A) Numbers of species and the percentages of biogeographical elements in living tonnoidean faunas. (B) Similarity indices of the living tonnoidean faunas listed in Table 5A, in order from highest to lowest similarity of Jaccard's and Dice's indices.

(A)	E Pacific	W Atlantic	W Africa-Med	I-W Pacific
Total species	38	68	51	235
Restricted	24 (63%)	25 (37%)	14 (27%)	203 (86%)
Shared with W Africa	5 (13%)	34 (50%)	-	24 (10%)
Shared with E Pacific	-	6 (9%)	5 (10%)	8 (3%)
Shared with W Atlantic	8 (21%)	-	34 (67%)	29 (12%)
Shared with I-W Pacific	8 (21%)	29 (43%)	24 (47%)	-

(B)	Jaccard	Simpson	Dice
E Atlantic: W Atlantic	0.4	0.666	0.444
W Atlantic: I-W Pacific	0.106	0.426	0.191
E Atlantic: I-W Pacific	0.084	0.471	0.155
W Atlantic: E Pacific	0.057	0.158	0.107
E Atlantic: E Pacific	0.056	0.132	0.112
E Pacific: I-W Pacific	0.03	0.211	0.059

GEOGRAPHICAL RESTRICTION OF GENERA

One rather surprising aspect of the faunal lists (above) is the restriction of some genera to particular faunal provinces. *Bufo* *naria*, *Bursina*, *Tutufa*, *Biplex*, *Gyrineum*, *Lotoria*, *Distorsionella*, *Distorsomina*, and *Phalium* apparently always have been limited to the Indo-West Pacific province (although, as noted in the Introduction, one specimen of *Lotoria lotoria* has been collected alive in Brazil). *Cymatiella* is limited to southern and eastern Australia at present, but the fossil record demonstrates a history of gradual migration from the Paris Basin (during Eocene time) via tropical America, documented here, and Indonesia (Beu, 2005: 104, figs 270-280; both Miocene) to Australia, where it is first recorded in Miocene rocks – presumably implying a formerly wide Tethyan distribution and gradual restriction to southern Australia. Similarly, *Eucorys* is restricted to the western Atlantic, and *Sconsia* is largely so [the two Indonesian Miocene species were reviewed by me (Beu, 2005), and a few Miocene-Pliocene occurrences in Darien and Ecuador are recorded below; *Sconsia* also has a long fossil record in Paleogene rocks of what is now Europe]. There is also no record of *Charonia*, *Tonna*, or any bursid genera other than *Bursa*, *Crossata*, and *Marsupina* ever occurring in the eastern Pacific (apart from rare non-breeding stragglers of *Charonia tritonis* at the present day; three specimens recorded). *Cassis* also has been at most a rare straggler in the eastern Pacific, as pseudopopulations recruited from the Atlantic, throughout its history. *Crossata* is an entirely eastern Pacific genus, perhaps descended from *Olequahia* Stewart, 1926 (type species *Cassidaria washingtoniana* Weaver, 1912, Eocene, Washington State; Beu, 1988: 74, pl. 1, figs 1-9) and it is feasible that *Crossata* and *Olequahia* are one clade. These generic restrictions seems strange if the eastern Pacific pro-

vided a widely open connection between the Atlantic and Pacific Oceans until recently, when such genera as *Cassis* and *Charonia* were diverse in both the Atlantic and the Indo-West Pacific throughout Cenozoic time, and still are at present, and yet do not occur in the eastern Pacific. However, *Cypraeacassis* was formerly more diverse than it is now in both the western Atlantic and the Indo-West Pacific, and its currently high diversity in the eastern Pacific (three species) is relict from a more widespread pattern of higher diversity during Miocene time. Similarly, the present distribution of *Malea* species is clearly relict, with the greatest diversity formerly occurring in the western Atlantic. It appears that some genera empirically have a low dispersibility, and have remained “fixed” in limited areas for long periods, whereas other genera have much higher dispersibility, and others again give a false impression as a result of a high rate of extinction in some areas.

LARVAL TRANSPORT FROM THE INDIAN TO THE ATLANTIC OCEAN

Why should the eastern Pacific have been singled out so sharply by high endemism and relatively low diversity, when there is clear evidence still at present (Emerson, 1991) of occasional transport of larvae across the eastern Pacific barrier? The West African-Mediterranean tonnoidean fauna, not considered to any great degree in the present report, has a moderately high proportion of restricted taxa (27%) and a proportion shared with the Indo-West Pacific that is slightly higher (47%) than in the western Atlantic fauna (43%). These two faunas stand out across the tropical realm as having > 40% of taxa in common with the tropical Indo-West Pacific. This implies that they have been able to establish genetic continuity with the Indo-West Pacific fauna after the pan-tropical American species became extinct in the Atlantic. The only way in which it seems possible for this to take place is by larval transport, in both directions, between the Indian Ocean and the Atlantic via South Africa. Species that demonstrate conclusively that at least some larval transport takes place westward around South Africa include *Bursa ranelloides*, *Ranularia cynocephalum* and *R. gallinago*, all of which occur in the Indian Ocean but not in the tropical western Pacific. If genetic exchange still occurs between the Indian Ocean and Atlantic populations of these three species, a westward route around southern Africa is the only possible one for transport of their larvae, despite the apparently dominant eastward transport around South Africa at present in the Antarctic Circumpolar Current.

Biogeographical evidence strengthening the significance

of westward larval transport around Africa is provided by the numerous species that are among the most common tonnoideans today in both the Indo-West Pacific and Atlantic faunas, but have no fossil record in the western Atlantic until Pleistocene time – if any fossil record there at all: *Bursa granularis*, *B. ranelloides*, *Distorsio perdistorta*, *Gutturium muricinum*, *Monoplex comptus*, *M. mundus*, *M. nicobaricus*, and *Ranularia cynocephalum*. Another group of species consists of less common stragglers (apparently pseudopopulations) that also can have entered the Atlantic only from the Indian Ocean: *Charonia tritonis* (one western Atlantic record), *Gelagna succincta*, *Monoplex exaratus* (one western Atlantic record), *M. vespaeus*, *Reticutriton pfeifferianus*, *Ranularia gallinago*, and *Malea pomum*. This list also possibly includes *Lotoria lotoria*, for which the single Atlantic record is unconfirmed. All of these species are absent, or occur only as rare members of pseudopopulations recruited from outside the region, in both the eastern Atlantic and the eastern Pacific. A few other taxa are represented in the western Atlantic by uncommon specimens indistinguishable from those living around South Africa at present (particularly *Charonia lampas* and *Ranella gemmifera*), again supporting a westward transport direction of larvae to Brazil. The only apparent explanation for the distribution of all of these species is larval dispersal into the Atlantic from South Africa during Pleistocene time and at present (see also Vermeij & Rosenberg, 1993: 182-184). The existence of the Agulhas leakage around southern Africa, a current allowing larvae to be dispersed from the Indian Ocean to the Atlantic, was described by Borowski (2003: 9), citing earlier descriptions and reviews by De Ruijter *et al.* (1999), Gordon (1985, 1986, 1996), and Gordon *et al.* (1992). De Ruiter *et al.* (2006) recently updated knowledge of this leakage, which occurs as westward-moving subsurface rings from eddies in the Mozambique Channel and south of Madagascar transported into the southern Atlantic Ocean. The Agulhas leakage also explains the size, shape, and color cline in the distribution of *Monoplex pilearis*, in which specimens from the southwestern Indian Ocean (Madagascar and Mozambique to Durban) are most similar to the western Atlantic population, although the fossil evidence reported here indicates that *M. pilearis* has occurred in the western Atlantic since at least late Early Miocene time (Baitoa Fm of the Dominican Republic).

Species that have no fossil record at all are more difficult to interpret. Were they absent until recently (*i.e.*, do they belong in the group of species that expanded their ranges recently from the Indian Ocean?) or do they just inhabit an environment that is poorly represented in the fossil record? The answer probably is “both.” Some of them (*e.g.*, *Ranularia rehderi*, *Sconsia alexarthuri*, and *Echinophoria coronadoi*) are distinctive, endemic western Atlantic species that cannot have arrived from elsewhere, and apparently lived in an environment

that is not fossilized. Others (*e.g.*, *Gelagna succincta*, *Monoplex comptus*, *M. exaratus*, and *Malea pomum*) are widespread in the Indo-West Pacific, some have a fossil record there (Beu, 2005), and they almost certainly belong in the group that has arrived geologically recently in the Atlantic from the Indian Ocean.

GEOGRAPHICAL RANGES AND UPLIFT OF THE CENTRAL AMERICAN ISTHMUS

The concept of a seaway through the present CAI, formerly uniting the tropical oceans, dates back to at least Spencer (1897), who envisaged a connection through the Isthmus of Tehuantepec, Mexico. Although it is still possible that such a seaway was present during Miocene time, as one was through the Atrato Basin in northern Colombia (Woodring, 1966; Duqué-Caro, 1990; Coates *et al.*, 2004), more recent research has concentrated on the concept of a younger seaway through approximately the position of the present Panama canal (*e.g.*, Coates *et al.*, 1992). It seems equally likely that one existed (perhaps at a similar time to the one through Panama) through lowland Costa Rica (Coates & Obando, 1996). Most statements about such a concept (*e.g.*, Keigwin, 1978) have implied a single, climactic uplift event in which the seaway suddenly was cut off and the “great American biotic interchange” of terrestrial mammals began, usually stated to have been at around 3.5-3 Ma. More gradual disconnection of the oceans and linking of the continents is indicated, however, by both recent geological and paleontological evidence (Coates & Obando, 1996; Collins *et al.*, 1996) and evidence from South American vertebrate paleontology of the earlier arrival of the first North American terrestrial mammals [*e.g.*, gomphotheres (Proboscidea), tapirs and camelids in Late Miocene rocks of Peru, Colombia and Brazil; Campbell & Frailey, 1996]. Mammals that can swim well arrived in South America by at least 12 Ma, indicating that a variety of stepping-stone islands lay across the CAI from that time. In contrast, South American mammals that were poor swimmers arrived in Mexico and giant South American ground birds arrived in Texas and Florida during Early to mid-Pliocene time (Flynn *et al.*, 2005; MacFadden *et al.*, 2007). Webb & Rancy (1996: 337) dated the “final emplacement of the isthmian link in Central America” at about 2.5 Ma, based on magnetostratigraphic dating of South American fossil mammal faunas. This merely indicates though, of course, that the earliest glacial lowering of sea level to provide access for terrestrial mammals happened at about that date, more-or-less coincident with the onset of glaciation in northern Europe; marine access between the oceans would still have been possible during the intervening interglacial highstands. Relationships between marine offshore foraminiferal faunas imply deep-water marine connections between the eastern Pacific and western Atlantic Oceans

up until approximately 3 Ma (Keigwin, 1978), even though the first evidence of break-down of planktonic faunal similarities between the two oceans is as early as 4.2-3.95 Ma (Ibaraki, 2002). These dates imply a gradual, complex uplift and closure of the CAI, presumably as a changing pattern of islands, marine basins, and seaways through at least 12-3 Ma.

The fossil record of tonnoideans lends support to such a long time-scale of CAI uplift. Occurrences of atlantiphile or paciphile species as fossils in the “wrong” biogeographical province offer the best support for this, and are listed here (following Beu, 2001; data for these records are provided under Systematic Paleontology, below). It should be noted that new dates on tropical American Neogene rocks published since Beu (2001) was written have all indicated earlier ages than were adopted formerly, weakening the evidence for a young date of final uplift of the CAI (Coates in Collins & Coates, 1999; Cotton, 1999; Coates *et al.*, 2003, 2004).

1. *Bursa rugosa*: This paciphile species is common and widespread in Neogene rocks of the Caribbean area. The youngest Caribbean occurrences are in the Late Miocene Gatun Fm, the Late Miocene-Pliocene Bocas del Toro Basin of Atlantic Panama, and Late Pliocene rocks of Florida. Collection NMB 18716 contains a single Pliocene specimen (Shark Hole Point Fm, 5.2-2.3 Ma; southern end of Playa Lorenzo, southern side Valiente Peninsula). It is also common in the Early Pliocene Punta Gavilán Fm of eastern Venezuela.

2. *Crossata ventricosa*: The sole Panama fossil record of this characteristic eastern Pacific species is also from the Pliocene Shark Hole Point Fm (5.2-2.3 Ma) at Shark Hole Point, Valiente Peninsula, Bocas del Toro Basin, on the Atlantic coast of Panama (NMB 17854, one specimen).

3. *Marsupina bufo* (Atlantic) and *M. nana* (Pacific): Although these are listed above as a possible example of a geminate species pair, they do not constitute such a pair in the sense of resulting from speciation *after uplift of the CAI* subdivided an originally single species. *Marsupina nana* is much closer morphologically (*i.e.*, presumably phylogenetically) to the Miocene *M. judensis* n. sp., on the Pacific coast, than it is to *M. bufo*, and *M. bufo* has a long (Miocene-Pleistocene) fossil record in the western Atlantic. This, then, seems to be another case, like *Semicassis centiquadrata*/*S. granulata*, of species pairs whose distinctions result from Miocene speciation events long before the final uplift of the CAI. It is conceivable that these species pairs reflect Miocene initiation of uplift, formation of isolated basins, and seaway constriction, as the uplift of the CAI commenced.

4. *Distorsio clathrata*: The eastern Pacific occurrences of this species are in the Early Pliocene Onzole Fm of Ecuador (three specimens listed here; two others recorded by Olsson, 1964: 175, pl. 30, figs 1-1b). All other fossil occurrences are in the western Atlantic area still inhabited by *D. clathrata*,

where there are few records before Pliocene time.

5. *Distorsio decussata*: The abundant occurrence of this species in Late Miocene-Pliocene rocks on both coasts of Panama indicates that the CAI was not yet uplifted. *Distorsio decussata* is limited to the eastern Pacific at present, but fossils are abundant in Atlantic Panama, clearly indicating an open isthmus (recorded below from ten Pliocene localities in the Bocas del Toro Basin, Atlantic Panama). The youngest record in the Atlantic (Table 2) is six specimens in the Escudo de Veraguas Fm (3.6-1.8 Ma) (NMB 17622, 1; 17628, 1; 17840, 4), confirming that planktotrophic molluscan larvae were carried through the Central American Seaway after 3.6 Ma, and possibly as late as earliest Pleistocene time.

6. *Monoplex panamensis*: A similar pattern to that of *Distorsio decussata* is shown by this extinct species, recorded below from Late Miocene-Pliocene rocks on both coasts of Panama. However, all localities have now been determined to be Late Miocene in age, except for two in the Pliocene Escudo de Veraguas Fm (3.6-1.8 Ma) at Cayo Agua, Bocas del Toro Basin (NMB 17633, 18719). These again are useful in demonstrating that the seaway remained open after 3.6 Ma.

7. *Linatella caudata*: This species seems to be the most significant, as it has not been recorded in the present-day eastern Pacific fauna, although it is very widespread in both the Indo-West Pacific and Atlantic present-day faunas. Nevertheless, fossils are recorded below from the eastern Pacific from both the Miocene of Punta Judas, Costa Rica (NMB 17764, 1) and the Pleistocene Armuelles Fm of the Burica Peninsula, northern Pacific Panama (NMB 17442, 5 juveniles; Pl. 63, Figs 8, 11). This locality (PPP 1761, blue silts, Río Rabo de Puerco, west of Puerto Armuelles, Burica Peninsula) is definitely stated to be within the Pleistocene Armuelles Fm in the PPP web database. This seems to be the youngest clear example of dispersal through the CAI and, interestingly, is in the opposite direction to most other examples – an atlantiphile tonnoidean in Pacific Panama. It indicates that at least shallow marine waters connected the Caribbean Sea with the eastern Pacific during Early Pleistocene interglacial periods of high sea level, until after 1.8 Ma. Alan Kohn (University of Washington, pers. comm., 2002) cautioned that it is not possible to completely discount dispersal across the eastern Pacific barrier to explain the occurrences of *L. caudata* in Pacific Panama. However, the low rate of occurrence of such dispersals, demonstrated by the very low similarity index between the Indo-West Pacific and eastern Pacific faunas in Table 5B, and the absence of any records of *L. caudata* from anywhere in the Pacific east of Hawaii (Beu, in prep.) makes such an explanation unlikely.

8. *Monoplex lignarius*: The Springvale Quarry locality in Trinidad, where this species occurs as fossil, is now known to be Early Pliocene (Donovan, 1994). *Monoplex lignarius* is now limited to the eastern Pacific, so this paciphile spe-

cies at least indicates that the CAI was still open during Early Pliocene time.

9. *Monoplex wiegmanni*: Again, this now-restricted eastern Pacific species has a single exception of biogeographical interest: one specimen is recorded below from the mid-Pliocene Banáno Fm of Río Banáno near La Bomba, on the Atlantic coast of Costa Rica. The age of this formation at La Bomba is 3.2-3.0 Ma (Coates, 1999: text-fig. 6).

10. *Halgyrineum louisae*: As pointed out by Robinson (1990, 1993), the sole fossil record of this species is in the latest Pliocene-Early Pleistocene (2.1-1.5 Ma) Moín Fm at Limón, Atlantic Costa Rica. Recent specimens are recorded widely but sparsely in the tropical western Pacific (Beu, 1998b: 64; see also below) and at the northern Atlantic islands and banks (Fechter, 1975; Gofas & Beu, 2002: 99). The Limón occurrence indicates that the Atlantic and Pacific populations were able to maintain genetic continuity until the final uplift of the CAI at around the Pliocene-Pleistocene boundary. As with *Bursa corrugata*, the lack of any obvious morphological differences between the shells of Pacific and Atlantic specimens needs to be confirmed by molecular evidence, but because *H. louisae* has a classic tonnoidean planktotrophic protoconch (Pl. 24, Figs 4, 7-10; Beu, 1998b: figs 19c, e-f), it is possibly one of the species still being kept in genetic continuity through larval transport around South Africa in the Agulhas leakage.

11. *Cassis*: As pointed out by Vokes (1990b), the genus *Cassis* s.s. is almost unknown in the eastern Pacific, although Hanna (1926: 444, pl. 20, fig. 8, pl. 29, figs 2-3) described *C. subtuberosa* (based on a specimen closely resembling *C. flammea*) from the Latrania Fm (Demere & Rugh, 2006) (Late Miocene/Early Pliocene) at Alverson Canyon, Coyote Mountains, California, USA. Vokes (1990b) recorded another *Cassis* specimen, probably belonging in *C. altispira* n. sp., from the Onzole Fm (Early Pliocene) at Quebrada Camarones, Ecuador. Two further eastern Pacific fossils are recorded below, tentatively identified as *C. altispira*: Río Tuquesa, Darien (Late Miocene), and Angostura Fm (Late Miocene), Punta Verde, 30 km east-northeast of Esmeraldas, Ecuador. *Cassis* was listed as an atlantiphile genus in the eastern Pacific by Woodring (1966), but seems more properly considered as an Atlantic and western Pacific-Indian Ocean genus that very occasionally was carried as planktotrophic larvae into the eastern Pacific through the Panama seaway, during Late Miocene-Early Pliocene time.

12. *Sconsia grayi*: Like *Cassis*, the genus *Sconsia* is almost entirely unknown in the eastern Pacific, fossil or Recent. The exceptions are two records of *S. grayi* from Late Miocene rocks of Darien, southern Pacific Panama (NMB 18184, Río Chucunaque, 4; NMB 18510, Río Tuquesa, 1; see below) and the records by Olsson (1964: 169) of fragments from the

Angostura Fm (Late Miocene) at three localities in Ecuador, indicating that the CAI was still open at the time of deposition of these rocks.

13. One of the most useful fossil records is that of *Malea ringens*. This occurs commonly as a fossil within its living range, along the Pacific coasts of Mexico, Costa Rica, Panama, Darien, Ecuador, and Peru, but also occurs commonly in the Late Miocene-Pliocene rocks of Atlantic Panama, in both the Bocas del Toro Basin and the Panama Canal Basin (24 Middle-Late Miocene and 16 Pliocene localities recorded below; Table 2: 26 specimens, 22 in Cayo Agua Fm, 5.0-3.5 Ma; 3 in Shark Hole Point Fm, 5.2-2.3 Ma, and 1 in Escudo de Veraguas Fm, 3.6-1.8 Ma), providing strong evidence for the CAI remaining open until late in Pliocene time. Here again, a single record from the latest Pliocene-Early Pleistocene (1.9-1.5 Ma) Moín Fm at Limón, Atlantic Costa Rica, by Aguilar & Denyer (1994: 63, pl. 1, fig. 10) is important for indicating that the CAI was still open during the deposition of this unit.

CONCLUSIONS

1. The record of tonnoideans in the tropical American region indicates that a seaway through the CAI (perhaps through Costa Rica, rather than, or as well as, Panama) was still open, at least intermittently, late in Pliocene time. The occurrences of the atlantiphile species *Linatella caudata* in the Pleistocene Armuelles Fm of the Burica Peninsula, northern Pacific coast of Panama, and of the paciphile species *Malea ringens* at Limón, Atlantic Costa Rica, indicate that some marine connections still occurred between the eastern Pacific and the Caribbean during at least latest Pliocene and perhaps earliest Pleistocene interglacial periods. Connections between the eastern Pacific and western Atlantic marine faunas would have occurred frequently, during interglacial periods of high sea level, for much of mid- to Late Pliocene and possibly earliest Pleistocene time, and conversely, connections between the terrestrial faunas of North and South America would have occurred frequently over the same period, during the alternating periods of glacial low sea level, i.e., after about 2.5 Ma. The closure of the Central American Seaway probably was a long-drawn-out, gradual series of events, finally closing permanently at around 2-1.8 Ma.

2. The lack of a fossil record before the Pleistocene in the western Atlantic of several species that are among the most common tonnoideans now in both the Indo-West Pacific and western Atlantic faunas indicates that they were able to reach the western Atlantic only very recently. The only feasible route for the transport of their larvae, particularly for *Bursa raneloides*, *Ranularia cynocephalum*, and *R. gallinago* (which occur in the Indian Ocean but not in the western Pacific, i.e., they cannot possibly have passed through the CAI) seems to have

been around South Africa, in the apparently opposite direction to that of the Antarctic Circumpolar Current. Such a route for larval dispersal, continuing still at present, is suggested also by the 43% of western Atlantic and 47% of West African species that are still shared with the Indo-West Pacific fauna, because the percentage of shared species is much lower (21%) for the eastern Pacific fauna, and most of the taxa in common with the Indo-West Pacific exist only as non-breeding pseudopopulations in the eastern Pacific (see also Vermeij & Rosenberg, 1993; Vermeij, 2005). Borowski (2003: 9) and De Ruiter *et al.* (2006) reviewed earlier publications on the Agulhas leakage, which occurs as subsurface eddies that transport water (and therefore larvae) between the Indian and Atlantic Oceans, explaining these distributions that at first sight seem counterintuitive.

3. Other tonnoideans indicate that reorganizations of distributions and speciation events occurred in tropical America during Miocene and Early Pliocene time. These include species pairs (such as *Marsupina nana*/*M. bufo* and *Semicassis centiquadrata*/*S. granulata*) and the complex taxonomy of such genera as *Cypraecassis* and *Dalium*, whose separations long predate the closure of the CAI, and indicate that uplift of the CAI was beginning as early as Middle or even Early Miocene time. Most apparently tonnoidean geminate pairs on the two sides of tropical America date from the period before CAI closure, when a filter barrier operated in the CAI. The only true geminate pairs formed by speciation *as a result of closure of the CAI* are subtle ones whose taxonomy is debated, such as *Monoplex pilearis*/*M. macrodon*, *Monoplex parthenopeus*/*M. keenae*, and possibly *Cypraecassis chipolana*/*C. wilmae* (the last uncertain because of the early extinction of *C. chipolana*). The subtle level of distinction between these taxa presumably results from the very recent date of final closure of the CAI.

4. Several lines of evidence indicate that the tropical western Atlantic region was subdivided into biogeographical subregions during Miocene and Pliocene time, with some tonnoidean species limited to one or two subregions (see also Vermeij, 2005). Distinctions between coeval pairs of species in one genus, such as cassids in the Panama basins and the Dominican Republic (*Sconsia grayi* and *S. laevigata*, *Semicassis granulata* and *S. reclusa*), seem to imply such subregions, as do the similarity indices discussed above. The limited geographical ranges of several *Malea* species, such as *M. densecostata*, point to the same conclusion. Iturralde-Vinent & MacPhee (1999: fig. 17) showed a relatively small Neogene pull-apart basin southwest of Margarita Island that would have included the Punta Gavilán-Cubagua area. Ostos *et al.* (2005; and other papers in the same volume) also provided an overview of the complex plate tectonic deformation along the Caribbean margin of Venezuela during Cenozoic time, defining a basin occupied by the Punta Gavilán-Cubagua region during Miocene-

Pliocene time. A recent update of the active tectonics of the southern Caribbean plate boundary zone also was provided by Levander *et al.* (2006). It appears that the restricted species at Punta Gavilán and Isla Cubagua were constrained by physical barriers. However, a filter barrier apparently also lay east of Panama. The evidence of tonnoidean distributions seems to indicate at least three subregions within the Late Miocene-Early Pliocene tropical western Atlantic: Panamic, northern Caribbean, and southern Caribbean. The northern Caribbean subregion seems to coincide with Vermeij's (2005) Caloosahatchian province, whereas the southern, Gatunian province recognized by Petuch (1982) and Vermeij (2005) deserves subdivision. The evidence for two subprovinces, in the Panamanian and Venezuelan regions, needs to be interpreted with caution, however. Several tonnoideans (*e.g.*, *Marsupina bufo*, *Sconsia grayi*, *Dalium solidum*, and *Echinophoria hadra*) are much more common now along the northern coast of South America and around the Lesser Antilles than elsewhere, and are apparently limited to highly productive upwelling areas. They seem to be limited by ecology rather than by physical or oceanographic barriers, and this would also have been a factor in the past.

5. The scenario indicated for the closure of the CAI is one of gradual constriction and fragmentation of waterways after mid-Miocene time (*ca.* 15 Ma), the frequent formation and disappearance of marine basins and seaways through a combination of active tectonics and the rapidly oscillating sea levels of Late Miocene-Early Pleistocene time, and the continuation of at least intermittent marine connections through a seaway during Late Pliocene and perhaps earliest Pleistocene interglacial periods of high sea level. This is discussed further below.

TIMING AND EFFECTS OF UPLIFT OF THE CENTRAL AMERICAN ISTHMUS

An enormous literature exists on the closure of the Central American seaway and the concomitant uplift of the CAI. This most major of relatively recent vicariant biogeographical events, the closure of the tropical gateway between the Atlantic and Pacific Oceans, has been studied closely because of the model it provides for similar situations in the past. It is *reasonably* well dated (it is at least certain that it occurred late in Neogene time), and so we understand it more fully than most similar but earlier events. It provides a "natural laboratory" for understanding the effects of the imposition of a vicariant barrier on speciation in the marine realm. Consequently, it has great utility as a calibration point for the "molecular clock." It also allowed the "great American interchange" of terrestrial mammals between North and South America (Stehli & Webb, 1985). Finally, it possibly was ultimately responsible for the initiation of the Pleistocene glacial-interglacial cycles through strengthening of the Gulf Stream and formation of

the Arctic Pond (Stanley, 1995) – and so, perhaps, the evolution of the genus *Homo* (Stanley, 1992, 1995). The significance of the closure of the CAI, combined with the complex geologically recent events in Caribbean plate tectonics, for tropical American biogeography has been explored by many authors (a few include Rosen, 1975; Hedges, 1982; Coney, 1982; Jones & Hasson, 1985; Vermeij & Petuch, 1986; White, 1986; Jackson *et al.*, 1993; Tsuchi, 1996; Jackson *et al.* (eds), 1996; Lessios *et al.*, 1999; and O'Dea *et al.*, 2007).

I state that the uplift is “reasonably” well dated because of uncertainty over exactly when the CAI finally closed. Three earlier publications of which I am aware have suggested what seems to me to be a reasonable, gradual scenario for closure of the CAI. Firstly, Jones & Hasson (1985: 349) concluded that “It seems reasonable that elevation of the Panama Isthmus proceeded gradually. The sedimentological and paleoceanographic studies suggest partial uplift and disruption of former current patterns by the late Miocene. ... Different microfossil groups that inhabit particular depths in the water column apparently showed a progressive pattern of isolation as the isthmus continued to emerge in the Pliocene ... Most evidence to date indicates 3.5 m.y.a. as the most likely time for isolation of the microfossil faunas, but total emergence of the entire isthmus probably did not occur until some time after 3.0 m.y.a., in the latest Pliocene or earliest Pleistocene.” Keller *et al.* (1989) also indicated a final uplift date for the CAI younger than the usually accepted 3.5–3.0 Ma, when they indicated four step-wise events in the faunal history of CAI closure, re-dated according to the timescale of Shackleton *et al.* (1996) at 6.8, 4.6, 2.5, and 1.9 Ma (Haug & Tiedeman, 1998: 674): “... initial closure of the Pacific-Caribbean gateway and cessation of sustained surface current flow between the Pacific and Caribbean occurred as late as [2.5] Ma. Maximum divergence of faunal provinces begins at [1.9] Ma and continues to the present. This implies that at least incipient littoral-neritic leakage occurred across the Pacific-Caribbean gateway between [2.5] and [1.9] Ma, with final closure at [1.9] Ma” (Keller *et al.*, 1989: 73). Finally, Coates & Obando (1996: 21) pointed out that although the Isthmus of Panama was “finally raised to a complete marine barrier about 3.1–2.8 Ma ... temporary breaching of this barrier may have occurred in the late Pliocene as a result of eustatic sea-level changes.”

The effects of and evidence for the uplift of the CAI have been described by (among many others) Keigwin (1978, 1982), Keller *et al.* (1989), Duqué-Caro (1990), L. S. Collins (1996), Collins *et al.* (1996), and Ibaraki (2002) based on Foraminifera; Marshall *et al.* (1982), Marshall (1985), Webb (1985), Campbell & Frailey (1996), Webb & Rancy (1996), and many others based on mammals; Kameo & Sato (2000) and Kameo (2002) based on calcareous nannofossils; Maier-Reimer & Mikolajewicz (1990), Mikolajewicz & Crowley

(1997), Haug & Tiedemann (1998), Chaisson & Ravelo (2000), Haug *et al.* (2001), Nof & Van Gorder (2002a, b), Gussone *et al.* (2004), and Schneider & Schmittner (2006) based on circulation through the CAI and effects of the closure on Atlantic circulation; and Fischer (1981), Vermeij & Petuch (1986), Coates *et al.* (1992), Vermeij (1993, 1997), Knowlton *et al.* (1993), Roopnarine (1996), Cronin & Dowsett (1996), L. S. Collins (1996), T. Collins (1996), Budd *et al.* (1996), Jackson *et al.* (1996), DeMaintenon (1998), Knowlton & Weigt (1998), Budd & Johnson (1999), Lessios *et al.* (1999), Anderson (2001), Marko (2002), Kirby & Jackson (2004), and O'Dea *et al.* (2007), a small selection of the huge literature on fossil and living macrofaunas and how these can be interpreted in terms of CAI closure. Among the many ideas that need reinterpretation if a late Pliocene or even earliest Pleistocene final closure of shallow-water transport through the CAI is accepted are Pleistocene faunal turnover of corals and mollusks in the western Atlantic (Allmon *et al.*, 1996; Allmon, 2001; Todd *et al.*, 2002), egg-size evolution in arcid bivalves on the two sides of the CAI at 2 Ma (Moran, 2004), and environmental change preceding Caribbean extinction by two million years (O'Dea *et al.*, 2007). These all were attributed to ecological changes in the western Atlantic, including productivity change (first suggested by Woodring, 1966: 430), because CAI closure was thought to be too early to explain them. It now seems more likely that the productivity change was caused by final closure of shallow-water connections by the final uplift of the CAI. Jackson *et al.* (2003) pointed out new evidence for an *increase* in Caribbean molluscan taxonomic diversity since Miocene time, rather than the Pliocene *decrease* in diversity that had been reported by previous workers “on the basis of inadequate data” (Jackson *et al.*, 2003: 1624). They also noted that “Upheaval of molluscan faunas did occur suddenly throughout tropical America at the end of the Pliocene as a result of more subtle, unknown causes” (Jackson *et al.*, 2003: 1624), and it now seems likely, again, that the “unknown cause” was the final closure of shallow-water connections, and consequent disruption of larval transport between the two oceans, by uplift of the CAI at about the Pliocene-Pleistocene boundary, *ca.* 2.0–1.8 Ma. Similarly, Landini *et al.* (2002) discussed the fish and molluscan fauna of the Late Pliocene Canoa Fm of Ecuador, assuming that this formation was deposited after the closure of the CAI. They particularly remarked on the 15 species of fishes in common with the boreal Pacific, but their pie graphs of faunal composition (Landini *et al.*, 2002: fig. 6) show that one species of benthic foraminiferan in the Canoa Fm is shared exclusively with the Atlantic and a further 18 species are shared with both the Californian Province and the Atlantic (Gulf of Mexico). Although the upwelling and circulation changes cited by Landini *et al.* (2002) might well have been factors altering

distributions as the CAI progressed toward final closure, their own evidence makes it just as likely that the CAI was still a seaway allowing dispersal of shallow-water species from the Gulf of Mexico to the eastern Pacific during Late Pliocene interglacial periods of high sea level. Another factor to bear in mind is that there is little evidence for coral reefs in the Caribbean until virtually the end of Pliocene time, when reef development became obvious in the Limón Basin in Atlantic Costa Rica (Aguilar & Alvarado, 1996; McNeill *et al.*, 2000; Johnson *et al.*, 2007) as well as in the Pleistocene forereef limestone of Swan Cay Fm in the Bocas del Toro Basin, Panama (Coates *et al.*, 2003: 272). It therefore appears likely that the cessation of shallow, near-surface current flow through the Central American seaway from the eastern Pacific into the Caribbean at approximately 2.0 Ma allowed the development of coral reefs. This was possibly another aspect of the resulting changes in productivity, or perhaps resulted from some other factor such as the extinction of predators of corals or their larvae. As pointed out by Johnson *et al.* (2007), the development of coral reefs in turn drove the increase in molluscan diversity in the Caribbean at the end of Pliocene time. Diaz (1995) also pointed out that environmentally homogeneous areas of the southern Caribbean at present have relatively low molluscan diversity, *e.g.*, the wide shelf off of the Orinoco River mouth, whereas environmentally heterogeneous, “patchy” areas and, in particular, the areas of upwelling induced by the trade winds along the northern coast of Colombia and Venezuela have the highest molluscan diversity at present. Presumably the “patchiness” invoked by Diaz includes coral reef development, and it is likely that both coral reefs and upwelling areas are diversity “hot spots” in the Caribbean. The trade winds will not have changed significantly through Neogene time (and presumably for much longer), so the development of coral reefs certainly seems likely to have been the main latest Pliocene change in the Caribbean that drove the coeval sharp increase in molluscan diversity. Shulman & Bermingham (1995: 908) pointed out an important apparent paradox to keep in mind when explaining the biogeography of widely dispersed marine animals, of which tonnoideans are among the best examples: the contrast between their high diversity within one area and the extensive gene flow between local populations. They followed Vermeij (1978) in suggesting that present-day sea levels, currents, and patterns of gene flow are not representative of the past marine environments in which much of today’s biodiversity developed. They therefore suggested that Plio-Pleistocene time might have been characterized by alternating periods of increased speciation during glacial periods of low sea level and decreased speciation during interglacial periods of high sea level. “Thus, speciation in the marine realm may ebb and flow with high and low sea level, respectively” (Shulman & Bermingham, 1995: 908). The

interplay of changing speciation rates with sea-level change, the development of Caribbean coral reefs from latest Pliocene time onward, and changes in current flows through the CAI as it gradually closed during Late Pliocene-Early Pleistocene time – with some surface larval exchange through the seaway still possible during interglacial periods until approximately 2 Ma, alternating with a dry land corridor during glacial periods of low sea level – seems to provide quite enough variation and complexity in drivers of biotic change to explain all of the patterns of diversity seen in tropical American molluscan biogeography.

Valuable independent evidence for the timing of marked uplift of the Atlantic coast of the CAI to near sea level was provided by L. S. Collins (1993) and Collins *et al.* (1996), who demonstrated no evidence of uplift of the Bocas del Toro and Limón basins throughout Pliocene time. The depositional facies represented by the lithologies and faunas of these basins indicate that uplift commenced only during Early Pleistocene time (*ca.* 1.6 Ma). Collins *et al.* (1996) pointed out that this coincides well with the geophysically determined dates of subduction of the Cocos Ridge under the CAI, because uplift of the Burica Peninsula in Pacific Panama commenced at *ca.* 3.6 Ma, but uplift did not commence in Atlantic Panama-Costa Rica until the Cocos Ridge had progressed under the CAI for 180 km at 9 cm/yr, reaching the Pacific coast at 1.6 Ma. A date for permanent drying of the CAI at 1.9 Ma was accepted by Keller *et al.* (1989; redated by Haug & Tiedemann, 1998) and Haug & Tiedemann (1998), and approximately 2.0–1.6 Ma seems a reasonable estimate of final closure based on both the evidence of transport of tonnoidean larvae through the CAI until *ca.* 2.0–1.8 Ma, and the geophysical evidence of uplift commencing at 1.6 Ma, reviewed by L. S. Collins (1993) and Collins *et al.* (1996). Questions of how South American mammals of North American origin, which are largely grassland herbivores, were exchanged through the tropical lowland forests of Central America are then answered by most exchange taking place during glacial lowstand periods, when part of Central America would have been grassed rather than forested. This question was considered by (among others) Colinvaux (1996), who concluded from extensive palynological evidence in Central and South America that much of Mexico to Yucatan and Honduras was savannah, but “most of the isthmus was elevated, with oak forest on mid-slopes” during glacial periods. “There was never a causeway of open savanna-land to connect the continents; rather, there was an ever-changing patchwork of plant communities that included tropical forest in the lowlands. This patchwork, constantly changing through succeeding glacial cycles, offered a filter bridge, possibly constraining the migrations of some animals more than others” (Colinvaux, 1996: 399).

This discussion leads to a cause-and-effect argument about

the initiation of the Pleistocene glaciations. The timing of CAI uplift steps – at 6.8, 4.6, 2.5, and 1.9 Ma (Keller *et al.*, 1989, as redated by Haug & Tiedemann, 1998) – now seems to coincide with the climatic shifts that they are supposed to have caused in (*e.g.*) Stanley's (1995) theory of causation of the Pleistocene glaciations by closure of the CAI. Of course, the position of the basal Pleistocene Global Standard Section and Point in the Vrica section, in southern Italy, at 1.81 Ma (Aguirre & Pasini, 1985) is contentious precisely because no particular event during Pliocene-Pleistocene history happened at this time (this "standard" boundary at 1.81 Ma is retained here, although a movement is under way to change it to 2.6 Ma). The boundary is located at just one of the many similar glacio-eustatic cycles through this period (in oxygen isotope stage 65) and no dramatic affect on world climates was caused by CAI closure, or anything else, at this level, despite the apparent (coincidental?) near-synchronicity between the boundary at Vrica and closure of the CAI. However, the whole argument becomes circular; did the lowering of sea level due to cooling climate cause the closure of the CAI, or did progressive, step-wise uplift of the CAI cause the Pliocene-Pleistocene climatic shifts? Is it a coincidence that they seem to have been coeval? Molnar (2008) published a similar conclusion, that initiation of glaciation was simply not related to uplift of the CAI, after the present manuscript was submitted. Preparation of the Earth for Pleistocene glaciation possibly began through a combination of constriction of the CAI with the Neogene thermal isolation of Antarctica through the development of the Antarctic Circumpolar Current (commencing at *ca.* 40 Ma, but Drake Passage possibly not open until 20 Ma; Lawver *et al.*, 1992; Drake Passage open early in Oligocene time, before 29 Ma; Livermore *et al.*, 2004). However, it seems likely that another cause must be sought for the initiation of major northern hemisphere glaciation at 2.7-2.5 Ma, a cause that probably acted in conjunction with constriction of flow through the CAI. A possible cause might well have been the reduction in volume of ocean water through Pliocene cooling shifts, and the consequent unloading of seafloor methane clathrates and release of large amounts of methane into the atmosphere (Kennett *et al.*, 2000, 2003). However, an alternative model that fits carbon isotope values better is the control of rapid glacial-interglacial temperature shifts by emissions of methane from either tropical or, more probably, northern high-latitude wetlands (Broecker, 2003; Hughen *et al.*, 2004; MacDonald *et al.*, 2006; Schaefer *et al.*, 2006; Sowers, 2006).

Paleoceanographers have relied upon the concept of the "ocean conveyor belt" driving world ocean currents, and changes in it such as reduction in the flow of the Gulf Stream leading to the onset of glaciations (*e.g.*, Broecker & Denton, 1989). This suggests the possibility that, rather than the

waxing and waning of the "Arctic Pond" as a driver of the Gulf Stream (Stanley, 1995), a major contribution of the closure of the CAI to paleoceanography and biogeography might have been strengthening of flow of the Gulf Stream in the northern Atlantic as a result of cessation of flow through the CAI. If any of the Gulf Stream formerly flowed through the CAI into the Pacific (although this was probably minor; Schneider & Schmittner, 2006), it would have had to flow northward in the Atlantic after closure of the CAI, presumably after a critical sill depth was reached at *ca.* 2.6 Ma, when significant northern hemisphere glaciation commenced. Wunsch (2002) argued that the sole driver of ocean currents is the wind field at the sea surface. Uplift of the CAI presumably was coeval with mountain uplift in Central America, so it is conceivable that mountain uplift would have altered the wind field at the sea surface significantly and so further changed surface currents on each side of the Americas. This remains a field for further research.

Nof & Van Gorder (2002a, b) argued that flow through the CAI was from east (Atlantic) to west (Pacific) before closure of the CAI. However, improved modeling of different sill depths and nutrient diffusivities allowed Schneider & Schmittner (2006) to conclude the opposite: water mainly flowed from the Pacific into the Atlantic before closure of the CAI. The corresponding constriction of throughflow due to shallowing of the CAI sill led to intensification of northern Atlantic circulation. More importantly, the loss of inflow of nutrient-rich Pacific water led to a reduction in productivity in the Atlantic and the corresponding nutrient accumulation in the eastern Pacific led to increased productivity there. Combined with the timing of CAI shallowing and closure suggested by me (Beu, 2001, and herein) from the evidence of tonnoidean gastropods, these conclusions produce a satisfying explanation of tropical American faunal history, as was also concluded by Landau *et al.* (2008). The greater number of paciphile than atlantiphile genera in the region is a strong indication that molluscan genera with planktotrophic larvae predominantly were carried from the Pacific into the Atlantic, rather than in the opposite direction. Increasing constriction of the CAI at *ca.* 6.8, 4.6, 2.5, and 1.9 Ma (Keller *et al.*, 1989; Haug & Tiedeman, 1998) decreased the numbers of larvae transported through the CAI into the Atlantic, particularly after 2.5 Ma, and the final closure of shallow surface throughflow at approximately 2.0-1.6 Ma extinguished the last paciphiles (a few taxa lingering in the Atlantic until *ca.* 1.5 Ma; Landau *et al.*, 2008) and caused the dramatic decrease in Atlantic productivity that led to marked molluscan extinction in the Atlantic after *ca.* 2 Ma.

TYPE MATERIAL OF EARLY-NAMED SPECIES

I began a list of collections and locations where type material

can be examined of early-named species of Tonnoidea (Beu, 1998b: 15), based largely on Dance (1966: appendix 4). Other useful catalogs of collection locations include those of Sherborn (1940) and, in particular, Cleevely (1983). Types of many of the species named by Linnaeus (1758, 1767, 1771) are present in either the Linnean Society of London's rooms in Burlington House, London (Dance, 1967) or Uppsala University Zoological Museum (now Museum of Evolution, Uppsala University; Wallin, 1993). However, the specimens cited by Linnaeus from illustrations in pre-Linnean iconographies have the same status as Linnaeus' own specimens as syntypes of Linnean species, and so if any remain today, their location is important to resolve. I concluded (Beu, 1998b: 16) that none of the specimens in Uppsala University Zoological Museum listed as possible syntypes of Linnaeus' species that I had been able to examine at that time is correctly identified; none bears an early label identifying it as a syntype and I considered that none of them actually is a syntype. However, Mats Eriksson (Uuzm) has recently pointed out to Gijs Kronenberg (Eindhoven, pers. comm., 12 February 2007) that these specimens might well all have been seen by Linnaeus, and so are potential syntypes (see discussion under the lectotype designation for *Cassis flammea*, below). Dance (1966: 291) reported that the collection of Link (1807) was in the Rostock Museum, but Kohn (1981: 301) stated that the collection, now in the Wilhelm-Pieck-Universität Rostock, is unlikely to contain any specimens that can be identified as Link types. Dance (1966: 297) reported also that some specimens illustrated by Perry (1811) are in BMNH, but unfortunately this is not so for any of Perry's tonnoideans. Dance (1966: 301) further reported that Schumacher's (1817) collection is in ZMC, but none of Schumacher's material of tonnoideans was present when I examined the collection in 1979. Most of the type material of species named by Lamarck (1816, 1822) is present in MHNG, along with the tonnoidean specimens illustrated by Kiener (1835a-c, 1841, 1842). It should be noted that almost all of Kiener's figured specimens of Cassidae, Bursidae, Personidae, and Ranellidae were chosen from Lamarck's type material (I have not checked the Tonnidae, but this seems likely to apply to the figured specimens in all Kiener's monographs). The type material of Japanese species described by Lischke (1868-1873) is in Löbbecke Museum und Aquazoo, Düsseldorf (Cosel, 1998). The location of the type material of the major iconographies of the 19th century has long been well-known, and is cited in the text below where relevant; most is in either BMNH (Reeve's, the Sowerbys', Gray's, some of Wood's, etc.) or MNHN (a few of Lamarck's, some of Valenciennes's, most of Quoy & Gaimard's, etc., and of all French authors up to Jousseaume and later).

Considerable further information on early types has since

come to light. The sole remaining almost intact pre-Linnean collection is that of Gualtieri (1742), which is owned by the Department of Zoology, University of Pisa, and can be examined at the Museo di Storia Naturale e del Territorio, in the Certosa di Calci, a beautiful old monastery in Calci, 20 km northeast of Pisa (curator Marco Zuffi). Gualtieri's collection is particularly important for its large number of potential Linnean types, because Linnaeus (1758, 1767) cited many of Gualtieri's (1742) figures as illustrations of his species. Of course, Adanson's (1757) collection also has long been well-known in MNHN, and was described by Fischer-Piette (1942). Stewart (1930: 35) pointed out that F. C. Schmidt purchased the Bolten collection (described by Röding, 1798) and at Schmidt's death, the collection was acquired by the Art and Natural History Museum of Gotha. A very small number of Bolten's shells has been recognized in the Museums der Natur de Gotha, Germany (Joost, 1990). Lamarck's and a few other early collections in MHNG have been described by Caillez (1995). The few specimens remaining from Bruguière's collection are also almost all in Geneva, apparently having been acquired by Lamarck, despite the fact that the French Government purchased Bruguière's collection in 1799 for the enormous sum of FF6,000 (Lamy, 1930); almost no specimens of Bruguière's can now be identified in MNHN (Virginie Héros, pers. comm., 2007). The location of the material from Cayenne, Guiana, described in the one-page paper by Bruguière (1792b) also is unknown, suggesting that it remained the property of the Société d'Histoire Naturelle de Paris and is long lost. A few type specimens from Lesson's descriptions have been recognized in MNHN, along with a few types from many other early collections, but unfortunately the holotype of *Tritocurris amphitridis* (= *Cymatium tigrinum*) has not been recognized. Deshayes' enormous collection is now at Centre des Sciences de la Terre, Université Claude Bernard Lyon-1, in Lyon, whereas that of Cossmann is in the Département de Paléontologie, MNHN, along with many other types of workers on French fossils. Most types of species described from the Aquitaine Basin, France, such as those of Grateloup, are stored in Université de Bordeaux-1, in Talence, outside Bordeaux, along with some of the types of Cossmann & Peyrot, among others [collections of Neuville, Duvergier (in part), Peyrot (in part), Magne, Vergneau-Saubade, and Reyt]. Several other collections containing the types of Cossmann & Peyrot are in the Muséum d'Histoire Naturelle de Bordeaux [Benoist, Degrange-Touzin, Duvergier (in part), and Peyrot (in part)], but many remained in private collections, some of which are now in MNHN (e.g., the Sylvestre de Sacy collection, the types of which are now in Malacologie; Marcomini, 1994), but many of which are now lost. A small part of Menke's collection was present in Bronn's collection of Recent shells, and is now in the Senckenberg Museum, Frankfurt

(Bronn's fossils were acquired by Agassiz, and are now in the Department of Geology, Museum of Comparative Zoology, Harvard University). Some (most?) of Chemnitz's apparently long-lost collection is now known to have been purchased for Peter the Great, and is in the Zoological Institute, Academy of Sciences of Russia, in St. Petersburg (Martynov, 2003), although a small number of specimens illustrated by Martini & Chemnitz belonged to Danish collectors such as Moltke and Spengler, and is in ZMC. Anton's collection has now been recognized in Staatlichen Museums für Tierkunde Dresden and is being recorded by Schniebs (1997, 2000). The late Harald Rehder (USNM) suggested to me that J. H. Redfield's collection [among tonnoideans, containing the type material of *Fusitriton oregonensis* and *Bufonaria thesites* (Redfield, 1846)] might be in the State Museum of New York, in Albany, but Johnson (2006) reported that it was willed to ANSP – where, however, these types have not been recognized, presumably because they belonged in other private collections. The fossils collected by Gay and described by Hupé (1854) from the Miocene and Pliocene of Chile are stored in the Département de l'Histoire de la Terre, MNHN, along with several other South American fossil collections, whereas d'Orbigny's South American fossils are stored in Salle d'Orbigny, Département de Paléontologie, MNHN (Griffin & Nielsen, 2008). The type material in Dunker's collection is in SMF and was listed by Jannsen (1993), although the types of Dunker's *Bursa* species were from Cuming's collection and are in BMNH. Type material of Maury (1917a) from the Dominican Republic is all available at PRI, whereas much earlier Dominican Republic material (Gabb and Pilsbry & co-authors) is in ANSP, and that of Sowerby is in the BMNH Palaeontology Department. Perhaps the most important collection from the "heroic days" of European malacology and paleontology that has not been available to modern science is that of R. A. Philippi. It is now known that his collection is stored in the Zoology Department, Museo Nacional de Historia Natural, Santiago, Chile (G. Pastorino, Buenos Aires, pers. comm., 2006).

SYSTEMATIC PALEONTOLOGY

ABBREVIATIONS USED IN THE TEXT

AMNH, American Museum of Natural History, New York; AMS, Australian Museum, Sydney; ANSP, Academy of Natural Sciences, Philadelphia (Recent Mollusca not prefixed; fossils prefixed "IP"); BMNH, The Natural History Museum, London; CAS, California Academy of Sciences, San Francisco, Invertebrate Paleontology collection; CASIZ, California Academy of Sciences, San Francisco, Invertebrate Zoology collection; FAU, Florida Atlantic University, Boca Raton, Florida; GNS, GNS Science, Lower Hutt, New Zealand (non-New Zealand mollusks prefixed "WM," Recent

New Zealand mollusks prefixed "RM"); IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels; LACM, Natural History Museum of Los Angeles Co, Los Angeles, California (Allan Hancock Foundation collections bear suffix "-AHF"); LACMIP, Invertebrate Paleontology Department collections at LACM; MACN, Museo Argentino de Ciencias Naturales "Bernadino Rivadavia," Buenos Aires, Argentina; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MLP, Museo de La Plata, La Plata, Argentina; MHNG, Muséum d'Histoire Naturelle de Genève, Geneva, Switzerland; MNHN, Muséum National d'Histoire Naturelle, Paris; MNRJ, Museu Nacional de Historia Natural de Brasil, Rio de Janeiro; NHMV, Naturhistorisches Museum Wien, Vienna, Austria; NMB, Naturhistorisches Museum Basel, Switzerland; NMP, Natal Museum, Pietermaritzburg, South Africa; NMW, National Museum of Wales, Cardiff; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington; RGM, fossil collections of the Netherlands Nationaal Museum van Natuurlijke Historie, Leiden (formerly Rijksmuseum van Geologie en Mineralogie); RMNH, Recent mollusk collection of Netherlands Nationaal Museum van Natuurlijke Historie, Leiden (formerly Rijksmuseum van Natuurlijke Historie); SDNHM, San Diego Natural History Museum, San Diego, California; SGO.PI, Museo Nacional de Historia Natural, Santiago, Chile (fossil collections in section Paleontología Invertebrados); SMF, Senckenberg Museum, Frankfurt (am Main), Germany; TFMCI, Museo de Ciencias Naturales, Santa Cruz de Tenerife, Canary Islands; TU, Tulane University, New Orleans (most material now in USNM; Dominican Republic material now in PRI; Florida material in UF); UCMP, University of California Museum of Paleontology, Berkeley; UF, Florida Museum of Natural History, University of Florida, Gainesville; USGS, United States Geological Survey, Washington, DC; USNM, National Museum of Natural History [formerly United States National Museum], Washington, DC; UUZM, Museum of Evolution, Uppsala University, Uppsala, Sweden; ZMA, Zoological Institute, University of Amsterdam, The Netherlands; ZMC, Zoological Museum, University of Copenhagen, Denmark.

Dimensions consistently are in mm, and are cited in the order H (height) and D (width, or maximum diameter). Other standard abbreviations are: Co = County, Fm = Formation, frag = fragment(s), and the usual N, S, E, W for north, south, east, west, and combinations of these. Unless stated otherwise, all type specimens listed under "Type material" have been examined by me.

LOCALITY DATA

All available locality details are provided for fossil specimens in this work. Many localities, principally in the Dominican Republic and Panama, for specimens in NMB, TU, and

USNM are cited in the text by their locality numbers only, and fuller details, in particular locating them on maps and sections, will be found in the publications by Saunders *et al.* (1986) and Collins & Coates (1999), as well as in the list here in Appendix 3. I have included locality details of Recent lots of some of the less common species of Bursidae, Personidae, and Ranellidae; localities for Recent material are not listed for Cassidae and Tonnidae, other than completely new records (*Cassis norae*, *Echinophoria hadra*). For Recent records of common species of Bursidae, Personidae, and Ranellidae, a full list of all the material examined is too long to cite in full. I have merely summarized the geographical ranges of these species.

SYSTEMATICS

Phylum **MOLLUSCA** Cuvier, 1795

Class **GASTROPODA** Cuvier, 1795

Superfamily **TONNOIDEA** Suter, 1913 (1825)
(following Bouchet *et al.*, 2005: 11, 253)

Remarks.—The standard classification of the superfamily Tonnoidea until recently has been that proposed by Thiele (1929). This classification recently has been modified and expanded by Warén & Bouchet (1990) and, in particular, by Riedel (1994, 1995, 2000). Following Riedel (1994), the Ficidae is removed to its own superfamily, Ficoidea, which contains also the family Thalassocynidae Riedel, 1994 (containing the single genus *Thalassocyron* Barnard, 1960; but note that Bouchet *et al.* (2005: 250) synonymized Thalassocynidae with Ficidae). Ficidae of the Dominican Republic are included in Appendix 1, but the many other Neogene *Ficus* species in tropical America are not covered in this report. The classification proposed by Riedel (1995, 2000) was rearranged by me (Beu, 2008), based on the conclusion on anterior gut glands by Andrews *et al.* (1999: 13) that “*Tonna* is further removed from the cassids than Riedel’s (1995) classification implies” [although Bouchet *et al.* (2005: 253), apparently unaware of Andrews *et al.*’s (1999) conclusion, followed Riedel in including Cassidae within the Tonnidae]. The family group taxa recognised here in Tonnoidea are:

1. Family Bursidae Thiele, 1925
2. Family Laubierinidae Warén & Bouchet, 1990 (= Pisanianurinae Warén & Bouchet, 1990; Beu & Bouchet, in prep.)
3. Family Personidae Gray, 1854
4. Family Ranellidae Gray, 1854
 - a. Subfamily Ranellinae Gray, 1854
 - b. Subfamily Cymatiinae Iredale, 1913 (1854)
5. Family Cassidae Latreille, 1825
 - a. Subfamily Cassinae Latreille, 1825
 - b. Subfamily Oocorythinae Fischer, 1885
 - c. Subfamily Phaliinae Beu, 1981

6. Family Tonnidae Suter, 1913 (1825)

Family Laubierinidae occurs only in the deep sea, has not been recorded fossil so far within the study area, and is not considered further. However, the recognition of some fossil species of *Pisanianura* within the study area eventually seems likely.

Family **BURSIDAE** Thiele, 1925

Remarks.—Riedel (1995) treated Bursidae as subfamily Bursinae of Ranellidae, but I argued (Beu, 1998a-b) that this expressed a closer relationship than the evidence allows, and retained Bursidae as a separate family. Warén & Bouchet (1990: 94) and Bouchet *et al.* (2005: 253) also supported family status for the Bursidae. The origins of Bursidae are mysterious at present, as there are few Eocene or older records assignable to this family, *e.g.*, there are none in the classic Eocene faunas of the Paris Basin, Indonesia, or the U.S. Gulf Coast. *Bursa*(?) *saundersi* Adegoke (1977: 209, pl. 31, figs 27-28) is the only possible Paleocene member of the family, but its position is uncertain because it lacks a posterior siphonal canal. Eocene species of *Marsupina* from Peru (Olsson, 1930) and the genus *Olequahia* Stewart, 1926 (Beu, 1988: 74, pl. 1, figs 1-9) in the western U.S.A. are the only convincing Eocene members. Bursidae continues to be maintained as a distinct family here.

Genus **BURSA** Röding, 1798

- Bursa* Röding, 1798: 128. Type species (by subsequent designation, Jousseaume, 1881: 174): *Bursa monitata* Röding, 1798 (= *Murex bufonius* Gmelin, 1791, by first reviser’s action of Winckworth, 1945: 137), Recent, Indo-West Pacific.
- Lampadopsis* Jousseaume, 1881: 175. Type species (by original designation): *Ranella rhodostoma* G. B. Sowerby II, 1835, Miocene to Recent, Indo-West Pacific and eastern and western Atlantic [*Lampadopsis* Jousseaume, 1881, justifiably emended to the genitive form by Fischer (1884b: 656)].
- Colubrellina* Fischer, 1884b: 656. Type species (by monotypy): *Ranella candisata* Lamarck, 1822 (= *Murex conditus* Gmelin, 1791), Recent, western Pacific.
- Talisman* de Folin, 1884: 212. Type species (by monotypy): *Talisman parfaiti* de Folin, 1884 (= larval shell of *Bursa scrobilator* (Linnaeus, 1758), *B. corrugata* (Perry, 1811) or *Aspa marginata* (Gmelin, 1791); Warén & Bouchet, 1990: 94).
- Pseudobursa* Rovereto, 1899: 6. Unnecessary replacement name for *Bursa* Röding, 1798.
- Bufonariella* Thiele, 1929: 284. Type species (by monotypy): *Murex scrobilator* Linnaeus, 1758, Pliocene to Recent, Mediterranean and eastern Atlantic; Pliocene and Pleistocene, Atlantic tropical America.
- Dulcerana* Iredale, 1931: 213 (unavailable; no differentiation from related taxa).

Annaperenna Iredale, 1936: 310. Type species (by original designation, Iredale, 1936: 337): *Ranella verrucosa* G. B. Sowerby I, 1825, Recent, southwestern Pacific.

Dulcerana Oyama, 1964: 332. Type species (by original designation): *Tritonium granulare* Röding, 1798, Pleistocene and Recent, Indo-West Pacific, eastern and western Atlantic, and eastern Pacific (Clipperton Island).

Tritonoranella Oyama, 1964: 332. Type species (by original designation): *Triton ranelloides* Reeve, 1844, Pliocene to Recent, eastern and western Atlantic, South Africa, Indian Ocean, Hawaii, and Japan-Taiwan.

Remarks.—I reconsidered (Beu, 1998b) the criteria previously used to subdivide the genus *Bursa* into subgenera, and concluded that, rather than hard-and-fast, “landmark” characters that could be used to subdivide it objectively, all characters that have been used by previous authors, including me (Beu, 1981), are matters of degree and form part of a broad character suite, which there is no means of subdividing without resorting to subjective assessments that will always leave some species in an unclear position. The single genus *Bursa* therefore was used for all Bursidae with an operculum that has an anterior terminal nucleus, with rather evenly inflated (as opposed to dorsoventrally compressed) shells, and with varices either aligned on opposing sides of the spire (at each 180°) or at each two-thirds of a whorl (at each 240° around the spiral). This usage is continued here.

The species with varices at each 240° and a red parietal area [*Bursa ranelloides* (Reeve, 1844) and the *B. latitudo* Garrard, 1961 species group, including *B. natalensis*; both discussed below] seem to be closely related phylogenetically, and might well constitute a distinct clade (for which genus or subgenus *Tritonoranella* Oyama, 1964, is available), but only a molecular study will resolve their phylogeny, and the *status quo* is retained until this is available. Also, the uncommon Indo-West Pacific species *Bursa fosteri* Beu, 1987, is similar to *B. latitudo* in most characters, but is smaller and has a more standard *Bursa* protoconch (shorter than in *B. latitudo*) and more nearly resembles other, more typical species of *Bursa*. Also, comments in the descriptions (below) on the variceal positions of several other *Bursa* species show that several species (e.g., *B. scrobilator*) have their varices a little offset down most of the teleoconch, and in several others (e.g., *B. granularis*, *B. chipolana*) the varices gradually change from strictly aligned on early spire whorls to more widely offset over the last few whorls. This indicates that variceal position intergrades in *Bursa*, and is not a useful character distinguishing clades.

Few radulae of Bursidae have been illustrated to date, but those that have (Beu, 1981; Ekawa & Toki, 2005) show subtle but consistent differences in tooth shape and the prominence of the interlocking basal hooks between the genera recognized here. Further study of radulae undoubtedly would help un-

derstanding of the classification of the family.

***Bursa amphitrites* Maury, 1917**

Pl. 1, Figs 1-4, 8

Bursa amphitrites Maury, 1917a: 273, pl. 17, fig. 9; Pilsbry, 1922: 360.

Not *Bursa* (*Colubrellina*) *caelata amphitrites*. Woodring, 1959: 207, pl. 28, figs 1-2, 7-8; Jung, 1965: 513, pl. 68, figs 12-13; pl. 69, fig. 2; Perrilliat, 1972: 76, pl. 37, figs 12-15 [= *Bursa rugosa* (G. B. Sowerby II, 1835)].

Not *Bursa amphitrites*. E. Vokes, 1973: 100 [in part = *Marsupina bufo* (Bruguière, 1792)].

Not *Bursa* (*Colubrellina*) *caelata amphitrites*. Aguilar, appendix in Seyfried *et al.*, 1985: 64 (?= *Marsupina judensis* n. sp.; not illustrated).

Not *Bursa amphitrites*. Petuch, 1992: 108, fig. 3G [= *Bursa rugosa* (G. B. Sowerby II, 1835)].

Not *Bursa* (*Lampasopsis*) (*sic*) *amphitrites*. Petuch, 1994: 120, pl. 39, figs L-M; Petuch, 1997: 224, fig. 83J [= *Bursa rugosa* (G. B. Sowerby II, 1835)].

Remarks.—The Dominican Republic Miocene and Pliocene collections, including Maury's type material of *Bursa amphitrites*, and extensive collections now available from throughout the tropical American region show that *B. amphitrites* is a relatively large, coarsely sculptured species that is less dorsoventrally compressed than most other tropical American *Bursa* species, and so is most similar to *B. chipolana* Schmelz (1997: 105, pl. 1) of other named species. Specimens are referred here to *B. amphitrites* only from the Dominican Republic and from the Buenevara Adentro beds (Gibson-Smith & Gibson-Smith, 1979; early Middle Miocene) of the Paraguaná Peninsula, Venezuela. The holotype (Pl. 1, Figs 2, 8) has numerous small, rounded nodules around the shoulder angle, a moderately coarse row of nodules around the second primary spiral cord, and a row of coarse, even granules in the center of each spiral interspace; specimens resembling the holotype or that are even more finely sculptured occur in both the Dominican Republic and Buenevara Adentro collections. However, the majority of specimens is more coarsely sculptured than the holotype, with relatively few, large, rounded nodules around the shoulder angle and smaller granules in the spiral interspaces. The spire height also is quite variable, ranging from significantly shorter than the holotype (Pl. 1, Fig. 1) to significantly taller (Pl. 1, Fig. 4). The species therefore differs from *B. chipolana* in its slightly to markedly more numerous shoulder nodules, its less strongly twisted anterior canal, producing a fasciole that is less obviously curved out to the left than in *B. chipolana*, in having lower varices that are less obviously buttressed by the spiral cords, and in therefore having an overall less extreme, slightly to markedly more weakly sculptured appearance.

The most common fossil *Bursa* species in the Caribbean area and Panama has consistently been identified as *B. amphitrites* or, perhaps more frequently, as *B. caelata amphitrites* [e.g., Woodring (1959: 207, pl. 28, figs 1-2, 7-8), Gatun Fm, Panama; Jung (1965: 513, pl. 68, figs 12-13; pl. 69, fig. 2), Cantaure Fm, Paraguaná Peninsula, Venezuela]. These authors included in the synonymy of *B. caelata amphitrites* Rutsch's (1934: 58, text-fig. 7, pl. 3, figs 3-4) name *B. (Marsupina) albofasciata boussingaulti*, from the Pliocene Punta Gavilán Fm in Venezuela. However, it is concluded here that (a) Rutsch's species is actually *B. rugosa* (G. B. Sowerby II, 1835), and he was correct to distinguish it from both *B. corrugata* (Perry, 1811) (= *B. caelata* Broderip, 1833) and *B. amphitrites*, and (b) the common *Bursa* species at most Panama and Caribbean Miocene and Pliocene localities is not *B. amphitrites*, but is *B. rugosa*. The type locality of *B. rugosa* is supposedly Manila, Philippine Islands, but it is actually the abundant living *Bursa* species in the eastern Pacific, despite only having been recorded from there previously by me (Beu, 2001). Keen (1971) seems to have confused *B. rugosa* with *B. calcipicta* Dall, 1908, a deep-water form concluded below to have been based on immature specimens of *Crossata ventricosa* (Broderip, 1833) (see Pl. 8, Figs 3-4). However, Olsson (1924: 124), when recording modern specimens from Peru and Ecuador, reached the correct conclusion when he noted that "my specimens ... appear to be closest to the *B. rugosa* Sowerby from Manila, according to Sowerby's figure."

The dorsoventrally compressed, more strongly nodulose species *Bursa pelouatensis* (Cossmann & Peyrot, 1924), illustrated by Schmelz (1997: pl. 1, figs 2a-c), seems unlikely to be related to either *B. amphitrites* or *B. chipolana*, in any close phylogenetic sense. On the other hand, *B. amphitrites* is similar to such living western Atlantic species (described below) as *B. natalensis* Matthews & Coelho, 1970, *B. ranelloides* (Reeve, 1844), and the very widespread *B. granularis* (Röding, 1798). A single, slightly incomplete, weakly sculptured, unusually tall-spined Dominican Republic specimen (Pl. 1, Fig. 4), referred with some hesitation to *B. amphitrites*, is almost as tall and finely sculptured as modern specimens of *B. natalensis*, indicating a possible close phylogenetic relationship between these species. As a whole, *B. amphitrites* bears a close resemblance to the taller, narrower, and usually more finely sculptured living species *B. granularis*. Because *B. granularis* is known as fossil only from Pleistocene rocks, a phylogenetic relationship between these species also is feasible.

Dimensions.—Holotype: H 46.4, D 29.3 mm; TU 1231, Dominican Republic: H 38.1, D 26.7 mm; TU 1293, Dominican Republic: H 53.8, D 32.1 mm; TU 1278, Dominican Republic, tall specimen resembling *Bursa natalensis*: H 60.9, D 33.0 mm.

Types.—*Bursa amphitrites*, holotype PRI 28763, from Bluff

3, Cercado de Mao, Dominican Republic; Cercado Fm, Late Miocene. Maury (1917a: 110) recorded material also from "Río Amina, between Hato Viejo and Potrero," but this was not identifiable in the PRI collection when I examined it.

Other material examined.—**Fossils: Dominican Republic: Late Miocene:** Gurabo Fm: NMB 16910 (1); Bluff 1 of Maury, Río Mao, collected M. Taviani (Institute of Zoology, University of Bologna, 2; one with more widely flared aperture than usual). **Late Miocene/Early Pliocene:** Gurabo Fm: TU 1231 (GNS WM16925, 1, short); 1292 (GNS WM18852, 1 frag); 1293 (GNS WM16933, 1; GNS WM18850, 1); USGS 8519 (2); 8528 (1). **Early Pliocene:** Gurabo Fm: Maury's loc. 200, "zone D," Río Gurabo (PRI, 1); TU 1219 (GNS WM18851, 2 frag); 1227 (GNS WM16919, 2); 1278 (GNS WM18849, 1, tall-spined, resembling *Bursa natalensis*); 1215, Gurabo Fm, Río Gurabo, collection of Bernard Landau (1); 1219, Río Amina, collection of Bernard Landau (1); 1354, Gurabo Fm, Cañada de Zamba, collection of Bernard Landau (1). **Venezuela: Early Middle Miocene:** NMB 17527, Buenevara Adentro beds (12).

Distribution.—*Bursa amphitrites* is recorded here only from the Late Miocene to Early Pliocene Gurabo Fm of the Dominican Republic and the early Middle Miocene Buenevara Adentro beds of the Paraguaná Peninsula, Venezuela.

Bursa asperrima Dunker, 1862

Pl. 1, Fig. 9

Bursa asperrima Dunker, 1862: 238; 1863: 57, pl. 19, figs 5-6; Yen, 1942: 217, pl. 19, fig. 114; Emerson, 1991: 68; 1994: 69; Finet, 1994: 41; Beu, 1998b: 146, fig. 43f; Kaiser, 2007: 39, pl. 26, figs 5a-b.

Ranella cruentata. Stearns, 1893: 347 (not *Ranella cruentata* G. B. Sowerby II, 1835).

Bursa cruentata. Hertlein & Allison, 1960: 15; Cernohorsky, 1970: 180 (in part); Salvat & Rives, 1975: 307, fig. 180; Okutani, 1986: 116-117, middle fig. second column; Okutani, 2000: 269, pl. 133, fig. 5 (not *Ranella cruentata* G. B. Sowerby II, 1835).

Lampadopsis cruentata. Oyama & Takemura, 1963: *Lampadopsis Tutufa* pl. 1, fig. 5 (not *Ranella cruentata* G. B. Sowerby II, 1835).

Bursa (Bursa) asperrima. Beu, 1985: 63; Cossignani, 1994: 43; Kaiser, 1997: 32.

Remarks.—I pointed out (Beu, 1998b: 146, fig. 43f) the few, slight, distinguishing characters of *Bursa asperrima* and noted that the most telling evidence for its status as a species separate from the common, widespread, Indo-West Pacific *B. cruentata* is their only partly sympatric ranges. *Bursa asperrima* occurs commonly at Clipperton Island, eastern Pacific, where *B. cruentata* has not been collected. *Bursa asperrima* also is the species present at most of the island groups of eastern

French Polynesia (*e.g.*, common in MNHN material from the Tuamotu Islands), whereas it is replaced by *B. cruentata* in the Marquesas Islands (Beu, in prep.). Emerson (1991) gave detailed locality data for the eastern Pacific records, adding records of two specimens from the Galápagos Islands. The shells of the two species differ mainly in *B. asperrima* lacking the dark red-brown to almost black bars on the parietal area of the inner apertural lip of *B. cruentata*. Other slight differences that seem to be constant are the wider shell of *B. asperrima* than of *B. cruentata*, especially at the periphery, and the more protruding outer-lip digitations in *B. asperrima* than in *B. cruentata*.

Dimensions.—Lectotype of *Bursa asperrima*: H 38.6, D 29.7 mm; WM12441, GNS, off of Nanakuli, Oahu, Hawaii: H 44.6, D 33.3 mm; NMP K.2826, Pitcairn Island: H 48.5, D 40.8 mm; GNS WM18460, Clipperton Island: H 34.1, D 25.3 mm; H 30.6, D 24.1 mm.

Types.—Lectotype of *Bursa asperrima*, Dunker's (1863: pl. 19, figs 5-6) figured syntype, BMNH 1968566/1, from the Cuming collection, designated by Yen (1942: 217); two paralectotypes, BMNH 1968566/2-3. The type locality was stated to be "China," but this seems likely to be one of Hugh Cuming's many "misremembered" localities, as there are no subsequent records from China; the most likely source for Cuming's specimens is Hawaii, although they could also have come from anywhere in eastern Polynesia. The type locality is here designated as Hawaii.

It should be noted that Hugh Cuming was famous for "remembering" in suspicious detail all the otherwise unrecorded localities for his 83,000 specimens, and history has shown that he was more usually wrong than right. Hedley (1913: 165) complained that Cuming was an "illiterate sailor," who convinced the well-known 19th century iconographers to describe his new species through sheer force of character, although Dance (1966: 164) refuted the charge of illiteracy. I discussed (Beu, 2006: 171-172) Cuming's localities, concluding that all are suspect unless verified by more recently collected material. The question is raised again several times through this monograph, because of such species as *Monoplex amictus* (Reeve, 1844) and *Bursa rugosa* G. B. Sowerby II, 1835, both said by Reeve and Sowerby (following Cuming) to be from the Philippines, but actually occurring only in the eastern Pacific.

Other material examined.—**Recent: Clipperton Island:** beach (B-4237, UCMP, 8); 10 m (B-6111, UCMP, 1); 40 m (B-6120, UCMP, 1); [no further data] (B-6551, UCMP, 1); [no further data] (B-6553, UCMP, 1); 5 May 1959 (LACM, C.19, 1); scuba, 15 m, under coral on coral reef terrace (GNS WM18460, 3).

Distribution.—I am not aware of any fossil record. *Bursa asperrima* occurs throughout the eastern and western Pacific

Ocean, but I am not aware of records from the Indian Ocean or from the Atlantic. It is common by itself (*i.e.*, without *B. cruentata*) at Clipperton Island, eastern Pacific (Hertlein & Allison, 1960; Kaiser, 2007: 39, pl. 26, figs 5a-b, recording material and several earlier misidentifications), and in eastern French Polynesia (Beu, in prep.), but is replaced by *B. cruentata* in the Marquesas Islands, and seems to be as common as *B. cruentata* in Hawaii, but is exceedingly rare further west in the western Pacific. Stearns (1893: 347) recorded *Ranella cruentata* Sowerby (*i.e.*, *Bursa asperrima*) from the American coast in the eastern Pacific: near Cape San Lucas, Baja California Sur, in 56 m, 22°52'N, 109°55'E (USNM 125665), and at Utila Island, Honduras. Emerson (1991: table 1) also recorded specimens from the Galápagos Islands (two specimens in CAS, from Jarvis and James islands). A single specimen from Pitcairn Island is present in NMP (K2826). The only records from west of Hawaii that I am aware of are the specimens illustrated by Oyama & Takemura (1963: *Lampadopsis-Tutufa* pl. 1, fig. 3), from Hachijo Island, southern Japan, and by Okutani (1986: 117; 2000: pl. 133, fig. 5), presumably also from southern Japan. An occurrence at Niue Island seems to be indicated by Cernohorsky's (1970: 180) record of specimens with and without "distinct black columellar bars." Salvat & Rives (1975: 307, fig. 180) illustrated specimens from Makemo Island, Tuamotu Islands, where it is moderately common. *Bursa asperrima* seems to be basically a far-eastern western Pacific species [like *Monoplex intermedius* (Pease, 1869), *Septa peasei* Beu, 1987, *Bursina nobilis* (Reeve, 1844) and *Distorsio graceiellae* Parth, 1989; Beu, in prep.], in the case of *B. asperrima* extending rarely to the eastern Pacific mainland. It occasionally extends its range to the west as planktotrophic larvae, but apparently is essentially out-competed by the closely similar *B. cruentata* to the west of its normal range.

Bursa chipolana Schmelz, 1997

Pl. 1, Figs 5-7, 10

Bursa (*Bufonariella*) *pelouatensis*. Vokes, 1973: 97, text-fig. 2 (not *Ranella pelouatensis* Cossmann & Peyrot, 1924).

Bursa (*Bufonariella*) *chipolana* Schmelz, 1997: 105, pl. 1, figs 1a-c; pl. 2, figs 1a-b, 2a-b; Vokes, 1997: 212.

Remarks.—Vokes (1973) pointed out the similarity of some fine material of *Bursa* from the Chipola Fm (late Early Miocene) of Florida to *Bursa pelouatensis*, from the Early Miocene of the Aquitaine Basin, France, and identified the Chipola material as *B. pelouatensis*. However, Schmelz (1997) compared further Chipola material with specimens of *B. pelouatensis* from the Aquitaine Basin (Schmelz, 1997: pl. 1, fig. 2a-c) and demonstrated significant differences between them. He therefore described the Chipola material as a new species.

It is clear from Schmelz's figures and from material of *Bursa chipolana* examined by me that Schmelz's action was well justified. *Bursa chipolana* does not seem to be related to *B. pelouatensis* in any close phylogenetic sense, but shares many characters with endemic American *Bursa* species, particularly *B. rugosa*. The strongly out-curved siphonal fasciole and widely flared, very strongly armed inner and outer apertural lips, the deeply semitubular, posteriorly extended posterior canals, the prominence of the varices, and the overall style of coarsely rugose sculpture are characters common to the two species. The most significant difference between the two is in the width and prominence of the spiral cords. The cords are markedly wider in *B. chipolana* than in *B. rugosa*, and form particularly prominent, wide nodules, with interspaces narrower than the nodules, where they cross the varices; the cords are narrower in *B. rugosa*, so that the interspaces are wider than the cords. *Bursa chipolana* also reaches a larger size than *B. rugosa*. There are also fewer, larger, more prominent nodules on the shoulder angle in *B. chipolana* than in *B. rugosa*. The wide spiral cord at the shoulder angle, raised into large nodules, also is more obviously subdivided by a weak median spiral groove in *B. chipolana* than in *B. rugosa*. These differences are slight enough to suggest the possibility that *B. chipolana* might have been the direct ancestor of *B. rugosa*. Most of the distinguishing characters are shared also with the younger and smaller, endemic western Atlantic species *B. grayana* Dunker, 1862 which, however, has markedly shorter posterior canals than either *B. chipolana* or *B. rugosa*.

Dimensions.—Holotype, H 46.0, D 29.0 mm (Schmelz, 1997); paratype, USNM 647108, from TU 547: H 48.2, D 31.6 mm.

Types.—*Bursa* (*Bufonariella*) *chipolana*, holotype UF 73199, from TU 546, Chipola Fm, Tenmile Creek, 3 km west of Chipola River, Calhoun Co, Florida (not seen); figured paratype USNM 647108, from TU 547, west bank Chipola River 600 m upstream from Fourmile Creek, Calhoun Co (Pl. 1, Figs 6-7; specimen figured by Vokes, 1973: text-figs 2a-b); figured paratype UF 73200, from TU 951, Tenmile Creek, Calhoun Co; 9 further paratypes from localities on or near the Chipola River listed by Schmelz (1997).

Other material examined.—**Fossils: Florida: Late Early Miocene**, Chipola Fm: TU 547, W bank Chipola River, second specimen accompanying paratype illustrated by Vokes (1973), USNM 647108; TU 546, basal bed, Tenmile Creek, Calhoun Co, collection of Bernard Landau (1); TU 830 (GNS WM16949, 4 frag); TU 951 (GNS WM16948, 2 incomplete); frags also seen in Chipola collections, TU 546, 787, 1051, and 1098.

Distribution.—*Bursa chipolana* is recorded only from the Chipola Fm (late Early Miocene) on and near the Chipola River, Calhoun Co, Florida, USA.

***Bursa corrugata* (Perry, 1811)**

Pl. 1, Figs 11-13; Pl. 2, Figs 1-4, 6-7

- Biplex corrugata* Perry, 1811: pl. 5, fig. 1.
Ranella semigranosa Lamarck, 1822: 153; Kiener, 1841: 19, pl. 11, fig. 2; Deshayes, 1843: 548; ?Coulon, 1933: 137.
Ranella caelata Broderip, 1833: 179; G. B. Sowerby II, 1835: pl. 85, fig. 8; Deshayes, 1843: 554; Reeve, 1844b: pl. 3, fig. 10; C. B. Adams, 1852: 118.
Ranella ponderosa Reeve, 1844b: pl. 3, fig. 14; 1844d: 137.
Ranella pustulosa Reeve, 1844b: pl. 3, fig. 11; 1844d: 137.
Ranella (*Apollon*) *caelata*. Mörch, 1860: 81.
Ranella (*Lampas*) *corrugata*. Mörch, 1877: 24.
Ranella calata (sic). Coulon, 1933: 137.
Bursa pustulosa var. *jabik* Fischer-Piette, 1942: 216.
Bursa caelata *louisiana* M. Smith, 1948: 28, pl. 9, fig. 4.
Bursa (*Colubrellina*) *corrugata*. Abbott, 1954: 198, pl. 9, fig. k; 1958: 60, text-fig. 2, pl. 1, fig. i; Warmke & Abbott, 1962: 103, pl. 18, fig. m; Coelho & Matthews, 1971: 51, figs 9-10; Rosewater, 1975: 18, fig. 8; H. & E. Vokes, 1983: 23, pl. 11, fig. 13; Rios, 1985: 79, pl. 28, fig. 345.
Bursa (*Colubrellina*) *caelata*. Hertlein & Strong, 1955b: 263.
Bursa mexicana Perrilliat, 1963: 19, pl. 4, figs 18-19.
Bursa corrugata. Kaufmann & Götting, 1970: 372, fig. 88; Abbott, 1974: 167, pl. 7, fig. 1780 (as *B. caelata* in plate caption); Rios, 1975: 81, pl. 22, fig. 330; Cosel, 1984: 221; Calvo, 1987: fig. 82 (radula); Leal, 1991: 110 (not pl. 16, figs C-D); Lipe & Abbott, 1991: 14, illus.; Paulmier, 1994: 9, fig. 22; Diaz & Puyana, 1994: 174, fig. 649.
Bursa caelata. Keen, 1971: 508, fig. 964; Finet, 1991: 270.
Bursa pustulosa. Burnay & Monteiro, 1977: 34, fig. 27.
Bursa (*Colubrellina*) *corrugata corrugata*. Beu, 1985: 64; Cossignani, 1994: 69; Kaiser, 1997: 33; López de la Fuente & Ramos, 2004: 86; Kaiser, 2007: 39, pl. 26, figs 6a-b.
Bursa (*Colubrellina*) *corrugata ponderosa*. Beu, 1985: 64; Cossignani, 1994: 70; Rios, 1994: 92, pl. 31, fig. 363; Redfern, 2001: 57, pl. 29, figs 246A-B.
Bursa (*Colubrellina*) *corrugata pustulosa*. Beu, 1985: 64; Cossignani, 1994: 71-72.
Bursa corrugata corrugata. Hickman & Finet, 1999: 73, fig. 66.
Bursa (*Bursa*) *corrugata pustulosa*. Guerreiro & Reiner, 2000: 118-119.
? *Bursa* (*Colubrellina*) cf. *corrugata*. Macsotay & Campos Villarroel, 2001: 70.
Bursa (*Colubrellina*) *granularis cubaniana*. Macsotay & Campos Villarroel, 2001: 70, pl. 13, fig. 5 (not *Bursa granularis* Röding, 1798).
Bursa corrugata pustulosa. Ardovini & Cossignani, 2004: 132, upper right fig. and central left 2 figs.

Remarks.—*Bursa corrugata* is a distinctive, widespread species, similar to the other relatively tall and narrow species of *Bursa*, such as *B. granularis*, in shape and general appearance. Most specimens have the varices extended more widely (*i.e.*, they are markedly more prominent) than in *B. granularis*. The external sculpture is highly variable, ranging from an almost complete-

ly smooth surface, to bearing only 3-5 large, rounded nodules in one peripheral row in each intervariceal interval, to coarsely, closely, and evenly granulose, with numerous similar rows of small, obvious, subrectangular nodules, 4 or 5 rows on the last whorl and 2 on the spire. The most distinctive characters are seen in the aperture, which (at least in large specimens) has much more widely flared lips, and in particular the outer lip, than any other *Bursa* species discussed here. It also bears numerous, narrow, prominent ridges on the inner part of both lips, and a unique sculpture of many small, narrowly rounded nodules on the outer areas of both lips. A further distinctive character of modern specimens is the color pattern, which is almost uniform pale to dark brown, including the aperture – a unique character among American *Bursa* species – with five or more markedly paler to white nodules on the varices and, on some specimens, slightly to markedly darker-brown spiral bands coinciding with the spiral cords.

Some authors have maintained that the distribution of the sculptural variants has a geographical expression [E. A. Smith, 1890a; Tomlin & Shackleford, 1914; Cooke, 1916b: 8 (but note that Cooke regarded *Bursa* “*caelata*” as limited to Pacific Panama); reviewed by Hertlein & Strong, 1955b: 264], and subspecies, or even separate species, have therefore been recognized in Panamic western America, in the western Atlantic, and in West Africa. Certainly, there is a tendency for the smoother forms, with relatively few large, rounded peripheral nodules, or with no nodules at all, to be more common at Ascension Island and in West Africa than they are in eastern or western America. However, the collections that I have examined all include a large proportion of finely and evenly granulose specimens, so that it is impossible to say with any certainty where most specimens came from without knowing the locality. This problem becomes particularly obvious when trying to determine the localities of early-named taxa, most of which have unlocalized type specimens; it is impossible to say which of the early names should be applied to which subspecies, if subspecies are to be recognized. The range of variation seems to me to be too great for subspecies to have any significance in *B. corrugata*. It also appears likely that the east-west gradient in nodule prominence and surface smoothness is regular enough in *B. corrugata* to constitute a cline, and it is desirable not to subdivide a cline formally with Latin names. Forms in this complex are illustrated excellently in color on a recent web page (<http://www.femorale.com.br/shellphotos>, last accessed 28 April 2006).

A rather surprising point about *Bursa corrugata* is its poor fossil record in the Americas. The collections examined here include no pre-Pleistocene fossils from the western Atlantic region, apart from a few records from the Pliocene of the Isthmus of Tehuantepec, Mexico, and a few records from the Pliocene and Pleistocene of the Galápagos Islands. However,

the Oligocene *B. victrix* Dall, 1916 (see below), is closely related to, or perhaps even conspecific with, *B. corrugata*, and the very similar *Tritonium edentatum* Gabb, 1877, possibly is even a Late Cretaceous relative (see under *B. victrix*). Therefore, rather than implying that this extremely widespread species has somehow achieved its distribution very recently (after the uplift of the CAI! – obviously impossible with its pan-American distribution), this poor fossil record apparently results from a more strictly intertidal habitat than most other bursids; the poor preservation potential of intertidal taxa is familiar to all paleontologists.

This makes it all the more surprising, though, that an exceedingly closely similar form to *Bursa corrugata* is common and widespread as a Miocene and Pliocene fossil in Europe: *B. papillosa* (Pusch, 1837) (e.g., Baluk, 1995: 209, pl. 18, figs 1-3). The specimens illustrated by Baluk (1995) have rather short spires compared with Recent specimens of *B. corrugata*, but other specimens are so closely similar (e.g., those illustrated by Hoernes & Auinger, 1879: pl. 23, figs 6-9) that specific distinctions are not obvious. I have examined Hoernes & Auinger's (1879) material, from Lapugy, Transylvania, Middle Miocene (NHMV 1854/35/165, 4; 1868/I/435, 1; 1890/33/76, 3; 1874/25/23, 2; 1863/15/171, 2; 1858/43/37, 1) and further material of *B. papillosa* has been examined at SMF, and I am unable to distinguish it from Recent specimens of *B. corrugata*. Another surprising fossil record of *B. corrugata* therefore is worth recording here; two specimens were collected by Paolo Crovato (Naples) from the late Pleistocene (Tyrrenian) conglomerate at Reggio Arangea, opposite Messina in southwestern Italy (one in GNS, WM17065). This species evidently (briefly) extended its range to include the Mediterranean Sea late in Pleistocene time, but could well merely have been returning to an area it inhabited throughout Miocene and Pliocene times. The extinction of deep-water corals and mollusks in the Mediterranean during early Holocene time, probably as a result of impoverished productivity following post-glacial warming, has been discussed by Raffi & Taviani (1984), and *B. corrugata* possibly was another taxon to reflect this phenomenon. *Bursa corrugata* is biogeographically unique in its long time range and very wide geographical range (e.g., it is the one tonnoidean species still remaining indistinguishable – at least on shell characters – on the two sides of the Isthmus of Panama following uplift of the Isthmus), and a genetic study of the Recent populations would be helpful.

Specimens recorded from Miocene and Pliocene localities in the western Pacific as *Bursa corrugata* (e.g., van Regteren Altena, 1942: 107: Kendeng beds of Java, Pliocene) have been examined at RGM, and are all based on *B. granularis*. I am not aware of any authentic fossil or Recent records of *B. corrugata* from the Indo-West Pacific region.

Dimensions.—*Ranella caelata*, lectotype: H 50.1, D 33.3 mm; paralectotypes: H 58.2, D 39.2 mm, and H 46.3, D 32.5 mm; *R. semigranosa*, lectotype: H 40.8, D 25.2 mm, paralectotype: H 31.7, D 21.3 mm; *R. ponderosa*, lectotype: H 67.2, D 43.1 mm; *R. pustulosa*, lectotype: H 54.0, D 42.9 mm; *Bursa mexicana*, holotype: H 36.0, D 21.4 mm; TU 1046, Agueguexquite Fm, figured specimen, NMB H 17890, from type locality of *B. mexicana*: H 32.8, D 21.2 mm; St. Helena, BMNH 1909.8.10.1-2: H 83.4, D 58.8 mm; H 72.5, D 46.6 mm.

Types.—*Biplex corrugata*, no original material known (as for all of Perry's Ranellidae and Bursidae; Beu, 1998b: 16). *Ranella semigranosa*, lectotype designated by me (Beu, 1998b: 154), the specimen illustrated by Kiener (1841: 19, pl. 11, fig. 2) and by Cossignani (1994: 77, top left 2 figs), MHNG 1098/86/2, with one paralectotype, MHNG 1098/86/1, both labeled "Amer. centr."; it is impossible to tell whether they are from the western or eastern coast of America, and a type locality is not selected here. *Ranella caelata*, 3 syntypes BMNH 1950.11.28.7-9, from "Panama," i.e., Panama Bay, eastern Pacific; the medium-sized syntype (H 50.1, D 33.3 mm) is labelled "holotype" and is the specimen figured by Reeve (1844b: pl. 3, fig. 10). This specimen is here designated the lectotype of *R. caelata* and the neotype of *Biplex corrugata* Perry, 1811. *Ranella ponderosa*, one "possible syntype" BMNH 1967654, unlocalized, not Reeve's (1844b) figured specimen. This form was based on relatively large specimens with little sculpture other than one row of large nodules at the periphery, and with a widely flared outer lip. Again, it is impossible to tell which coast of America this specimen was collected on, although large specimens of this type have mostly been collected from Florida and the West Indies during the 20th century; a type locality is not selected here. *Ranella pustulosa*, 3 syntypes BMNH 1967653, from Ascension Island; the smallest, slightly incomplete syntype is that illustrated by Reeve (1844b: pl. 3, fig. 11). This form was based on relatively small, sparsely nodulose specimens of a deep maroon-brown color, which tend to predominate in collections from Ascension and West Africa. *Bursa pustulosa* var. *jabik*, holotype in collection Adanson, MNHN, from Sénégal, West Africa. This variety, proposed from among the names erected by Adanson (1757), is based on West African specimens of the sparsely nodulose variety that was also named *Ranella pustulosa* by Reeve (1844b). *Bursa caelata louisa*, repository of type material unknown, presumably originally in the private collection of M. Smith; type locality "Perlas Archipelago, Gulf of Panama"; proposed as a "subspecies" in the sense of variety, because Smith (1948: 28) also recorded *B. caelata* from "Panama and the coasts of central America," and differentiated *B. caelata louisa* as "a smaller and more compact form than the typical *caelata*." *Bursa mexicana*, holotype in Universidad Nacional

Autonoma de Mexico, Instituto de Geologia, no. 1109-G (Perrilliat, 1963: 43), not seen; from the Agueguexquite Fm (Pliocene), Isthmus of Tehuantepec, Mexico. Perrilliat (1963) differentiated her species from Recent specimens of "*Bursa caelata*" by trivial differences in the sculpture, which is highly variable in this species; her illustration clearly shows *B. corrugata*, and specimens collected from the type locality of *B. mexicana* by E. & H. Vokes (TU 1046) are typical, if small and thin-shelled, specimens of *B. corrugata*, closely resembling the Recent specimen from Clipperton Island illustrated by Kaiser (2007: 39; pl. 26, figs 6a-b).

Other material examined.—**Recent: E Pacific:** 103 lots at AMNH, GNS, LACM, RMNH, SMF, ZMA, BMNH; from W Mexico (northernmost: 10-20 m, Saladita Cove and first cove to north, near Guaymas, Sonora, 27°53'15"N, 110°58'W, LACM 68-27, 1), Nicaragua, W Costa Rica, W Panama, W Colombia, Ecuador and Peru (southernmost: 2-10 m, rocks and sand, Isla Lobos de Afuera, Peru, 06°57.1'S, 80°42.3'W, LACM 74-6, 1). **W Atlantic:** 85 lots at AMNH, ANSP, BMNH, C. J. Finlay collection (now at FAU), DMNH, GNS, LACM, MCZ, RMNH, SMF, USNM, ZMA; from Florida (northernmost: 10 m, off of Palm Beach, AMNH 125514, 1), Bahamas, Atlantic Costa Rica, Cuba, Jamaica, Cayman Islands, Dominican Republic, Puerto Rico, Antillean Islands (St. Croix, Tobago, Grenada, St. Barthelemy, Martinique, Antigua, Dominica, Barbados), Aruba, Bonaire, Curaçao, Colombia, Venezuela, Guiana, and Brazil (southernmost: Bahia de Todos Santos, Bahia, ANSP 263514, 1; and Maceio, Algoes, LACM 31446, 1). **Central Atlantic: St. Helena:** 11 lots (BMNH, 3 lots; GNS, 1 lot; MCZ, 2 lots; MNHN, 1 lot; NMP, 1 lot; USNM, 3 lots). **Ascension:** 6 lots (Dautzenberg collection, IRSNB, 1 lot; BMNH, 1 lot; MCZ 136156, 2 lots; USNM, 2 lots). **E Atlantic:** 69 lots at BMNH, Dautzenberg collection, GNS, IRSNB, MCZ, MNHN, RMNH, NMP, USNM; from Madeira, Cape Verde Islands, Mauritania, Sénégal, São Tomé, Spanish Guinea, Ile Principé, Liberia, Cameroon, Ivory Coast, Gold Coast, Nigeria, Congo, Gabon, Angola (southernmost: intertidal rocks, Lucira, Praia de Cesar, Prov. Moçamedes, Angola, MNHN, 4).

Fossils: Mexico: Pliocene: Agueguexquite Fm: TU 638 (10 frag); TU 1046 (= NMB 19020), Perrilliat's loc. [6, 11 frag; including illustrated specimen (Pl. 1, Fig. 12), NMB H 17890; GNS WM16947, 2 frag; WM 18854, 9 frag]. **Galápagos Islands:** "Tertiary" (Pliocene-Pleistocene?), Chatham Island, Galápagos Islands, coll. M. J. Barrande (BMNH Palaeontology Department, G9670, 3). Pitt *et al.* (1986: 276, fig. 11) also recorded five Pliocene or Pleistocene fossil specimens of *Bursa corrugata* (as *B. caelata*) from the Cerro Gallina tuff cone, Isla Santa Cruz, Galápagos Islands. **Venezuela: Holocene:** Tortuga Fm, Las Calderas Canyon, Cubagua Island, collection of Bernard Landau (1). **Ecuador:**

Pleistocene: NMB 19149 (1, aperture only). **Italy:** Tyrrhenian (Pleistocene) conglomerate, Reggio Aranea, opposite Messina in Reggio Calabria, southern Italy, two specimens collected by Paolo Crovato, Naples (including GNS WM17065, 1).

Distribution.—*Bursa corrugata* lives at present in Panamic western America, from Sonora to northern Peru (Keen, 1971; and data above), in the western Atlantic, from Florida, USA, and the Bahamas to northern Brazil (Abbott, 1974; and data above; “Ceará to São Paulo; Trindade I.”, Rios, 1994), at St. Helena and Ascension Island in the mid-Atlantic (Rosewater, 1975: 18, fig. 8; and listed above), and in tropical West Africa, from Madeira (listed above), the Canary Islands (Nordsieck & Garcia-Talavera, 1979: 127, pl. 28, fig. 5), and Mauretania to at least as far south as Gabon (Bernard, 1984: 64, fig. 102) and Angola (Gofas *et al.*, 1984: 132, as *B. pustulosa*). It was recorded also from the Galápagos Islands by Hickman & Finet (1999), Cocos Island, Costa Rica, eastern Pacific, by Montoya (1983, 1984) and Skoglund (1992), from Clipperton Island by Kaiser (2007: 39), and from Gorgona Island, Pacific Colombia, by Cantera *et al.* (1979) and Cosel (1984). Specimens from 125 m, off of Martinique, Caribbean, were illustrated by Paulmier (1994: 9, fig. 22). Matthews (1968) recorded specimens found rarely in the gut of the toadfish or “pacomon,” *Amphichthys cryptocentrus* (Valenciennes, 1837), caught off of Fortaleza, Ceará, Brazil. Fossils are widespread in Europe in Miocene, Pliocene, and late Pleistocene rocks, but in the Americas are recorded only from the Agueguexquite Fm, Isthmus of Tehuantepec, Mexico (Pliocene), and the Galápagos Islands (Pleistocene). Like *Monoplex trigonus* (Gmelin, 1791) (see below), *B. corrugata* does not live in the Mediterranean at present, but young Pleistocene (Tyrrhenian) fossils occur at at least one locality in southern Italy, demonstrating that it entered briefly during interglacial warm periods. *Bursa corrugata* is among the widest-ranging of the tonnoideans that have *not* entered the tropical Indo-West Pacific, and its full range – both geographical and stratigraphical – is still poorly known.

***Bursa granularis* (Röding, 1798)**

Pl. 3, Figs 1, 3

Tritonium granulare Röding, 1798: 127.

Tritonium jabick Röding, 1798: 127.

Biplex rubicola Perry, 1811: pl. 5, fig. 4.

Ranella granifera Lamarck, 1816: pl. 414, fig. 4, “Liste des objets”: 4; 1822: 153; Kiener, 1841: 16, pl. 11, fig. 1; Deshayes, 1843: 548; Reeve, 1844b: pl. 6, fig. 30; Küster & Kobelt, 1871: 143, pl. 39, fig. 1; Coulon, 1933: 137.

Ranella affinis Broderip, 1833: 179; G. B. Sowerby II, 1835: pl. 89, fig. 12; Reeve, 1844b: pl. 4, fig. 19; Küster & Kobelt, 1871: 142, pl. 38a, fig. 5.

Ranella cubaniana d’Orbigny, 1841a: 165, pl. 23, fig. 24; Mörch,

1877: 24.

Ranella livida Reeve, 1844b: pl. 6, fig. 28; 1844d: 138; Krauss, 1848: 113.

Ranella semigranosa. Reeve, 1844b: pl. 6, fig. 25; Krauss, 1848: 113 (not *Ranella semigranosa* Lamarck, 1822).

Bursa granularis. H. & A. Adams, 1852: 106; Hedley, 1916: 196; Hertlein & Allison, 1960: 15; Barnard, 1963: 17; Hinton, 1972: 12, pl. 6, fig. 22; Salvat & Rives, 1975: 307, fig. 179; Hinton, 1978: 32, fig. 8; Kay, 1979: 227, fig. 80A; Kilburn & Rippey, 1982: 73, pl. 16, fig. 14; Drivas & Jay, 1988: 62, pl. 16, fig. 4; Leal, 1991: 111, pl. 16, figs C-D; Lipe & Abbott, 1991: 14-15, illus.; Wilson, 1993: 226, pl. 43, figs 11a-b, 12; Kubo in Kubo & Kurozumi, 1995: 74, 78, fig. 7; Beu, 1998b: 150, figs 48a-e, 58d; 1999: 44, fig. 85; 2005: 19, figs 27-28; Lee & Chao, 2003: 40, pl. 4, fig. 93.

Ranella (Lampas) granifera. Tryon, 1880: 41, pl. 22, figs 35-40; Watson, 1886: 399.

Bursa cumingiana Dunker, 1862: 238; 1863: 59, pl. 19, figs 7-8.

Gyrineum affine var. *cubanianum*. Dall, 1889: 224.

Gyrineum affine. Dall, 1903b: 132.

Bursa affinis. Maury, 1922: 114.

Dulcerana granularis. Iredale, 1931: 213; Rippingale & McMichael, 1961: 69, pl. 7, fig. 19.

Dulcerana jabick. Iredale, 1931: 213.

Bursa alfredensis Turton, 1932: 107, pl. 24, fig. 781.

Bursa kowiensis Turton, 1932: 108, pl. 24, fig. 782.

Ranella (Bursa) affinis. Trechmann, 1933: 39.

Gyrineum affine (sic) cubanianum. Morretes, 1949: 92.

Dulcerana versigranulata (sic). Jackson, 1952: 46.

Bursa (Colubrellina) cubaniana. Abbott, 1958: 57, text-fig. 2, pl. 1, fig. k; Warmke & Abbott, 1961: 103, pl. 18, fig. i; Rios, 1970: 70; Coelho & Matthews, 1971: 52, figs 11-12; Humfrey, 1975: 126, pl. 14, figs 4, 4a; H. & E. Vokes, 1983: 23, pl. 11, fig. 14.

Bursa cubaniana. Nowell-Usticke, 1959: 61; Work, 1969: 663; Kaufmann & Götting, 1970: 372, fig. 87; Matthews & Kempf, 1970: 28; de Jong & Coomans, 1988: 214, pl. 16, fig. 382.

Bursa cubaniana intermedia Nowell-Usticke, 1959: 62, pl. 3, fig. 13; 1969: 15, pl. 3, fig. 634.

Bursa corrugata lineata Nowell-Usticke, 1959: 62, pl. 3, fig. 12; 1969: 14, pl. 3, fig. 632; 1971: 11, pl. 2, fig. 632.

Bursa granularis affinis. Hertlein & Allison, 1960: 15.

Colubrellina corrugata. Oyama & Takemura, 1960: *Colubrellina* pl., figs 1-2 (not *Biplex corrugata* Perry, 1811).

Colubrellina jabick. Oyama & Takemura, 1960: *Colubrellina* pl., figs 3-4.

Colubrellina semigranosa. Oyama & Takemura, 1960: *Colubrellina* pl., figs 5, 7 (not *Ranella semigranosa* Lamarck, 1822).

Colubrellina granularis. Habe, 1961: 47, pl. 24, fig. 5; Okutani, 1986: 116-117, top left fig.

Colubrellina (Dulcerana) granularis. Habe, 1964: 76, pl. 24, fig. 5; Wilson & Gillett, 1971: 80, pl. 54, figs 7-7b.

Bursa granularis cubaniana. Abbott, 1974: 167, pl. 7, fig. 1781 (as *B. granularis* in pl. caption); Rios, 1975: 81, pl. 23, fig. 331; Finlay, 1978: 149; Bandel, 1984: 102, pl. 10, figs 3, 8; Diaz & Götting, 1988: 156; Diaz, 1990: 19; Diaz & Puyana, 1994: 174, fig. 650; Redfern, 2001: 58, pl. 29, figs 247A-B.

Bursa (Colubrellina) granularis cubaniana. Rios, 1975: 81, pl. 23, fig.

331; Beu, 1985: 64; Cossignani, 1994: 78.

Bursa (Colubrellina) granularia (sic). Rios, 1985: 79, pl. 28, fig. 347.

Bursa (Colubrellina) granularis granularis. Beu, 1985: 64; Cossignani, 1994: 75-77.

Bursa (Colubrellina) granularia (sic) cubaniana. Rios, 1994: 92, pl. 31, fig. 365.

Bursa (Bufonariella) granularis. Bosch *et al.*, 1995: 102, fig. 737.

Bursa (Colubrellina) granularis. Okutani, 2000: 269, pl. 133, fig. 1; Zhang & Ma, 2004: 182, text-figs 113a-c, pl. 5, figs 1-3; Kaiser, 2007: 39, pl. 26, figs 7a-b.

Remarks.—*Bursa granularis* is extremely widespread and common in both the intertidal zone and the shallow subtidal zone throughout the Indo-West Pacific province, occurs commonly also in the western Atlantic, and rarely in the eastern Pacific and the eastern Atlantic. It is highly variable in spire height, in sculptural prominence, and in color pattern, and consequently has received many names. I reviewed (Beu, 1998b) the variation, synonymy, and type material of *B. granularis*, and most of this need not be repeated here. The above synonymy includes all of the names of which I am aware that refer to this species, but is a very incomplete listing of the published references; it cites most of the usages of which I am familiar in the Atlantic, a few of the Pacific ones, and some modern books with good illustrations. I provided (Beu, 1998b) a fuller synonymy.

Bursa granularis is easily recognized by its relatively tall, narrow shape for a bursid and by its thin teleoconch, giving it an overall appearance more nearly resembling that of Ranellidae such as *Monoplex* than is common in the Bursidae. The varices are strictly aligned for most of the spire height, becoming a little displaced only on the last whorl or two of large specimens. There seems to be no intritacalx present on any material that I have examined. All specimens have three major spiral cords on the last whorl, forming nodules where they cross the varices, and most have small and numerous to few, large nodules on the major cords; a few specimens lack nodules altogether (such as the holotype of *B. kowiensis*). The width of the varices and the size of the nodules on the varices are highly variable. The abapertural face of each varix is deeply excavated, and is buttressed by the spiral cords. The aperture has a deeply excavated columella, and so is nearly circular. The apertural lips are well flared, and bear numerous prominent, narrow transverse ridges. In many specimens, the aperture is only slightly paler than the external teleoconch color, whereas in others, it is white. The protoconch is of the most common type in *Bursa*, of 2.5 whorls, of rather tall-turbiniiform shape with a weakly impressed suture, with a finely reticulate protoconch I of 0.5 whorls, and with reticulate sculpture on the first whorl of protoconch II, fading out before the end of the last protoconch whorl.

The color pattern of the teleoconch exterior of Indo-West Pacific specimens of *Bursa granularis* is highly variable, from off-white, pale brown or pale orange to deep reddish brown, with or without various combinations of spiral and/or axial bands and irregular spots and streaks. Atlantic specimens have a markedly less-variable color pattern, with a moderately dark tan or pale orange background (highly variable in tone among specimens) bearing a paler (cream on most specimens) diffuse peribasal band and dorsum of the anterior canal, with the varices darker brown than the rest of the surface but banded with cream where they are crossed by the spiral cords. Indo-West Pacific specimens bearing the same color pattern as Atlantic specimens are not uncommon (seen from Grand Récif de Tuléar, Madagascar; Horseshoe Reef, Okinawa; Tuamotu Islands, Polynesia; and common in Hawaii) and I concluded (Beu, 1998b) that the Atlantic *cubaniana* form is best regarded as part of the variation of a single taxon, *B. granularis*. It appears from the color pattern that the Atlantic population might have been derived from the Indo-Pacific one through a classic founder population as a spat-fall of only a few larvae, *i.e.*, an initially low genetic variability (low diversity of alleles?) in the original small population has resulted in a narrow range of variation in color pattern in the present Atlantic population – as also seems likely for apertural color in *B. rhodostoma* (see below). I am unable to see any other differences between the Atlantic and Indo-West Pacific populations. The lack of a fossil record in the Atlantic before Pleistocene time (despite a record in the western Pacific from Miocene time onward: Martin, 1899: 147; 1919: 88, 130; Tesch, 1920: 42, pl. 129, fig. 154; van Regeteren Altena, 1943: 108, as *B. corrugata*; Beu, 2005) suggests that this colonization event occurred relatively late in Pleistocene time, and that this is one of the many species that colonized the Atlantic from the Indian Ocean via South Africa, in the manner suggested by Vermeij & Rosenberg (1993).

Dimensions.—Neotype of *Tritonium granulare* and lectotype of *Ranella granifera*: H 51.7, D 33.1 mm; lectotype of *R. affinis*: H 62.5, D 35.7 mm; lectotype of *R. livida*: H 56.8, D 32.0 mm; lectotype of *Bursa cumingiana*: H 46.5, D 31.3 mm (Beu, 1998b); *R. cubaniana*, holotype: H 51.7, D 33.1 mm; ANSP 272722, Boca Chica, Isla Tierra Bomba, E Colombia: H 70.8, D 39.2 mm; Pleistocene, Barbados, collection of Bernard Landau: H 80.2, D 41.0 mm.

Types.—*Ranella granifera*, lectotype designated by me (Beu, 1998b), MHNG 1098/85/1, with 2 paralectotypes, from the Red Sea; this specimen is also the neotype of *Tritonium granulare* Röding, 1798, of *T. jabick* Röding, 1798, and of *Biplex rubicola* Perry, 1811. *Ranella affinis*, lectotype [designated by me (Beu, 1998b)] and 2 paralectotypes BMNH 1950.11.28.4-6, supposedly from “Annaa,” Tuamotu Islands. *Ranella cubaniana*, holotype BMNH 1854.10.4.412, from

"St. Lucie," West Indies (Pl. 3, Figs 1, 3), an abraded and slightly incomplete specimen of the Atlantic form of *Bursa granularis*. *Ranella livida*, lectotype (designated by me; Beu, 1998b) and 2 paralectotypes BMNH 1967657, supposedly from "Anaa," Tuamotu Islands. *Bursa cumingiana*, lectotype (designated by me; Beu, 1998b) and one paralectotype BMNH 1968530, from New Caledonia. *Bursa alfredensis* and *B. kowiensis* of Turton (1932), types not seen, presumably in the collection from Port Alfred, South Africa, presented to the Oxford University Museum by Turton (1932). *Bursa corrugata lineata*, holotype AMNH 195427, from Krause's Lagoon, St. Croix, Virgin Islands, Caribbean, a small specimen of the Atlantic form of *B. granularis*. *Bursa cubaniana intermedia*, type material not recognizable in Nowell-Usticke's collection (now in AMNH), as was also stated by Faber (1988: 81).

Other material examined.—The abundant Indo-West Pacific lots in world collections are not listed. **Recent: E Pacific: Clipperton Island:** [no further data] (UCMP, B-4237, 18; B-6101, 1; B-6104, 2; B-6205, 1; B-6566, 1; UCMP 37062, 23; MNHN, 20); dived 6-20 m (ZMA, 1). **W Atlantic:** 136 lots examined, at AMNH, ANSP, DMNH, GNS, LACM, MCZ, NMB, NMP, RMNH, USNM, ZMA, Zoological Museum, University of Bologna, and C. J. Finlay collection (now at FAU), plus 30 lots at R. von Cosel's material in SMF; from Bermuda, Bahamas, Florida, E Mexico, E Honduras, E Panama, Cuba, Cayman Islands, Jamaica, Puerto Rico, Antillean Islands (St. Croix, Dominica, Barbados, Tobago, Grenada, Martinique, Bequia, Windward Isles, St. Kitts, St. Thomas, Saba, St. Martin, St. Eustatius), Aruba, Bonaire, Curaçao, E Colombia, Venezuela, and Brazil (GNS WM14010, off of Mucuripe, Fortaleza, Ceará State, 1).

Fossils: Atlantic Panama: Pleistocene: Colon, Panama (BMNH Palaeontology Department, G23167, 1). **Cuba: Pleistocene:** Las Puercas Beach, Oriente, ex Johns Hopkins University (USNM, 2 large). **Dominican Republic: Pleistocene:** La Isabella Fm, El Castillo, La Isabella, collection of Bernard Landau (6). **Barbados: Pleistocene:** USGS 18383, coral rock (1); USGS 18381, coral rock (2); coral rock, Barbados (BMNH Palaeontology Department, G69350-2, 3); coral rock, Bridgetown (BMNH Palaeontology Department, G69283-4, 2; G3680, 2); low-level reefs, Bishopscourt (BMNH Palaeontology Department, G10941, 8 large); post-coral rock, Silver Sands (BMNH Palaeontology Department, GG4245, 1); Coral Rock, Barbados, collection of Bernard Landau (3).

Distribution.—In the living fauna, *Bursa granularis* is common throughout the Indo-West Pacific province, from Jeffreys Bay, South Africa, throughout eastern Africa and the Red Sea to the northern Indian Ocean, in the western Pacific from Kii Peninsula and Yamaguchi Prefecture, Honshu, Japan (Beu, 1999), south to Rottneest Island in Western Australia

(Wilson, 1993: 226) and to Sydney Harbor, New South Wales, Australia, and throughout Polynesia to Hawaii (Beu, 1998b). In the eastern Pacific, particularly large specimens are common at Clipperton Island (UCMP 37062, 23; Hertlein & Allison, 1960; Kaiser, 2007: 39, pl. 26, figs 7a-b, much material listed) and specimens were recorded by Emerson (1991: table 1) from the Revillagigedo Islands, Cocos Island, and the mainland coast at Bahia Chamela, Jalisco, western Mexico (LACM 38-6). In the western Atlantic, it is recorded from southeastern Florida (Abbott, 1974), USA, south to Bahia, Brazil ("Pará to Bahia, Fernando de Noronha Is., Atoll das Rocas"; Rios, 1985, 1994). Matthews (1968) recorded specimens found uncommonly in the gut of the toadfish or "pacomon," *Amphichthys cryptocentrus*, caught off of Fortaleza, Ceará, Brazil. In the eastern Atlantic, it is recorded only from the Cape Verde Islands (Garcia-Talavera, 1983: 141). Although *B. granularis* has a Miocene-Recent time range in the Pacific (see above), it is recorded only from Pleistocene rocks and in the living fauna in the western Atlantic, and so apparently is a geologically recent arrival there. The record by Gregory (1895: 288, table) from Pleistocene rocks of Barbados as "*Ranella (Lampas) aff. affinis*" presumably refers to this species. Robinson (1991) recorded *B. granularis* from the Late Pliocene-Early Pleistocene Moín Fm at Limón, Costa Rica, on the basis of a personal communication from me, but I have since reidentified these specimens as *B. scrobilator* (Linnaeus, 1758) (see below). Fossils have not been reported in the eastern Pacific.

Bursa grayana Dunker, 1862

Pl. 3, Figs 2, 4-9

Bursa grayana Dunker, 1862: 238; 1863: pl. 19, figs 5-6.

Bursa bufoniopsis Maury, 1917a: 108, pl. 17, fig. 8; Pilsbry, 1922: 360.

Bursa aff. thomae. Matthews & Kempf, 1970: 28.

Bursa (Bursa) pacomoni Matthews & Coelho, 1971: 2, figs 1-5; Coelho & Matthews, 1971: 48, figs 4-8; Leal, 1991: 113, pl. 16, fig. E.

Bursa (Bursa) grayana. Beu, 1985: 63; 1987: 317, figs 157-164; Rios, 1985: 78, pl. 28, fig. 343; 1994: 92, pl. 30, fig. 361; Cossignani, 1995: 48.

Remarks.—*Bursa grayana* is easily recognized by its relatively small size (height to 40 mm); the only smaller species in the fauna considered here is *B. rhodostoma* (G. B. Sowerby II, 1835). *Bursa grayana* is similar in shape to *B. rhodostoma*, although the spire is slightly taller in some specimens than in *B. rhodostoma*, and in most specimens the shell is a little wider than in *B. rhodostoma* because of (a) slightly wider and more prominent varices, and (b) a slightly more dorsoventrally compressed shell. Modern specimens are easily distinguished

by the pale lavender to deep-red aperture of most specimens of *B. rhodostoma* (a few have a white aperture), which contrasts with the uniformly white aperture of *B. grayana*. The outer lip of *B. grayana* also is more widely flared than in *B. rhodostoma* and, most notably, the posterior siphonal canals of *B. grayana* are markedly longer and more deeply tubular and protrude to form short, spine-like tubes in a manner not seen in most specimens of *B. rhodostoma*. *Bursa grayana* differs from *B. rhodostoma* further in its more coarsely nodulose sculpture, with many rather small, rounded to subrectangular nodules on the primary spiral cords, and the spiral interspaces largely filled by smaller, rounded nodules on the secondary cords. Also, the upper two main spiral cords, at the shoulder angle and just below it, consistently are subdivided by a shallow median groove in *B. grayana*, but this groove has not been observed in *B. rhodostoma*. The siphonal fasciole also is more prominent and more coarsely sculptured in *B. grayana* than in *B. rhodostoma*, and curves out strongly to the left of the aperture. A final consistent and easily recognized character present in *B. grayana* but not in *B. rhodostoma* is the subsutural row of short, prominent, radial ridges, fading out at about half the height of the sutural ramp.

This species was first recognized during the 20th century as the Dominican Republic Miocene fossil *Bursa bufoniopsis* Maury, 1917, and in the living western Atlantic fauna as *B. pacomoni* by Matthews & Coelho (1971); their material was obtained from the stomach of the “pacomon,” *Amphichthys cryptocentrus*, from off of the coast of Brazil (States of Pará and Bahia, and from the Fernando de Noronha Islands and Atol das Rocas). I pointed out (Beu, 1987: 318) that most of the type material of *B. grayana*, supposedly from the Red Sea, is conspecific with *B. bufoniopsis* and *B. pacomoni*, and selected a specimen of this species as the lectotype of *B. grayana*. [I cited (Beu, 1987) the wrong BMNH specimen number for the specimen intended to be designated as the lectotype; the correct registration number for the lectotype is BMNH 1988064/1].

Dimensions.—Figured specimen, NMB H 18053, from NMB 15863, Dominican Republic: H 41.9, D 28.1 mm; figured specimen, NMB H 17891, from NMB 18734, Cayo Agua, Panama: H 29.5, D 19.9 mm; Recent, Dry Rocks, off of Key Largo, Florida, C. J. Finlay collection (now at FAU): H 55.5, D 36.7 mm; lectotype of *Bursa grayana*: H 28.0, D 19.1 mm; *B. bufoniopsis* holotype: H 38.3, D 26.3 mm; *B. pacomoni* holotype: H 28, D 22 mm, largest paratype: H 34, D 22 mm (Matthews & Coelho, 1971: 6, table of 12 specimens).

Types.—Lectotype of *Bursa grayana* (designated by me; Beu, 1987: 318) BMNH 1988064/1, with one paralectotype 1988064/2, and 3 further paralectotypes 1968529/1-3, all incorrectly labelled “Red Sea” (actually Recent, west-

ern Atlantic). The type locality is here designated as off of Mucuripe, Fortaleza, Brazil. *Bursa bufoniopsis*, holotype PRI 28762, from Río Gurabo at Los Quemados, Dominican Republic; presumed paratypes, PRI, Maury’s loc. 200, zone D, Río Gurabo (1, incomplete); Maury’s loc. 210, zone B, Río Gurabo (1). *Bursa pacomoni*, holotype MNRJ 3528, taken from stomach of “pacomon” off of Mucuripe, Fortaleza, Ceará, Brazil; 3 paratypes in MNRJ, 4 paratypes in Laboratorio de Ciencias do Mar, Universidade de Río Grande, Río Grande do Sul, Brazil; and 4 paratypes in Museu Oceanografico de Río Grande, Río Grande do Sul, Brazil (not seen; Matthews & Coelho, 1971: 6, table).

Other material examined.—**Recent: W Atlantic: Florida:** Dry Rocks, off of Key Largo, 1948, C. J. Finlay collection (now at FAU; 1); dredge fill, Dania Beach (USNM 797966, 1). **Belize:** Belize (MCZ, 1). **San Salvador:** off of E coast of San Salvador (GNS WM16679, 1). **Puerto Rico:** [no further data] (AMNH 190479, 1). **Brazil:** Fortaleza, Ceará, from fishermen (MCZ 277369, 1); Praia de Checo Negro, Cidade da Bahia (MCZ, 1); Natal (AMNH 112180, 2); *ex pisce*, 30-60 m, off of Mucuripe, Fortaleza, Ceará (AMNH 163333, 10; ANSP 316116, 2); on rocks, Itapoa, Bahia (ANSP 274397, 1; 276358, 1); 15 m, fishermen, off of Fortaleza, Ceará (ANSP 340904, 1); off of Fortaleza, Ceará (DMNH 38455, 1; 40924, 1); off of Mucuripe, Fortaleza, Ceará (DMNH 51632, 1; GNS WM16678, 1); U.S. Fish Commission sta. 2758, 40 m, SE of Cape Roque (USNM 417784, 2); beach, Atol das Rocas (GNS WM13665, 1).

Fossils: Mexico: Pliocene: USGS 18688 (1). **Dominican Republic: Late Miocene:** Cercado Fm: TU 1230 (GNS WM16899, 1; WM18839, 3); 1422 (GNS WM18848, 5); NMB 16982, Cercado Fm, Río Cana, collection of Bernard Landau (20). **Late Miocene/Early Pliocene:** Gurabo Fm: NMB 16809 (1); TU 1225 (GNS WM18838, 1 frag); 1231 (GNS WM18840, 4; GNS WM18845, 3); 1246 (GNS WM18846, 1 frag); 1250 (GNS WM18841, 1); 1277 (GNS WM16902, 1); 1296 (GNS WM18842, 1); “Miocene,” Yaque River, Dominican Republic, coll. T. S. Heneken (BMNH Palaeontology Department, GG20413, 1). **Early Pliocene:** Gurabo Fm: NMB 15803 (1); 15817 (1); 15843 (1); 15846 (1); 15850 (2); 15863 (2; 1 figured, NMB H 18053); 15865 (1); 15866 (1); 16817 (2); 16879 (1); TU 1210 (GNS WM18844, 1 frag); 1212 (GNS WM16898, 1); 1215 (10, incl. GNS WM16894, 4; WM 18837, 5); 1354 (GNS WM18843, 1); USGS 8544 (1); 8714 (1); Gurabo Fm, Río Gurabo, collection of Bernard Landau (11); Mao Fm: TU 1365 (GNS WM18847, 1). **Atlantic Panama: Pliocene:** NMB 18734, Cayo Agua Fm, 300 m WNW of Punta Piedro Roja, Cayo Agua, Bocas del Toro Basin (2, including illustrated specimen (Pl. 3, Figs 7-8), NMB H 17891).

Distribution.—*Bursa grayana* occurs in the living fauna

from southern Florida, USA, throughout the western Atlantic to Bahia, Brazil, and to Fernando de Noronha Island and Atol das Rocas (Rios, 1994), although it is much less common in collections than the shallow-water species *B. corrugata*, *B. granularis*, and *B. rhodostoma*. Most specimens are from divers or from fish stomachs, although a few have been found cast ashore on beaches. There are no records from either the eastern Atlantic or the eastern Pacific. Miocene and Pliocene fossils are moderately common in the northern Dominican Republic, probably reflecting the offshore habitat of the species at present, and the correspondingly offshore deposition sites of most Dominican Republic units. However, the only other fossils of which I am aware are two specimens from the Pliocene Cayo Agua Fm in the Bocas del Toro Basin, eastern Panama, and one poorly localized specimen from Mexico, of Pliocene age.

***Bursa natalensis* Coelho & Matthews, 1970**

Pl. 3, Figs 10-13

Bursa finlayi McGinty, 1962: 39, pl. 3, figs 1-1a, 2 (in part; holotype is *B. ranelloides* Reeve, 1844); Laursen, 1981: 30, pl. 3, figs 2a-b.

Bursa (Colubrellina) natalensis Coelho & Matthews, 1970: 1, figs 1-3.

Bursa (Colubrellina) finlayi. Coelho & Matthews, 1971: 53, figs 13-15.

Bursa (Bufonariella) latitudo natalensis. Beu, 1981: 288, figs 16a-f.

Bursa (Colubrellina) latitudo natalensis. Beu, 1985: 64; Cossignani, 1995: 82.

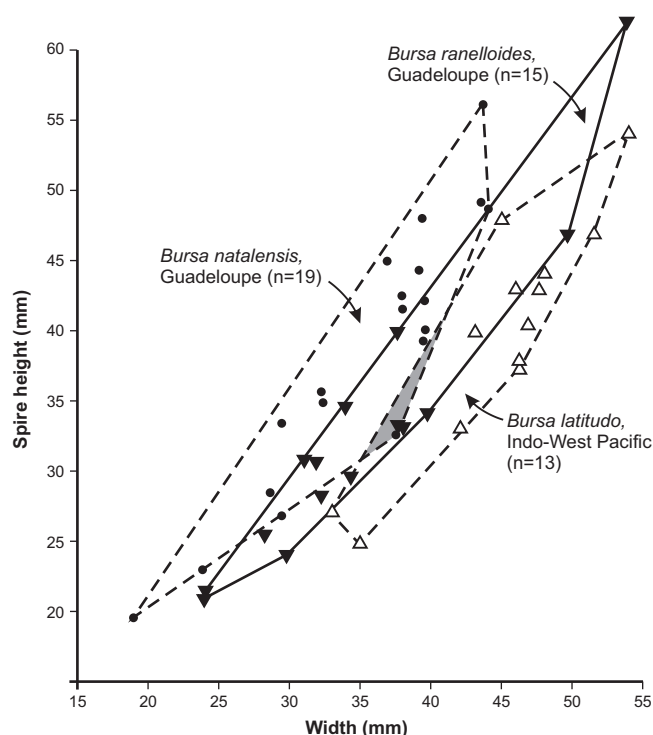
Bursa latitudo natalensis. Calvo, 1987: fig. 83 (radula); Paulmier, 1994: 9, fig. 23.

Bursa natalensis. Leal, 1991: 113.

Remarks.—*Bursa natalensis* is easily recognized by its extremely tall and narrow shape. Although not as tall and narrow as the rare western Pacific species *B. condita* (Gmelin, 1791), *B. natalensis* is the next-tallest known bursid, and is much the tallest of the western Atlantic species. The varices are situated at each two thirds of a whorl (at each 240° around the spiral) as in *B. ranelloides* and in the Indo-West Pacific species *B. latitudo* Garrard, 1961, the parietal area of the inner lip bears a weakly to quite strongly defined red-brown color patch, or bars between the white ridges on some specimens, as are seen also in both *B. ranelloides* and *B. latitudo*, and the sculptural style, with two moderately prominent, nodulose whorl angulations and several rows of small nodules between them, also is closely similar to that of both *B. ranelloides* and *B. latitudo*. Although this species was compared with *B. condita* by Coelho & Matthews (1970), *B. condita* is still taller and narrower, has its varices aligned or at most a little offset (Beu, 1998b: figs 43a-d), has still finer exterior sculpture with no large nodules, and lacks the red parietal color patch of *B. ranelloides*, *B. latitudo*,

and *B. natalensis*. It is clear that the real phylogenetic affinities of *B. natalensis* are with *B. ranelloides* (discussed below) and, even more closely, with *B. latitudo*, which was discussed in detail by me (Beu, 1998b). The protoconch of *B. natalensis* (*vide* Beu, 1998b: fig. 45d) is unusually tall and narrow, and is indistinguishable from that of *B. latitudo*, and there can be little doubt that these are sister species. *Bursa natalensis* differs from *B. latitudo* in its smaller maximum size (*B. latitudo* reaches ca. 105 mm in height, whereas *B. natalensis* reaches 95 mm but rarely exceeds ca. 80 mm) and in its consistently, markedly narrower shape. The two have a similar range of sculptural variation. Both species have at least 3 or 4 rows of small granules on interstitial spiral cords between the two major cords, and similar finely granulose sculpture over the rest of the shell surface. They also both lack an obvious intritacal, having a very thin, rarely preserved periostracum which, on a few very fresh shells, bears short, thin, pliable bristles on protected parts of the shell. Specimens are illustrated excellently in color on a recent web page (<http://www.femorale.com.br/shellphotos>, last accessed 28 April 2006).

The excellent lots of unusually large specimens loaned and presented to me by Dominique Lamy (Guadeloupe) (40 specimens from Racket Bank, 3 from Saba Bank, 3 from off of Îlot Pidgeon, all in the West Indies) demonstrate that *Bursa natalensis* is extremely similar to *B. latitudo* in all characters other than width and spire height, but a scatter diagram comparing dimensions of Pacific and western Atlantic specimens (Text-fig. 7) shows that they scarcely overlap at all in shape. The greatest factor in the variation in width is the size of the peripheral nodules; both species vary from very coarsely sculptured, with only 6 or 7 large, pointed nodules at the periphery in the last intervariceal interval, to very finely sculptured, with 10 or more very small, closely spaced nodules at the periphery in the last intervariceal interval, or even to having no nodules at all on the last whorl or two of a few specimens. The specimens that overlap in Text-fig. 7 are the most coarsely sculptured ones of *B. natalensis* and the most weakly sculptured ones of *B. latitudo*. There can be little doubt that these are very closely related species. Their close similarity suggests that *B. natalensis* evolved from a former population of *B. latitudo* that became isolated in the Atlantic, presumably through subdivision of a formerly larger population by closure of the CAI. It is now clear that *B. latitudo* occurs widely in the eastern West Pacific, among the island groups of eastern French Polynesia (Beu, in prep.) and so an apparent former distribution in the eastern Pacific seems not to have left a fossil record, presumably because of the offshore hard substratum inhabited by this species group. The close similarity in shape of *B. natalensis* to *B. ranelloides* in the scatter diagram (Text-fig. 7) suggests that the change in shape might have been driven by competition with *B. ranelloides*, which occurs in the Atlantic but not in the



Text-fig. 7. Scatter diagram comparing proportions of *Bursa natalensis*, *B. latitudo*, and *B. ranelloides*; overlap area of *B. natalensis* and *B. latitudo* is shaded.

western Pacific (other than rarely in Hawaii and commonly in southern Japan-Taiwan).

The partly sympatric species *Bursa ranelloides* differs from *B. natalensis* in its smaller average size (*B. ranelloides* rarely exceeds 65 mm in height, although the largest specimen seen, from Guadeloupe, is 109.7 mm high, larger than all specimens that I have seen of *B. natalensis*), in being markedly shorter and wider, in the majority of specimens having small nodules at the periphery (large nodules are present in about 20-30% of specimens of *B. ranelloides*, compared with about 70-80% of specimens of *B. natalensis*), in the peripheral nodules of large-noduled specimens being evenly rounded, rather than sharply pointed as in *B. natalensis*, in the numerous, closely spaced rows of gemmules on the surface being low and rounded, rather than taller, more widely spaced, and more sharply defined as in *B. natalensis*, in having a more narrowly flared outer lip flange with shorter transverse ridges, in having markedly shorter and less prominent transverse ridges on the inner lip, in having a paler, more yellow-brown exterior with more clearly axially aligned color bands than in *B. natalensis*, in which the exterior is a darker red-brown and the darker bands are more consistently arranged between nodules on the spiral cords, in the anterior siphonal canal being shorter and more strongly twisted to the right (in apertural view), in the aperture being consistently white, rather than pale mauve on

the interior and, in a few specimens, pale mauve on the outer lip in *B. natalensis*, and in bearing an obvious, thin, very finely reticulate, silky-looking intritacalx on unabraded specimens, whereas *B. natalensis* does not have an intritacalx. The fine, close spiral lirae covering the entire exterior remain on the one definite fossil specimen (a small spire) of *B. natalensis* that I have examined, and it clearly lacks the equally fine and closely spaced axial threads of *B. ranelloides*, leaving no doubt of the identification.

McGinty (1962: 39) clearly intended to provide a name for *Bursa natalensis* when he named *B. finlayi*, because his figured paratype is a specimen of *B. natalensis*. Unfortunately, McGinty (1962) selected a short specimen as the holotype of *B. finlayi*, and examination of this specimen (USNM 634570) showed that it is a specimen of *B. ranelloides* with moderately large nodules, intermediate between the extreme *ranelloides* and *tenuisculpta* forms. Laursen (1981: 30, pl. 3, fig. 2) continued the usage of the name *B. finlayi* for this species in his monograph of North Atlantic gastropod planktonic larvae. He provided excellent SEM pictures of the larval shells of *B. corrugata*, *B. granularis*, and *B. natalensis*.

Dimensions.—Figured paratype of *Bursa finlayi*, Bay of Matanzas, Cuba, ANSP 304276: H 76.7, D 39.6; paratype of *B. finlayi*, Bay of Matanzas, C. J. Finlay collection (now at FAU): H 81.6, D 41.8 mm; Bahia de Anasco, Puerto Rico, C. J. Finlay collection (now at FAU): H 89.0, D 43.2 mm; off S shore of Bermuda, DMNH: H 91.3, D 45.7 mm; largest seen, collection of D. Lamy, Guadeloupe, from 120-180 m, Raket Bank, off of St. Barthelemy, Lesser Antilles: H 94.3, D 47.5 mm.

Types.—*Bursa (Colubrellina) natalensis*, holotype MNRJ 3527; one paratype in Laboratorio de Ciencias do Mar, Universidade Federal do Ceará, Brazil, no. 462; one paratype in Museu Oceanografico de Rio Grande, Rio Grande do Sul, Brazil, no. 14731 (Coelho & Matthews, 1970: 4); all from lobster traps in 40-50 m, off of Natal, Rio Grande do Norte, Brazil (none seen). *Bursa finlayi*, holotype USNM 634570, *Triton* sta. 615, dredged off of Sombrero Key Light, Florida Keys, "on the rocky Pourtales Plateau" in 210 m (McGinty, 1962: 39, pl. 3, fig. 2), a specimen of *B. ranelloides* (Reeve, 1844); all paratypes are *B. natalensis*: 3 paratypes in McGinty collection from off of Sand Key Light, Key West, Florida, in 128-137 m (not seen); paratype in McGinty collection from fish traps in 180-200 m, off of Gibara, Oriente Province, Cuba (not seen); paratypes from the same station in collection of C. J. Finlay (now at FAU), and one in USNM.

Other material examined.—**Recent: E Atlantic: Madeira(?):** A single moderately large, very tall and narrow specimen of *Bursa natalensis* is present in Dautzenberg's collection (IRSNB), labeled "Pr. Alice stn. 1242, 240 m, 10 Sept. 1901, Banc de la Seine, Madeira" (*i.e.*, the locality of 6 of the 7 syn-

types of *B. ranelloides* var. *tenuisculpta*), among Dautzenberg's material identified as *B. ranelloides* var. *tenuisculpta*. However, it seems likely that this specimen has been accidentally exchanged with another western Atlantic specimen in the same drawer; a specimen of *B. ranelloides* var. *tenuisculpta* labeled "Martinique, coll. Crosse" lies in the box alongside the specimen of *B. natalensis*, both specimens are unnumbered, and it seems likely that the specimens in the two boxes have been mixed. This is the sole specimen of which I am aware supposedly originating from the eastern Atlantic. **W Atlantic:** **Bermuda:** 300 m, crab pots, 4 km off S shore of Bermuda (DMNH, 3). **Florida:** shrimp boats off of Marquesas Key (AMNH 162793, 2). **Cuba:** off of Habana, 250 m, *Blake* sta. 14 (MCZ 202065, 1); Bay of Matanzas, crab trap (ANSP 304276, 1, the paratype of *B. finlayi* figured by McGinty, 1962: pl. 3, figs 1, 1a); Bay of Matanzas, fish traps in 240 m, C. J. Finlay collection (now at FAU; 1, paratype of *B. finlayi*); off of Gibara, Oriente, fish traps, 180-200 m, C. J. Finlay collection (now at FAU, 1); Bay of Matanzas, fish trap in 240 m (USNM 673601, 1; paratype of *B. finlayi*). **Puerto Rico:** fish trap, 200 m, Bahia de Anasco (MCZ, 1); 240 m, fish traps, Bahia de Anasco (AMNH 190485, 2); fish traps in 180 m, Bahia de Anasco, 1971, C. J. Finlay collection (now at FAU, 3). **Nevis, British West Indies:** WSW of Charlestown, shell trap set in 250 m, Bredin-Smithsonian Expedition (USNM 735915, 1). **Guadeloupe:** 120-180 m, Racket Bank, off of St. Barthelemy Island, collection of D. Lamy (40); 150-200 m, Saba Bank, collection of D. Lamy (2); côte sous le Vent, Îlot Pidgeon, collection of D. Lamy (3); fishermen's traps, 300 m, off of Îlot Pidgeon, D. Lamy (GNS WM17174, 16); 200 m, off of St. Barthelemy Island, D. Lamy (GNS WM17178, 12; WM17390, 1); 180 m, Saba Bank, D. Lamy (GNS WM16996, 2); 120-180 m, off of Racket Bank, D. Lamy (GNS WM16987, 4); 250 m, Racket Bank, D. Lamy (GNS WM17013, 7); 500 m, off of Pointe Noire (GNS WM17169, 1); 250 m, off of Vieux Habitants, D. Lamy (GNS WM17179, 1); 500 m, off of Basse Terre, D. Lamy (GNS WM17155, 1). **Martinique:** 80-90 m, traps off of Martinique, *M/V Le François* (GNS WM15381, 2). **Barbados:** *Diadema* sta. 130, off of Paynes Bay, St. James, 180 m, 1961, C. J. Finlay collection (now at FAU, 1); Sandy Lane Bay, W coast, crab trap, 200 m (ZMA, 1); 210 m, off W coast of Barbados (GNS WM15213, 2).

Fossils: Atlantic Costa Rica: Latest Pliocene-Early Pleistocene, Moín Fm (crosses the Pliocene-Pleistocene boundary; McNeill *et al.*, 2000): TU 1240 (GNS WM18853, 1 spire). Robinson (1991) recorded another specimen from Limón (in TU 1239) that I have not seen and that probably belongs here, identified as *B. granularis* following correspondence with me.

Distribution.—*Bursa natalensis* lives now in the western

Atlantic, from southern Florida, USA, to Bahia, Brazil, in relatively deep water (*ca.* 100-500 m). Most material that I have seen is from the Lesser Antilles, particularly near Guadeloupe. Paulmier (1994: 9, fig. 23) illustrated a specimen, and reported *B. natalensis* from depths of 125-380 m off of the French Antilles, Caribbean. I am aware of only the one fossil specimen (and a possible second specimen) of *B. natalensis*, recorded above from Limón, Costa Rica.

***Bursa ranelloides* (Reeve, 1844)**

Pl. 4, Figs 1-9; Pl. 5, Figs 1-4, 6, 8

- Triton ranelloides* Reeve, 1844a: pl. 3, fig. 10; Reeve, 1844c: 111.
Simulium papillosum A. Adams, 1870: 49; Beu, 1971: 110, pl. 8, fig. 8.
Lotorium ranelloides. G. B. Sowerby III, 1902: 95.
Bursa (Lampas) ranelloides var. *tenuisculpta* Dautzenberg & Fischer, 1906: 36, pl. 2, figs 15-18.
Bufonariella ranelloides. Oyama & Takemura, 1960: pl. *Colubrellina-Bufonariella*, figs 8-11; Habe, 1961: 47, pl. 24, fig. 3; 1964: 76, pl. 24, fig. 3; Beu, 1971: 110, pl. 8, fig. 8; Kuroda *et al.*, 1971: 203, pl. 33, figs 5-6.
Bursa finlayi McGinty, 1962: 39, pl. 3, fig. 2 (in part; holotype only).
Tritonoranella ranelloides. Oyama, 1964: 332.
Bursa (Colubrinella) (sic) canarica Nordsieck, 1975: 4, fig. 16.
Bursa (Colubrellina) benvegnuae Penna-Neme & Leme, 1978: 285, figs 25-26.
Bursa ranelloides. Finlay, 1978: 148; Gofas & Beu, 2002: 102, figs 8A-J; Beu, 1998b: figs 49f-g; Zhang & Ma, 2004: 180, text-fig. 112, pl. 4, fig. 8.
Bursa (Colubrellina) tenuisculpta. Abbott, 1974: 166, fig. 1778; Penna-Neme & Leme, 1978: 284, figs 1-10, 24, 27.
Bursa pygmaea Kosuge, 1979: 31, pl. 5, fig. 5, pl. 6, fig. 23.
Bursa (Bufonariella) ranelloides ranelloides. Beu, 1981: 290, figs 18d, f-i.
Bursa (Bufonariella) ranelloides tenuisculpta. Beu, 1981: 292, figs 19a-k.
Bursa (Colubrellina) ranelloides ranelloides. Beu, 1985: 64.
Bursa (Colubrellina) ranelloides tenuisculpta. Beu, 1985: 64; Rios, 1985: 79, pl. 28, fig. 349; 1994: 92, pl. 31, fig. 366.
Bursa (Colubrellina) ranelloides benvegnuae. Rios, 1985: 79, pl. 28, fig. 348.
Bursa ranelloides tenuisculpta. Paulmier, 1994: 9, fig. 24; Ardovini & Cossignani, 2004: 132, central right and lower left figs.
Bursa (Colubrellina) ranelloides and formae *tenuisculpta* and *benvegnuae*. Cossignani, 1994: 86-87.
Bursa ranelloides benvegnuae. Coltro, 1995: 52, fig. 4.
Bursa (Tritonoranella) ranelloides. Okutani, 2000: 269, pl. 133, fig. 3; Higo *et al.*, 2001: pl. 49, fig. G1622.

Remarks.—*Bursa ranelloides* is one of the most commonly dredged *Bursa* species (in *ca.* 80-500 m, reaching as deep as at least 1,250 m) in both the eastern and western Atlantic, as well as off of Japan and Taiwan. It is therefore rather surprising to

find that it has almost no fossil record in the area studied here. The species is easily recognized by varices that, unlike those of most other *Bursa* species, are not aligned up opposing sides of the shell, but are situated at each 240° around the spiral, as in the Ranellidae Cymatiinae, combined with a red to dark brown parietal color patch in the inner lip, with an obvious, thin, white to pale gray, finely reticulate intritacalx on fresh shells, giving them a silky sheen, with relatively small average size (reaching 110 mm, but rarely exceeding 65 mm H), and with sculpture resembling that of *B. natalensis*, but with more rounded nodules and with lower and more rounded granules between the major spiral cords. Other differences from *B. natalensis* are listed above.

Bursa ranelloides exhibits a great range of variation in the size and number of the nodules on the two whorl angulations throughout its geographical range, so that samples consisting of relatively few specimens have been considered by numerous authors over the years to be species distinct from *B. ranelloides*. This is particularly so in the western Atlantic, where most authors have considered the variety *tenuisculpta* to be a species distinct from *B. ranelloides*, even though Finlay (1978: 148) recognized some specimens in the western Atlantic that conform to the “typical *ranelloides*” form, until then supposedly limited to Japan. *Bursa canarica* and *B. benvegnuae* were proposed for specimens intermediate between the *ranelloides* and *tenuisculpta* sculptural extremes. It is clear, though, that Dautzenberg & Fischer (1906: 36) appreciated that their new variety was merely an infrasubspecific sculptural variant, because they illustrated Japanese shells that they considered to fall into both their variety *tenuisculpta* and “specimens intermediate between the type and the var. *tenuisculpta*.” Examination of numerous specimens from the western Atlantic and the collection of Indian Ocean specimens that fill the apparent range gap between the previously known Japanese and South African populations (Beu, 1998b: 161, reporting specimens dredged off of Réunion Island and the Comores Islands by MNHN, Paris) have shown that (a) the same variation in sculpture is present throughout the range, and (b) this is a single, widespread, highly variable species. Part of the apparent difference in the range of sculptural variation between the Japanese and Atlantic populations probably results from many of the Japanese specimens having been collected in shallower water than the Atlantic, South African, or Indian Ocean ones, because this species appears to follow the usual tendency of ranellids and bursids to be progressively taller, narrower, more finely sculptured, and paler in color in progressively deeper water. However, the excellent range of large, beautiful specimens from Guadeloupe, West Indies, loaned to me by Dominique Lamy, shows that specimens with few, large, strongly rounded nodules at the periphery, identical to Japanese ones, are common in some areas in the

western Atlantic.

As is also noted above for *Bursa corrugata*, some European Miocene fossil specimens resemble *B. ranelloides* so closely that specific distinctions are not obvious. The specimens from the Vienna Basin described as *Ranella (Lampas) austriaca* by Hoernes & Auinger (1879: 186, pl. 23, figs 10-12) were not present in the collections that I examined at NHMV in 1998, but one specimen (NHMV 1894/24/37, from Vosgau, Vienna Basin) was examined that was identified as “*Ranella scrobiculata* Kiener,” the name that Hoernes & Auinger (1879) said that they were replacing with the new name *R. austriaca*. This specimen appeared to be a normal specimen of the finely sculptured form of *Bursa ranelloides* that is so common in Recent deep-water populations. Cossmann & Peyrot (1924: 312, pl. 16, figs 16-17) named and illustrated an exceedingly similar but slightly narrower shell from Miocene rocks of the Aquitaine Basin, southwestern France, under the name “*Bursa lessonae* race *occidentalis*.” These occurrences suggest that several of the *Bursa* species that are widespread in the Indo-West Pacific and Atlantic at present, such as *B. granularis* and *B. ranelloides*, had their origins in the Tethys and Paratethys seaways (see maps and dates by Rögl, 1998), along with some *Monoplex* species such as *M. corrugatus*.

Bursa pygmaea appears to be another synonym of *B. ranelloides*. The shape, sculpture and widely separated varices (situated at each 240°) are identical to those of *B. ranelloides*, and Kosuge (1979) described the “fine, linen-like sculpture,” i.e., the finely cancellate intritacalx. The type locality is “off Midway Island [the northernmost island of the Hawaiian chain] at the depth of 380 m,” and at first I was inclined to doubt the validity of this locality. The locality “Midway” is misinformation that has been applied to several other mollusks by Japanese fishermen to disguise their sources, and it seemed possible that the type material actually was collected in southern Japan. The case would then parallel that of *Nesiocypraea midwayensis* Azuma & Kurohara, 1967; Okutani (1975: 191) reported a specimen from Kurose Bank, off of Hachijo Island, southeastern Japan. He pointed out that doubts previously had been expressed about its type locality, and suggested that the holotype came from submarine banks off of southern Japan, rather than from Midway Island. A similar case is “*Fusitriton*” (actually *Sassia*) *midwayensis* Habe & Kosuge, 1968, supposedly from Midway, but since recollected around Taiwan (Lai & Ou-Yang, 1999; Zhang & Ma, 2004: 94, pl. 2, fig. 8). However, Robert Moffitt (Honolulu Laboratory, U.S. National Marine Fisheries Service; pers. comm., August 2003) reported that the Hawaiian Biological Survey has collected further material of *B. ranelloides* around Hawaii. The type material of *B. pygmaea* was collected during an oceanographic expedition by *R/V Kaiyomaru*; material has been collected again around the Hawaiian Islands, and the

Midway locality evidently is correct.

Dimensions.—*Triton ranelloides*, holotype: H 49.6, D 32.2 mm; *Simpulum papillosum*, holotype: H 40.3, D 25.1 mm; *Bursa pygmaea*, holotype: H 26.2, D 15.8 mm (Kosuge, 1979); Seamount 1 cruise, sta. CP79, Seine Banc, near Madeira, eastern Atlantic: H 61.1, D 34.1 mm; AMNH 190483, off of Key West, Florida: H 71.6, D 40.1 mm; H 66.3, D 38.4 mm; H 55.7, D 31.9 mm; H 53.3, D 31.2 mm; AMNH 190484, off of Key West, Florida: H 66.2, D 36.0 mm; DMNH, off of Gurnet Rock, S shore of Bermuda: H 75.5, D 40.8 mm; H 74.3, D 37.5 mm; USNM 417773, off of Key West, Florida: H 77.2, D 38.1 mm; figured specimen, NMB H 17892, from NMB 17830, Cayo Agua, Panama (Pliocene): H 33.8, D 22.5 mm; largest seen, from Raket Bank, off of St. Barthelemy Island, Guadeloupe: H 109.7, D 53.8 mm (an almost completely smooth specimen of the *tenuisculpta* form); next largest, same locality, coarsely nodulose: H 93 (incomplete), D 48 mm (incomplete); next largest, same locality, coarsely nodulose: H 85.9, D 49.4 mm.

Types.—*Triton ranelloides*, holotype BMNH 1967594, labelled "Philippines." This locality evidently is yet another incorrect Hugh Cuming label, because *B. ranelloides* has not been recollected from the Philippine Islands, and the holotype appears to have been abraded on a beach; it is almost certainly from southern Japan. The type locality is here designated as Sagami Bay, Honshu, Japan. *Simpulum papillosum*, holotype (Pl. 5, Figs 1, 4; figured also by Beu, 1971: pl. 8, fig. 8) BMNH 1967680, from "Takano-Sima," Japan. *Bursa (Lampas) ranelloides* var. *tenuisculpta*, 7 presumed syntypes, most not seen, from: (1) sta. 899 (1897 expedition), 200 m, Princess Alice Bank, Azores Islands, North Atlantic, one alive; and (2) sta. 1242 (1901 expedition), 240 m, Seine Bank, Madeira, northern Atlantic, 6 empty shells. Dautzenberg's collection in IRSNB contains several specimens identified as "*Ranella ranelloides* var. *tenuisculpta*": (1) Martinique, West Indies, coll. Crosse (one, very finely sculptured but as noted above, seems likely to have been muddled with the neighbouring specimen of *B. natalensis*, supposedly from *Princesse Alice* sta. 1242, Seine Banc, near Madeira); (2) sta. 2034, 26 July 1905, 185 m, "pres. Monaco Inst." (one, *i.e.*, possibly one of the syntypes of *R. ranelloides* var. *tenuisculpta*). Another specimen bears identical data to no. (1) here, but bears very fine peripheral nodules and is labeled only as "*Ranella ranelloides* Reeve." It therefore appears that (a) Dautzenberg & Fischer's (1906) varietal name was intended to apply only to *exceedingly* finely sculptured specimens, with no peripheral nodules whatsoever, and (b) most or all of the syntypes illustrated by Dautzenberg & Fischer (1906) are in the Musée Oceanographique, Monaco; two syntypes in MNHN, from *Princesse Alice* sta. 1242, Seine Bank, Madeira, 240 m, 10 September 1901, *ex* collection H. Fischer. *Bursa finlayi*, holotype USNM 634570, *Triton* sta.

615, dredged on Pourtales Plateau off of Sombrero Key Light, Florida Keys, in 210 m, by T. L. McGinty, 8 July 1951; 3 paratypes in T. L. McGinty collection, dredged off of Sand Key Light, Florida, in 130-137 m; further paratypes from fish traps off of Gibara, Oriente Province, Cuba, collected by C. J. Finlay, and from Matanzas Bay, Cuba, collected by C. J. Finlay, in USNM, collections of T. L. McGinty and of C. J. Finlay (now at FAU) (but all except the holotype are specimens of *B. natalensis*). *Bursa (Colubrinella) (sic) canarica*, holotype (not seen) originally in Nordsieck collection, no. 67.02, from "Gran Canaria" (Nordsieck, 1975: 4), present location not known to me. *Bursa (Colubrellina) benvegnuae*, holotype (not seen) in Museu de Zoologia, Universidade de São Paulo, Brazil, MZUSP no. 18477, from W. Besnard sta. 444, off of Mostardas, Rio Grande do Sul, Brazil, 31°31'S, 49°47'W; 2 paratypes from the same station MZUSP 18478. *Bursa pygmaea*, holotype (not seen) in the Institute of Malacology of Tokyo (Kosuge, 1979), from Midway, Hawaiian Islands (discussed above).

Other material examined.—**Recent:** South African, Indian Ocean, and Japanese material not listed here. **E Atlantic:** 42 lots at MNHN, largely from the Seamount cruises 1 & 2, material listed and illustrated by Gofas & Beu (2002), from Canary Islands, Azores Islands, Lusitanian Seamounts, Meteor Bank, Hyères Bank, Irving Bank, Plato Bank, Atlantis Bank; La Palma, Canary Islands (GNS, 2 lots). **W Atlantic:** 60 lots, at AMNH, ANSP, DMNH, GNS, LACM, MCZ, USNM, C. J. Finlay collection (now at FAU), and D. Lamy collection (the USNM Florida material is largely from J. B. Henderson's *Eolis* stations, which were discussed, with a web address for more accurate stations, by Bieler & Mikkelsen, 2003); from Bermuda, Florida, E Mexico, Cuba, Puerto Rico, and Antillean islands (Virgin Islands, Martinique, Guadeloupe).

Fossils: **Trinidad:** **Middle Miocene(?)**: USGS 19865, Trinity Hill Sandstone member of Moruga Fm (USNM, 2). **Atlantic Panama:** **Pliocene:** NMB 17830, Cayo Agua Fm, E coast Cayo Agua, small island 1.3 km SE of Punta de Tiburón, Bocas del Toro Basin (NMB H 17892, 1, Pl. 5, Fig. 8).

Distribution.—*Bursa ranelloides* is moderately common in offshore (particularly rocky) habitats in the eastern and western Atlantic. In the western Atlantic, it is recorded from Bermuda and southern Florida (where it seems to be quite common), USA, south to "northeast Brazil" (Rios, 1994: 92). Paulmier (1994: 9, fig. 24) illustrated a specimen from 320 m, off of Martinique, West Indies. Its range is poorly documented in the central and eastern Atlantic, but it is recorded from at least the Azores (Gofas & Beu, 2002), Madeira, and the Cape Verde Islands and on many of the offshore banks, and presumably occurs much more widely than this in depths of 100 m to more than 1,200 m. However, no specimens have been collected from close to the African mainland. An inter-

esting record is from Vema Seamount, east of Walvis Ridge, SE Atlantic (NMP D.4374, 1). In South Africa, it is recorded from 168 m, 13 km WNW of Scottsburgh Lighthouse, Natal (G. B. Sowerby III, 1902: 95) and 46 lots have been examined at NMP, ranging from the Transkei coast (southwesternmost: NMP C.1176, *R/V Meiring Naudé* sta. D2, off of Port Grosvenor, 120-128 m, 39°57'9"S, 31°25'9"E, 1 specimen) to northern Zululand (northeasternmost: NMP D.8368, *R/V Meiring Naudé* sta. ZA16, SE of Kosi River mouth, 200 m, 26°54.6'S, 32°58.6'E, 1 specimen). There it is part of the northern, warm-water fauna, the tail of the Indian Ocean fauna rather than the cool-water endemic South African fauna, indicating that it ranges farther northeastward into the western Indian Ocean; NMP sampling ceased at the Mozambique border. In the Indian Ocean, it is recorded from six samples taken in 80-340 m off of Réunion Island and from *Benthesi* sta. 49, 300-450 m, W of Passe Boueni, off of Mayotte, Comores Islands (Beu, 1998b: 161; material in MNHN). It will presumably be found to occur much more widely in the western Indian Ocean once more extensive deep-water sampling has been carried out. In Japan, *B. ranelloides* is a well known shell in relatively shallow water, from Boso Peninsula southward (Kuroda *et al.*, 1971: 134); Okutani (2000: 269) recorded that in Japan, specimens occur from the "intertidal zone down to 200 m deep," whereas it is definitely an outer shelf and upper bathyal species throughout the rest of its range. Kuroda *et al.* (1971: 134, as *Bufonariella ranelloides*) recorded specimens dredged in Sagami Bay, Honshu (its northern limit, Boso Peninsula, forms the northern margin of Sagami Bay), at five localities in 65-87 m. Specimens were recorded also from Taiwan by Lai (1987: 20, fig. 3, as *Tutufa ranelloides*), and material in MNHN was dredged recently off of eastern and northeastern Taiwan (25 specimens at nine stations, in 221-532 m). No fossil or Recent material is recorded from the eastern Pacific, but fossils are recorded from a few Miocene and Pliocene localities in the western Atlantic. This distribution pattern is unique for a tonnoidean, as far as I am aware. I know of no authentic records from the Philippine Islands (despite the original locality data for the holotype of *Triton ranelloides*) or from the northwestern Pacific area between Taiwan and the northern Indian Ocean. The Japanese and Hawaiian populations evidently are isolated from the Indian Ocean to the Atlantic, suggesting that the occurrences in Japan-Taiwan and Hawaii are relict from a formerly wider distribution in the Pacific. Fossil specimens have been reported previously from the Pliocene Shinzato Fm of Okinawa, Japan, (Ogasawara, 2002: 328) and the late Middle Pleistocene (oxygen isotope stage 5e) Ryukyu Limestone of Kikaijima, Ryukyu Islands, southern Japan (Ogasawara, 2002: 329), but the only others known to me are those listed here.

Bursa rhodostoma (G. B. Sowerby II, 1835)

Pl. 5, Figs 5, 7, 10-12, 15

- Ranella rhodostoma* G. B. Sowerby II, 1835: pl. 88, fig. 10; 1841b: 52; Deshayes, 1843: 552; Reeve, 1844b: pl. 7, fig. 32; Chenu, 1859: 155, fig. 712; Küster & Kobelt, 1871: 155, pl. 34a, fig. 11.
- Ranella thomae* d'Orbigny, 1841a: 250, pl. 23, figs 23-24; Krebs, 1864: 25; Mörch, 1877: 24; E. A. Smith, 1890b: 269.
- Ranella venustula* Reeve, 1844b: pl. 7, fig. 37; 1844d: 138; Angas, 1877: 180.
- Ranella paulucciana* Tapparone-Canefri, 1876b: 244; 1881: 51, pl. 2, figs 16-17.
- Ranella rhodostoma* var. *xantostoma* Tapparone-Canefri, 1878: 249.
- Ranella (Lampas) cruentata* var. *rhodostoma*. Tryon, 1880: 40, pl. 21, fig. 25.
- Ranella bergeri* "Sowerby." Tapparone-Canefri, 1881: 50, pl. 2, fig. 1, 2.
- Ranella (Lampas) thomae*. Watson, 1886: 400; Gregory, 1895: 288.
- Gyrineum cruentatum*. Dall & Simpson, 1901: 416 (not *Ranella cruentata* G. B. Sowerby II, 1835).
- Bursa mammata*. Hedley, 1915: 28; Iredale, 1931: 212; Iredale & McMichael, 1962: 55 (not *Bursa mammata* Röding, 1798, = *Murex bufonius* Gmelin, 1791).
- Ranella (Lampadopsis)* cf. *thomae*. Trechmann, 1930: 208, pl. 12, fig. 18.
- Ranella (Bursa) thomae*. Trechmann, 1933: 39.
- Bursa (Bursa) thomae*. Morrison, 1949: 11; Abbott, 1954: 197; Rios, 1975: 81, pl. 22, fig. 329.
- Lampadopsis rhodostoma*. Habe, 1961: 47, pl. 24, fig. 1; Oyama & Takemura, 1963: *Lampadopsis* plate, figs 1-2; Habe, 1964: 75, pl. 24, fig. 1; Okutani, 1986: 116-117, top center fig.
- Bursa thomae*. McGinty, 1962: 40; Warmke & Abbott, 1962: 103, pl. 18j; Humfrey, 1975: 126, pl. 14, figs 5, 5a; Finlay, 1978: 149; Bandel, 1984: 101, fig. 162, pl. 10, fig. 4; de Jong & Coomans, 1988: 70; Diaz & Götting, 1988: 156; Leal, 1991: 112; Lipe & Abbott, 1991: 14-15, illus.; Diaz & Puyana, 1994: 174, fig. 652.
- Bursa (Bursa)* aff. *thomae*. Jung, 1969: 486, pl. 49, figs 1-2; Rios, 1970: 74.
- Bursa (Bursa) thomae*. Matthews & Coelho, 1971: 4, figs 6-7; Coelho & Matthews, 1971: 47, figs 1-3.
- Bursa (Lampasopsis) thomae*. Abbott, 1974: 166, pl. 7, fig. 1777.
- Bursa rhodostoma*. Salvat & Rives, 1975: 307, fig. 181; Hinton, 1978: 32, figs 5, 5a; Kay, 1979: 229, figs 80C-D; Garcia-Talavera, 1983: 33, 135; Drivas & Jay, 1988: 60, pl. 15, fig. 9; Lai, 1989: 21, fig. 4; Wilson, 1993: 227, pl. 43, fig. 5; Kubo in Kubo & Kurozumi, 1995: 78, fig. 5; Beu, 1998b: 163, fig. 47g, 52h, k, 58e; Zhang & Ma, 2004: 176, text-fig. 109.
- Bursa (Lampasopsis) rhodostoma*. Nordsieck & Garcia-Talavera, 1979: 126, pl. 28, fig. 2.
- Bursa (Bursa) rhodostoma rhodostoma*. Beu, 1985: 63; Cossignani, 1994: 56.
- Bursa (Bursa) rhodostoma thomae*. Beu, 1985: 63; Rios, 1985: 79 (not pl. 28, fig. 344, = *B. grayana*); Cossignani, 1994: 57; Rios, 1994: 92 (not pl. 30, fig. 362, = *B. grayana*); Guerreiro & Reiner,

2000: 119-120; Redfern, 2001: 57, pl. 29, figs 245A-B, pl. 109, fig. 245C.

Bursa (Bursa) rhodostoma. Springsteen & Leobrera, 1986: 124, pl. 34, fig. 9.

Bursa bergeri. Drivas & Jay, 1988: 60, pl. 15, fig. 8.

Bursa venustula. Drivas & Jay, 1988: 60, pl. 15, fig. 10.

Bursa (Bursa) venustula. Cossignani, 1994: 62, illus.

Bursa (Ranella) rhodostoma. Okutani, 2000: 269, pl. 133, fig. 4.

Bursa rhodostoma thomae. Ardovini & Cossignani, 2004: 132, 2 lower right figs, 133, upper left fig.

Remarks.—*Bursa rhodostoma* is easily recognized by being the smallest species of Bursidae in the region studied here (rarely reaching 50 mm H, although most specimens do not exceed 30 mm), by its white (in a few specimens) to purple, lavender, or deep red aperture (rather than consistently white as in the similar species *B. grayana*), by its less obviously coarse and nodulose sculpture than in *B. grayana*, by its siphonal fasciole being less prominent (less strongly curved to the left) than in *B. grayana*, by lacking the short radial ridges around the top of the sutural ramp that are consistently present in *B. grayana*, and by most specimens having short posterior canals that do not protrude beyond the varices, as they do consistently in *B. grayana*.

Bursa rhodostoma is highly variable in apertural color (from white, in a few specimens, through mauve to deep purple and deep red), in the prominence of the apertural ridges and nodules, in the prominence of the external sculpture, and in the external coloration. Most specimens are encrusted with coralline algae; unencrusted specimens range from plain white through weakly spotted with pale brown on and/or between the spiral cords, to a pale brown background with many dark brown spots or streaks on and between the spiral cords. The various forms have received several names, but are all part of a single variable species (Beu, 1998b). I have not previously included *Ranella venustula* in the synonymy of *B. rhodostoma*, because this is based on a rather distinctive form (types illustrated by Cossignani, 1994: 62) from eastern French Polynesia with a reddish purple aperture, and it has always seemed that it might turn out to be a distinct species. However, the extensive, carefully, and systematically collected faunas of eastern French Polynesian island groups now available in MNHN (tonnoideans being surveyed by me, in prep.) demonstrate that a separate eastern Polynesian species does not exist; *B. venustula* is merely a further form in the range of variation of *B. rhodostoma*.

I treated (Beu, 1998b: 163) the Atlantic and Pacific forms of *Bursa rhodostoma* as geographical subspecies, although morphological differences were not detected, and the only difference between them is the lower incidence of specimens with red or dark purple apertures in the Atlantic than in the Pacific populations, i.e., most Atlantic shells have a pale mauve aper-

ture, whereas this color form occurs in only about a third of Pacific specimens. This character was considered also by Leal (1991: 112) to separate these forms as full species. However, because specimens from both the Pacific and Atlantic populations seem to show a similarly wide range of variation in adult size, in teleoconch sculpture and external color, and in apertural armature (low nodules to quite prominent teeth inside the outer lip), and because Nordsieck & Garcia-Talavera (1979: 126, pl. 28, fig. 2) have illustrated an eastern Atlantic specimen with a red aperture, the differences between the Atlantic and Pacific populations now seem so trivial as not to separate discrete taxa. I regard this as one widespread, highly variable species of *Bursa*. Again, the Atlantic population seems merely to have lower genetic variation than the Indo-West Pacific one, possibly as the result of an initial appearance in the Atlantic of a spat-fall of very few specimens.

Such points of taxonomic decision are, of course, critical to the conclusions reached about biogeographical relationships. The taxonomy will only be certain after molecular studies, but the decision comes down to one question: can the fossil shells be distinguished? In this case they certainly cannot, and I am satisfied that the named forms all belong to a single species, living in both the Atlantic and Indo-West Pacific Oceans, and kept in genetic continuity by transport of occasional larvae around South Africa in the Agulhas leakage.

Dimensions.—*Ranella rhodostoma*, lectotype: H 22.0, D 16.2 mm; paralectotype: H 28.4, D 20.2 mm; *R. thomae*, holotype: H 18.4, D 14.1 mm; Recent, Washerwoman Key, Florida, MCZ 250675: H 34.1, D 24.7 mm; Recent, 25 m, Pompano Beach, Florida, C. J. Finlay collection (now at FAU): H 39.3, D 27.3 mm; DMNH 96974, 4 km off S shore of Bermuda: H 40.0, D 28.7 mm; figured specimen, NMB H 17893, from NMB 19007 (TU 1239), Limón, Costa Rica: H 22.6, D 16.8 mm; figured specimen, NMB H 17894, from NMB 17516, Cantaura, Venezuela: H 27.7, D 20.9 mm.

Types.—*Ranella rhodostoma*, lectotype designated by me (Beu, 1998b: 165) BMNH 1966542/1, with 2 paralectotypes BMNH 1966542/2-3, from "Isl. Masbate, of the Philippines." *Ranella thomae*, holotype BMNH 1854.10.4.414, from "St. Thomas," West Indies. *Ranella venustula*, 3 syntypes BMNH 1966541, from "Lord Hood's Island" (South Marutea Island, Gambier Islands) (Cossignani, 1994: 62, syntypes illustrated). Type material of *R. bergeri*, of *R. paulucciana*, and of *R. rhodostoma* var. *xantostoma* not seen. Cossignani (1994: 57) reported that 15 specimens (presumably syntypes) of *Bursa bergeri* are present in Tapparone-Canefri's collection, in Museo Civico di Storia Naturale "Giacomo Doria," in Genoa, and the type material of the other two taxa named by Tapparone-Canefri is presumably in the same museum.

Other material examined.—Recent: **E Atlantic: Canary Islands:** Medano, Tenerife (DMNH 47525, 2); Santa Cruz,

Tenerife (BMNH 1887.2.9.1220, 2); Candelaria, Tenerife (TFMC 1566, 11); 3-10 m, Bahia del Puerto, La Palma (GNS WM14953, 2); 3 m, La Palma (GNS WM15190, 1); Los Christianos, Tenerife (GNS WM17407, 4). **Madeira:** [no further data] (BMNH 1911.10.26.11134-5, 2). **Cape Verde Islands:** beach, Baia Algodoeiro, Ilha Sal (MNHN, 3); beach, Mindelo, Baia Porto Grande, São Vicente (MNHN, 1); St. Vincent (USNM 253391, 3; BMNH 1959.10.12.72, 2); Îles du Cap Vert, coll. Petit de la Saussaye (MNHN, 1); Cape Verde Islands (MNHN, 1; BMNH, 6); Cap Vert (MNHN, 1); *Calypso* sta. 84, Sal, 19-22 m, 16°34.5'S, 22°52.5'W (MNHN, 2); *Calypso* sta. 83, Sal, 27-45 m, 16°34.6'S, 22°54.6'W (MNHN, 1); *Cancap-VI* sta. 6.174, Tydeman Cape Verde Islands Expedition 1982, 75 m, NW of São Vicente, 16°55'N, 25°02'W (RMNH, 1); 10 m, Mاتیota Bay, St. Vincent (GNS WM16694, 1), St. Vincent (GNS WM15191, 1); 12 m, scuba, Mاتیota Bay, St. Vincent, "always with blue sea urchin" (GNS WM13778, 1). **Central Atlantic Islands:** St. Helena (USNM 123969, 2; BMNH 1889.10.1.2416-20, 7); Ascension Island (LACM 55279, 2). **W Atlantic:** 113 lots, at ANSP, BMNH, DMNH, GNS, MCZ, RMNH, SMF, USNM, ZMA, Zoological Museum, University of Bologna, and C. J. Finlay collection (now at FAU); from Bermuda, Bahamas, Florida, Louisiana, E Mexico, Cuba, Dominican Republic, Puerto Rico, Jamaica, Cayman Islands, Antillean islands (St. John, St. Croix, St. Lucia, Dominica, Martinique), E Colombia, Aruba, Bonaire, Curaçao, Guiana (OCPS sta. H59, 49 m, off of Suriname, 7°08.5'N, 56°57.0'W; RMNH, 1).

Fossils: **Florida:** Late Early Miocene, Chipola Fm: TU 547, *ex* S. Hoerle collection (1, USNM). **Jamaica:** **Pleistocene:** Manchioneal beds, Navy Island, Port Antonio [BMNH Palaeontology Department, GG5358, 1, specimen figured by Trechman (1930: 208, pl. 12, fig. 18), *pres.* C. T. Trechman, 1936]. **Barbados:** **Pleistocene or Holocene?:** low-level reefs, Bishopscourt (BMNH Palaeontology Department, G10866, 2); post-coral rock, near Silversands [BMNH Palaeontology Department, G69042, 1, specimen listed by Trechman (1937: 355), *pres.* C. T. Trechman, 1938]. **Trinidad:** **Middle Miocene:** 400 m past Brasso River on road to Brasso (UCMP S-8137, 1). **Early Pliocene:** USGS 18634 (USNM, 1; specimen illustrated by Jung, 1969: pl. 49, fig. 1, 2); Springvale Fm, Claxton Bay exit from motorway, collection of Bernard Landau (1). **Atlantic Costa Rica:** **Latest Pliocene-Early Pleistocene,** Limón (McNeill *et al.*, 2000): USGS 2693 (USNM, 1); 21051 (USNM, 1); TU 1239 = NMB 19007 (NMB H 17893, 1, illustrated, Pl. 5, Fig. 15); basal Moín Fm mudstone (Late Pliocene), Rte. 32, 3 km W of Puerto Limón (BMNH Palaeontology Department, 1). Recorded also from the Moín Fm by Robinson (1991, 1993). **Venezuela:** Late Early Miocene, Cantaure Fm: NMB

17516, lower shellbed (NMB H 17894, 8; 1 illustrated, Pl. 5, Figs 10, 12); same locality (UCMP S-8360, 1); same locality, collection of Bernard Landau (11). **Pliocene:** USGS 24704, Cumaná Fm (USNM, 1).

Distribution.—*Bursa rhodostoma* lives today throughout the Indo-West Pacific Province, from Madagascar (and possibly eastern South Africa) to the northern Indian Ocean and the Red Sea, from southern Honshu, Japan, south to Sydney Harbour, New South Wales (where a specimen was collected alive at Bottle and Glass Rocks during the 19th century), and eastward throughout Melanesia and Polynesia to Hawaii (Beu, 1998b). In the western Atlantic, it ranges from South Carolina (Merrill & Petit, 1965: 63), USA, to Bahia, Brazil (Abbott, 1974; Coelho & Matthews, 1971), including Louisiana, USA, and from Fernando de Noronha and Martin Vas Islands and many seamounts off of Brazil (Rios, 1994: 92; Leal, 1991: 112). Matthews (1968) recorded specimens found commonly in the gut of the toadfish or "pacomon," *Amphichthys cryptocentrus*, caught off of Fortaleza, Ceará, Brazil. E. A. Smith (1890b) recorded it also from St. Helena, and specimens are listed above from St. Helena and Ascension Island. In the eastern Atlantic, it is recorded from Madeira, the Canary Islands, and the Cape Verde Islands (Nordsieck & Garcia-Talavera, 1979; and above). There are no fossil or Recent records from the eastern Pacific. In the western Atlantic, fossils range in age from late Early Miocene to late Pleistocene, although this is a very uncommon fossil, not known from many of the classical localities in the study area. Gregory (1895: 288) recorded Pleistocene fossils from Barbados.

***Bursa rugosa* (G. B. Sowerby II, 1835)**

Pl. 5, Figs 9, 13-14; Pl. 6, Figs 1-10

Ranella rugosa G. B. Sowerby II, 1835: pl. 85, fig. 7; 1841b: 53; Reeve, 1844b: pl. 5, figs 21a-b.

?*Tritonium commutatum*. Gabb, 1873: 211 [according to Gabb (1881: 353), not *Triton commutatum* "Dunker," but Dunker's name is a *nomen nudum*, listed below under *Charonia variegata* (Lamarck, 1816)].

Bursa (Marsupina) albofasciata boussingaulti Rutsch, 1934: 58-59, fig. 7; pl. 3, figs 3-4.

Bursa (Ranella) sp. Trechman, 1935: 542, pl. 21, fig. 20 (as *Bursa (Ranella)* cf. *amphitrites* in caption to pl. 21).

Bursa (Colubrellina) caelata amphitrites. Woodring, 1959: 207, pl. 28, figs 1-2, 7-8; Jung, 1965: 513, pl. 68, figs 12-13, pl. 69, fig. 2; Perrilliat, 1972: 76, pl. 37, figs 12-15 (not *Bursa amphitrites* Maury, 1917).

Bursa calcipicta. Keen, 1958: 348, fig. 328; 1971: 508, fig. 965; Finet, 1991: 270 [in part not *Bursa (Lampadopsis) calcipicta* Dall, 1908, = *Crossata ventricosa* (Broderip, 1833)].

Bursa (Colubrellina) sp. Olsson, 1964: 172, pl. 30, fig. 4.

Bursa (Colubrellina) species A. Jung, 1971: 189, pl. 11, figs 5-7.

?*Bursa* sp. Cosel, 1984: 221.

Bursa (Bursa) rugosa. Beu, 1985: 63, fig. 39; Cossignani, 1994: 50; Kaiser, 1997: 33.

Bursa (Colubrellina) sp. Perrilliat, 1987: 15, pl. 4, figs 3-4.

Bursa amphitrites. Petuch, 1992: 108, fig. 3G (not *Bursa amphitrites* Maury, 1917).

Bursa (Lampasopsis) (sic) amphitrites. Petuch, 1994: 120, pl. 39, figs. L-M; 1997: 224, fig. 83J (not *Bursa amphitrites* Maury, 1917).

Bursa (Bursa) calcipicta. Kaiser, 1997: 32 [not *Bursa (Lampadopsis) calcipicta* Dall, 1908].

Bursa rugosa. Beu, 2001: 711, figs 1.3, 1.5.

Remarks.—*Bursa rugosa* is distinguished from the other, similar *Bursa* species in the study region (a) by its moderately large size (up to ca. 70 mm H), (b) by its very prominent, strongly curved siphonal fasciole, curving to the left of the aperture and then back to the right, to form a deep pseudumbilicus that is covered over in almost all specimens by a wide flare of the inner lip to the left of the lower columellar area, (c) by its equally widely flared outer lip with a weakly digitate outer margin, (d) by its prominent apertural ridges, the inner lip bearing many large, rather closely spaced, weakly anastomosing transverse ridges and the inner edge of the outer lip bearing five pairs of prominent transverse ridges corresponding to the interspaces between the exterior spiral cords (three ridges are present in a few of these groups, rather than two, in a few specimens), (e) by its short to moderately tall spire with moderately to strongly stepped outlines, caused by the weakly concave sutural ramp above the moderately large shoulder nodules of most specimens, (f) by its external sculpture of four major spiral cords, bearing numerous, small to few, large, rounded nodules on at least the upper two cords, forming obvious buttresses where the cords cross the adapertural and abapertural variceal hollows, and forming low, rounded but obvious nodules where the cords cross the varices, (g) by its varices being strictly aligned up the opposing sides of the spire until the last whorl or two of large specimens, when they become progressively further offset as the shell grows, (h) by its moderately long (on Recent specimens and well preserved fossils) semitubular posterior siphonal canals, protruding above the varices on most specimens to produce blunt spines, and (i) by its finely to moderately prominently rugose surface between the major spiral cords.

Bursa rugosa is the most common intertidal *Bursa* species in the Panama Bay area at present (material listed below) and is much the most common fossil *Bursa* species in tropical America (recorded here from nine faunas), and yet the mention of the similarity of his material to *B. rugosa* by Olsson (1924: 124) is the sole reference to this name in the modern literature before Beu (2001). Experience of the living Indo-West Pacific fauna (e.g., identifications contributed to Springsteen & Leobrera, 1986; Beu, 1987, 1998b; Beu in Poppe, 2008) leaves no doubt that *B. rugosa* does not occur in

the Indo-West Pacific province, and this is presumably yet another example of Hugh Cumming's mislocalized material. The abundant Recent material from Panama (notably DMNH 91396, 6; DMNH 39411, 26) agrees precisely with Sowerby's type material (Pl. 5, Figs 9, 13) in all characters, and there is no doubt about the identity of the Panamic species. The material from Gorgona Island, eastern Colombia, identified as "*Bursa* sp." by Cosel (1984: 221) also is *B. rugosa* (examined at SMF).

Rutsch's name *Bursa (Marsupina) albofasciata boussingaulti* was proposed as a result of several misconceptions. This species belongs in *Bursa sensu stricto*, no matter what subgeneric position is used for other species. *Marsupina* is reserved here for species closely related, in a phylogenetic sense, to the type species, the western Atlantic *M. bufo* (Bruguière, 1792). The only Pliocene to Recent eastern Pacific species belonging to *Marsupina* are *Ranella nana* Broderip & Sowerby, 1832, and "*Gyrineum*" *strongi* Jordan, 1926 (see below); *Ranella albofasciata* was based on a coarsely sculptured variant that occurs in most samples of *M. nana*. Also, larger collections from the type locality of *B. albofasciata boussingaulti*, most notably the excellent lot of 30 specimens collected by Jack and Win Gibson-Smith (NMB 17531), demonstrate that the holotype is a small, immature specimen, and larger shells agree with the population living in Panama Bay in all characters. Most of the large lots of fossils collected at the many other Caribbean and Panamic localities where this species occurs also consist mainly of rather small specimens, but a few large ones are seen in most large samples, and the smaller ones agree with *B. rugosa* in all essential characters.

The specimens from the Grand Bay Fm at Carriacou Island, West Indies, identified by Jung (1971: 189) as "*Bursa (Colubrellina)* species A" are calcite neomorphs (as is all the rest of this collection), and nearly all of them have the shell surface severely abraded, to the extent that the shell shape is substantially modified and the original sculpture is not determinable. One specimen has a small area of original sculpture preserved, and its coarsely nodulose sculpture appears to be that of *B. rugosa*. Also, the specimen from the same source illustrated by Trechman (1935: pl. 21, fig. 10; BMNH Palaeontology Department, GG4400) has better-preserved sculpture than all of the NMB material, showing two peripheral rows of small, rounded nodules, with 7 nodules in the upper and 8 in the lower row in the last intervariceal interval. However, all material lacks apertural characters, and the Carriacou form is not certainly identifiable. Donovan *et al.* (2003) pointed out that Grand Bay Fm is a slumped, tubiditic formation deposited in deep water (> 150-200 m) and so it is not surprising that aragonitic fossils contained in it have been altered to calcite.

Dimensions.—*Ranella rugosa*, lectotype: H 49.1, D 33.7

mm; paralectotypes: H 48.4, D 32.3 mm, and H 46.6, D 31.2 mm; Recent, Panama Bay, AMNH 122936: H 60.4, D 39.5 mm; *Bursa albofasciata boussingaulti*, holotype: H 36.7, D 24.5 mm; figured specimen, NMB H 17895, from NMB 18306, Panama: H 41.2, D 29.5 mm; figured specimens from NMB 17531, Punta Gavilán, Venezuela: NMB H 17896 (largest): H 71.2, D 41.8 mm; NMB H 17897: H 61.2, D 36.1 mm; NMB H 17898, smallest: H 22.9, D 16.9 mm.

Types.—*Ranella rugosa*, three syntypes BMNH 1989133, from “Manila,” Philippine Islands (wrong), *ex* Cuming collection; the type locality is here designated as Perlas Islands, Panama Bay. The largest syntype most nearly resembles Sowerby’s (1835: pl. 85, fig. 7) figure. *Bursa (Marsupina) albofasciata boussingaulti*, holotype NMB H 1870 (Pl. 5, Fig. 14), from Punta Gavilán, Venezuela (Early Pliocene); with 2 paratypes NMB H 1871/1-2, all data as for the holotype; one paratype NMB H 1872, Punta Gavilán beds, coast near Sabanas Altas, northern Venezuela (localities shown by Rutsch, 1934: fig. 2).

Other material examined.—Full material is listed for this species, because it has not been recognized under this name previously. **Recent: E Pacific: W Mexico:** 5-22 m, S side Bahia Cuastocomate, 5 km NW of Barra de Navidad, Jalisco (LACM 68-41, 1). **Pacific Costa Rica:** 1-2 m, N side Bahia de Culebra (ANSP 308538, 1); 2-10 m, E Bahia Cocos, 9 km SW of Puerto Culebra (ANSP 307934, 1); Islas Tortugas (MCZ, 4); 10-25 m, small islets off of Punta Quepos, Puntarenas Province, *Searcher* sta. 462-464 (LACM 72-58, 2); 40 m, off of Bahia Herradura, Puntarenas Province, *Searcher* sta. 451, 456-7 (LACM 72-54, 1); 10-14 m, Bahia Herradura, *Searcher* sta. 447 (LACM 72-52, 3); 8-13 m, N side Isla del Caño, Puntarenas Province, *Searcher* sta. 471-4 (LACM 72-63, 1). **Pacific Panama:** Venado Island, Panama Bay (MCZ, 1); Panama Bay (AMNH 122936, 1); 10 m, E side Tabogo Island (ANSP 314498, 3); Pacific Panama (DMNH 91328, 1; DMNH 91396, 6); Balboa, Pacific Panama (DMNH 39411, 26); 10-30 m, Isla Otoque, Bona Islands, Panama Bay (LACM 65-21, 1); Veracruz (LACM B-119, 2); intertidal, Venado Island (LACM 55014, 3); 50-100 m, on rock, off of Bahia Honda (LACM-AHF 863-38, 1); 60-70 m, on rock, off of Medidor Island, Bahia Honda (LACM-AHF 948-39, 1); 6 m, Bahia Honda (LACM 45117, 1); dredged, 73 m, off of Canal de Afuera Island (GNS WM15229, 2); low tide, Venado Island (GNS WM14065, 2); intertidal, Balboa (GNS WM12445, 1; WM12466, 2); dredged, 30-45 m, Canal de Adentro (GNS WM15227, 1). **W Colombia:** shallow water with *Pocillopora*, Gorgona Island (LACM-AHF 411-35, 1); 40 m, on mud, off of Monkey Point, Gorgona Island (LACM-AHF 407-35, 1); 90 m, on mud, off of Port Utria (LACM-AHF 415-35, 1); R. von Cosel’s material in SMF: on boulder at 1 m, Ensenada de Utria (1 live); *Cassique* haul

18, off of Bueneventura (1); beach, Gorgonilla, S end of Isla Gorgona (2). **Ecuador:** 10 m, rocks, S of Salinas, N side Santa Elena Peninsula, *Anton Bruun* cruise 16, sta. 6670 (LACM 66-114, 1); 16-20 m, on rock with gorgonians, off of Bahia Santa Elena (LACM-AHF 209-34, 1). **Peru:** Mancora (ANSP 225130, 1); intertidal, Punta Telagrafo, Paita (LACM 72-86, 1). **Galápagos Islands:** Jervis Island (DMNH 66169, 1); N side Jervis Island (DMNH 64561, 2); 90 m, on rock, Tagus Cove, Albemarle Island (LACM-AHF 324-35, 1); Sombrero, San Salvador Island (AMNH 117924, 4); 2.5 m, N shore of Isla Rabida (Jervis Island) (AMNH 156376, 1); Isla Rabida (AMNH 156379, 2); dredged, 50 m, Academy Bay, Santa Cruz Island (AMNH 156378, 1); dredged, 5 m, Las Cuevas, Isla Santa Maria (AMNH 156337, 1); beach, Bahia Urbina, Isla Isabella (GNS WM15988, 1); 10-15 m, Bahia Isabel, Fernandina (Narborough) I (GNS WM17454, 1).

Fossils: Mexico: Pliocene: Agueguexquite Fm: TU 1046 (GNS WM18823, 1). **Carriacou:** Grenadine Islands: **Middle Miocene:** All material is from Grand Bay Fm: NMB H 15448, Grand Bay cliff (NMB, 1, specimen figured by Jung, 1971; H 15449, 1; Pl. 6, Figs 3-4); 10703 (2); 10709 (2); 10710 (7); 13770 (3). **Pacific Costa Rica: Pleistocene:** NMB 17771 (2). **Atlantic Panama: Middle Miocene:** Gatun Fm: NMB 17637 (1); 17638 (2); 17639 (1); 17649 (5); lower Gatun Fm, bed 1 of Todd, quarry floor, Los Lomos Suites, Cativa, Colon (BMNH Palaeontology Department, GG 22586, 1, large and typical). **Late Miocene:** Gatun Fm: NMB 17644 (2); 17868 (1); 17871 (1); 18257 (1); 18258 (3); 18261 (1); 18308 (1); 18322 (12); 18389 (1); 18390 (1); 18663 (1); USGS 16909 (4); 16926 (2, including specimen illustrated by Woodring, 1959: pl. 28, figs 1-2, USNM 562609); 16949 (2, including specimen illustrated by Woodring, 1959: pl. 28, figs 7-8, USNM 562608); 21956 (6); 22016 (1); 25281 (1); CAS loc. 2653, Gatun third locks excavation, Canal Zone, Gatun Fm (2); CAS 60190, hill N of Sabanita, Gatun Fm (2); TU 757 (GNS WM16956, 10; WM18820, 43); 958 (GNS, WM 11988, 16; GNS WM18819, 51); 961 (1); 962 (GNS WM18822, 1); Woodring’s loc. 138, Gatun Fm, Transisthmian Highway 1.6 km E of Canal Zone, Panama (GNS, WM7971, 3); TU 961, Cativa, Colon, collection of Bernard Landau (4); Valiente Fm: NMB 17629 (3); NMB 17824 (2); 18375 (1); 18771 (1). **Pliocene:** Shark Hole Point Fm: NMB 18716, S end of Playa Lorenzo, S side Valiente Peninsula (1). **Pacific Panama: Pleistocene:** NMB 17439 (2); 17443 (1); 18306 (1, illustrated, NMB H 17895; Pl. 6, Fig. 2, 6). **Panama, Darien: Late Miocene:** NMB 18504 (1). **Colombia: Pliocene(?):** USGS 10927 (1); 11625 (1); UCMP S-48, Lower Cibarco Fm, 250 m E of Tubará, Departamento de Atlantico (1); UCMP S-57, low hills W of Río Magdalena, Departamento de Bolivar (1); UCMP S-7423, Arroyo Cibarco, N of Usiacuri, Departamento de Atlantico (1). **Venezuela:**

Late Early Miocene: Cantaure: NMB 12842 (2); 17241 (3); 17242 (1); 17243 (NMB H 13699, 1, specimen illustrated by Jung (1965: pl. 68, figs 12-13; illustrated here, Pl. 6, Fig. 7); H 13700 (1, specimen illustrated by Jung, 1965: pl. 69, fig. 2); 17248 (1); 17516 (37); locality same as last, collection of Bernard Landau (11, + GNS WM17449, 4); 17517 (11); 17518 (8); 17519 (31); 17520 (49); 17521 (11); same as last, collection of Bernard Landau (1); USGS 25171 (4). **Late Miocene:** NMB 13112 (4); 16526 (1); 17530 (22); UCMP S-106, Mataruca Member, Caujarao Fm, Carrizal, E of La Vela de Coro, Falcón (12). **Pliocene:** NMB 12045 (3, topotypes of *B. boussingaulti*); 12879 (2); 12887, Cubagua Fm, Araya Peninsula (18; 1 illustrated, NMB H 18050; Pl. 6, Fig. 9); NMB 13116 (1); 17531 (30, topotypes of *B. boussingaulti*; 2 illustrated, NMB H 17896-17897; Pl. 6, Figs 1, 5, 8, 10); locality same as last, collection of Bernard Landau (3); 17532 (9); USNM, A. A. Olsson's loc. 210, Cerro Negro Member, Cubagua Fm, Cañon de los Calderas, Cubagua Island, Nueva Esparta (1); same as last, collection of Bernard Landau (5); UCMP S-122, Cubagua Fm, 400 m SW of house at Las Calderas, Nueva Esparta (1). **Ecuador: Late Miocene:** NMB 19122 (2 juveniles); USGS 23487 (1). **Pliocene:** Onzole Fm, Punta Gorda (USNM 644042, 1; illustrated by Olsson, 1964: pl. 30, fig. 4).

Distribution:—In the living fauna, the distribution of *Bursa rugosa* has been poorly defined until now, because of Keen's (1971) confusion of this species with *B. calcipicta* (= *Crossata ventricosa*; see below), but because all of the material that I have seen that might be assigned to *B. calcipicta* was collected well offshore, *B. rugosa* is presumably the species on which Keen (1971: 508) based the range of "Tenacatita Bay, Jalisco, Mexico, 9 to 11 m, to Panama Bay ... and La Plata, Ecuador"; also recorded by Olsson (1924: 124) from Ecuador and Peru, although unfortunately he did not record precise localities for this species, unlike the others in his paper. The LACM material listed above makes it clear that *B. rugosa* lives now from southern Mexico to at least Paíta, Peru. Records of "*Bursa calcipicta*" from Cocos Island, Costa Rica (Montoya, 1983, 1984; Skoglund, 1992) and the Galápagos Islands (Finet, 1985) almost certainly are also based on *B. rugosa*. Certainly, *B. rugosa* is limited to tropical western America at present. It is therefore particularly interesting for Panamic biogeography that *B. rugosa* occurs in Florida [if rarely; specimens identified by Petuch (1992, 1994, 1997) as *B. amphitrites*], USA, and is abundant in Caribbean, Venezuelan, and Colombian shallow-water fossil localities of Early Miocene to Pliocene age; this is one of the clearest examples of a paciphile tonnoidean species. Other than in the Panama Isthmus itself, where it is common in Pliocene rocks on both coasts, there seem to be no records of *B. rugosa* in the western Atlantic after the end of Pliocene time. In 1985, I identified a specimen in USGS

8343 (Moín Fm, latest Pliocene-Early Pleistocene, Limón, Atlantic Costa Rica) as possibly *B. rugosa*, a biogeographically important record if it could be substantiated, but T. R. Waller (USNM, pers. comm., September 2008) found only *Marsupina bufo* in this collection. There are also no records at all from the Dominican Republic, apparently reflecting the mostly coral reef or offshore, soft-bottom nature of the Dominican Republic units, and the shallow rocky habitat of *B. rugosa*. The specimens identified as *B. (Colubrellina)* sp. by Perrilliat (1987: pl. 4, fig. 3, 4) also are clearly *B. rugosa*, from the Middle Miocene Ferrotepec Fm in Michoacan, Mexico.

***Bursa scrobilator* (Linnaeus, 1758)**

Pl. 7, Figs 3-4, 6-7

Murex scrobilator Linnaeus, 1758: 749; 1767: 1218.

Murex scrobiculator. Gmelin, 1791: 3535.

Tritonium scrobiculator. Röding, 1798: 127.

Murex rana var. Brocchi, 1814: 401 (not *Murex rana* Linnaeus, 1758).

Triton scrobiculator. Lamarck, 1816: pl. 414, fig. 1, "Liste des objets": 4; 1822: 180; Deshayes, 1843: 626; Bellardi & Michellotti, 1840: 33, pl. 2, fig. 7; Philippi, 1843: 213; Reeve, 1844a: pl. 8, fig. 28; Petit de la Saussaye, 1852c: 194.

Bufonaria pesleonis Schumacher, 1817: 252.

Murex nodosus Borson, 1825: 310.

Ranella tuberculata Risso, 1826b: 203, pl. 9, fig. 123; Arnaud, 1977: 139, pl. 10, fig. 167.

Ranella scrobiculata. G. B. Sowerby II, 1836: pl. 93, fig. 21; Kiener, 1841: 22, pl. 3, fig. 2; pl. 10, fig. 1; Kobelt, 1883: 9, pl. 31, figs 1-8.

Ranella coriacea Reeve, 1844b: pl. 4, fig. 26; 1844d: 137.

Tritonium scrobilator. Philippi, 1844: 184; Aradas & Benoit, 1876: 280.

Ranella nodosa. Sismonda, 1847: 40; D'Ancona, 1872: 61, pl. 8, figs 5a-b; Bellardi, 1873: 233, pl. 15, fig. 5.

Apollon quercina Mörch, 1853: 106.

Ranella scrobiculata. Hörnes, 1856: 212, pl. 21, figs 3-4.

Tritonium scrobiculator. Drouët, 1858: 34.

Ranella scrobiculator. Weinkauff, 1868: 73.

Bufonaria scrobiculator var. *minor* Pallary, 1900: 296.

Ranella (Apollon) nodosa vars. *subanodosa* and *mioquineseriata* Sacco, 1904: 39, pl. 11, figs 1-2.

Bursa (Bufonariella) scrobiculator. Thiele, 1929: 284, illus.

Bursa (Bufonariella) scrobiculata and var. *nodulosa* Segre, 1954: 64, pl. 3, figs 4-6d.

Bursa (Bufonariella) scrobiculata, with vars. *major*, *peculiaris*, *fasciata*, *undulata*, *nodulata*, *nodulosa elongata*, *seminodulosa*, and *seminodulosa fasciata* Settepassi, 1970: Cymatiidae vii, pl. 5, figs 14a-b, 15a-b, pl. 6, figs 16a-b, 17-18 (with further synonymy).

Bursa (Bufonariella) scrobiculator nodosa. Caprotti, 1970: 172, pl. 6, fig. 3.

Bursa scrobiculator. Micali, 1975: 202, illus. (living animal); Melone, 1975: 203, illus. (radula); Ávila *et al.*, 1998: 500; Verdejo Guirao, 2001: 14-18, figs 2-17.

- Bursa (Bufonariella) nodosa*. Pavia, 1976: 153, pl. 2, figs 2, 5; Baluk, 1995: 210, pl. 18, figs 4-5.
- Bursa (Bufonariella) scrobilator*. Nordsieck & Garcia-Talavera, 1979: 126, pl. 28, fig. 1.
- Bursa scrobilator*. Russo, 1981: 20, illus. (living animal); Robinson, 1993: 253; Cachia *et al.*, 1996: 116, pl. 12, fig. 2; Gofas & Beu, 2002: 102; Ardovalini & Cossignani, 2004: 133, three central figs; Landau *et al.*, 2004: 66, pl. 5, figs 3-5, pl. 10, fig. 1; Chirli, 2007: 103, pl. 37, figs 11-16, pl. 38, figs 1-4 (with long synonymy).
- Bursa (Colubrellina) scrobilator scrobilator*. Beu, 1985: 64; Cossignani, 1994: 88-89; Giannuzzi-Savelli *et al.*, 1997: 242, figs 903-904.
- Bursa (Colubrellina) scrobilator coriacea*. Beu, 1985: 64, fig. 43; Cossignani, 1994: 89.
- Bursa scrobilator (sic)*. Guerreiro & Reiner, 2000: 120-121.
- Bursa scrobilator* f. *coriacea*. Ardovalini & Cossignani, 2004: 133, two upper right figs.

Remarks.—*Bursa scrobilator* is distinguished from the other *Bursa* species in the study area (a) by its tall, narrow spire (second only to that of *B. natalensis*), (b) by its varices being slightly offset down the spire sides rather than strictly aligned, (c) by its unusually long anterior siphonal canal for a *Bursa* species, (d) by its short, widely open posterior siphonal canal, forming little more than a notch in the outer lip flange anterior to the varix in many specimens, (e) by its narrowly rounded, well-raised varices with concave hollows between the main variceal ridge and the rest of the shell surface on both adapertural and abapertural faces, so that the four well-raised spiral cords form very prominent buttresses on both sides of each varix, particularly on the last few whorls, and the cords form four low, rounded nodules on the outer ridge of each varix, (f) by its sculpture of many, low, rounded nodules to (on most specimens) few, large, rounded, widely spaced nodules on the cord at the shoulder angle, and many smaller rounded nodules on most or all of the three lower major cords, and (g) by its sculpture of crisp, narrow, well-defined, closely spaced spiral ridges over the entire teleoconch surface, the ridges bearing small, closely spaced, spirally elongate granules on many specimens. Its protoconch is of the relatively tall-mammillate type, of 3.75 whorls, with a low protoconch I of 0.75 whorl bearing fine reticulate ridges, followed by fine, cancellate spiral and axial ridgelets on the first whorl of protoconch II, fading out over the second whorl.

Bursa scrobilator is the single living *Bursa* species of the Mediterranean Sea; the only other present-day eastern Atlantic bursid, "*Bursa*" *marginata* (Gmelin, 1791), is not reliably recorded from the Mediterranean, and is referred below to *Aspa* H. & A. Adams, 1852. Although it is an exceedingly rare species in the Mediterranean today, *B. scrobilator* has been well known in biological and paleontological literature since pre-Linnean time, and has been referred to and illustrated in so many early works and modern-day shell books that no at-

tempt has been made here to compile a full synonymy. The synonymy given above merely lists the actual synonyms, some of the main early works, and a few recent illustrations; Priolo (1964: 536) and Chirli (2007: 103) provided useful, extensive lists of further references in the European literature. The European Miocene and Pliocene fossils of this species group have usually been considered to belong to a distinct species, *B. nodosa* (Borson, 1825), which supposedly differs from all Recent Mediterranean and Atlantic specimens in having only three, rather than four, major spiral cords on the last whorl. However, Landau *et al.* (2004) demonstrated that Pliocene fossils from Estepona, Spain, and other localities on the Iberian Peninsula include some specimens resembling *B. scrobilator* and some resembling *B. nodosa*, and considered that the two forms intergrade and are not distinct species. Miocene specimens from the Vienna Basin illustrated by Hörnes (1856: pl. 21, figs 3-4) and those from Korytnica, Poland, illustrated by Baluk (1995: pl. 18, figs 4-5) also are typical of *B. scrobilator* in having four prominent spiral cords. In the American records of *B. scrobilator* newly recognized here, all material consistently has four major spiral cords on the last whorl. This distinction therefore is interesting for biogeography; the American Pliocene-Pleistocene specimens seem, from this character, to have originated from an eastern Atlantic-Iberian Peninsula population, with four major spiral cords, rather than from a Mediterranean-southern European population, with only three major spiral cords. Given the now generally accepted concept of desiccation of the Mediterranean Sea during Messinian time (latest Miocene) (Hsü *et al.*, 1973, 1978; Cita, 1982; but see Grecchi, 1978 and Sabelli & Taviani, 1983, 1984, for a contrary viewpoint), it seems likely that the Mediterranean was repopulated from the New World and eastern Atlantic by specimens bearing four spiral cords, after the extinction during the period of desiccation of specimens with three spiral cords.

The West African population of *Bursa scrobilator*, living along the mainland coast from Sénégal to Angola, is distinctive in bearing the finely granulose sculpture and fine to prominent shoulder nodules described above, whereas all Mediterranean specimens have a smoother, polished surface bearing little of the fine granulation and, on the last whorl or two of large shells, none of the shoulder nodules seen on West African specimens. Reeve (1844b: pl. 4, fig. 26) provided the name *Ranella coriacea* for the more coarsely sculptured West African form. The West African specimens are the ones from the Old World that match the American ones most closely. Most or all of the Mediterranean-southern European fossil material assigned to *B. nodosa* also bears fine granulose sculpture and obvious shoulder nodules. However, the distribution of sculptural variants in the eastern Atlantic is more complex than this. Specimens from the Canary Islands (20 m, Tenerife,

GNS WM15185, 1, pres. F. Garcia-Talavera; 5 m, Lanzarote, GNS WM17413, 1), some from the Azores Islands (GNS, WM15966, Praia, Santa Maria Island, beach specimen collected by AGB, February 1998; and one of 3 specimens in MNHN), and Pleistocene fossil specimens from the Azores (GNS WM15963, coll. AGB & B. Landau, February 1998) and near Penedo, Porto Santo, Madeira Archipelago (Gerber *et al.*, 1989: 24; GNS WM15129, 1), lack the fine granulate sculpture and shoulder nodules and are indistinguishable from Mediterranean Recent specimens, whereas two other Azores specimens in MNHN have fine granules on the exterior, intermediate between those of West African specimens and the smooth Mediterranean shells. It therefore seems likely that the fine granulate sculpture and the shoulder nodules are trivial (phenotypic?) characters of no taxonomic significance. Verdejo Guirao (2001) illustrated a large range of variation in this species, demonstrating that the evenly granulate form is strictly limited to the West African coast, from Morocco to Angola.

Although the spelling "*scrobiculator*" for the name of this species is well entrenched in the literature, Linnaeus (1758: 749; 1767: 1218) spelled the name *scrobilator* in both the tenth and twelfth editions of "Systema Naturae." Despite considerable argument over the years about the meaning of the name, and whether it might have been a spelling error, Linnaeus clearly intended this original spelling, and I can see no justification for changing it.

Dimensions.—Figured specimens, from NMB 19008 (TU 1240), Limón, Costa Rica: NMB H 17899: H 54.7, D 32.3 mm; NMB H 17900: H 50.3, D 30.9 mm.; lectotype of *Murex scrobilator*: H 61.9, D 38.1 mm; paralectotype, H 52.7, D 33.0 mm; lectotype of *Ranella coriacea*: H 43.8, D 27.4 mm; paralectotype, H 59.8, D 37.4 mm; paralectotype, H 32.4, D 21.5 mm.

Types.—*Murex scrobilator*, two syntypes in Linnaeus' collection, housed by the Linnean Society of London, Burlington House, London; both bear the number "537" inside the outer lip (the number of this species in Linnaeus' 1767 work; Linnaeus, 1767: 1218) and are therefore authentic Linnaeus syntypes. The larger specimen (H 61.9 mm) is here designated the lectotype of *Murex scrobilator*. This designation is necessary because the syntypes include the specimen illustrated in the reference cited by Linnaeus (1758: 749): Gualtieri (1742: pl. 49, fig. B). This specimen, examined by me in Museo di Storia Naturale e del Territorio, Università di Pisa, in the Certosa di Calci, outside Pisa, is a specimen of *Bursa corrugata* (Gualtieri collection no. 2627). The type locality of *B. scrobilator* is here designated as Palermo, Sicily. In the absence of any known type material of Schumacher (1817), the lectotype of *M. scrobilator* is also here designated the neotype of *Bufonaria pesleonis* Schumacher, 1817. *Ranella coriacea*, 3

syntypes BMNH 1967656, without locality. The medium-sized syntype is marked "F" on the columella and "c" inside the outer lip, showing it to be the one illustrated by Reeve (1844b: pl. 4, fig. 26). The type locality is here designated as Île Gorée, Sénégal. I discussed (Beu, 1987: 333) the identity of *Apollon quercina* Mörch (1853: 106), and designated the lectotype as the specimen figured by Lister (1691: 943, fig. 39). This figure clearly shows *Bursa scrobilator*. The location of any original material referred to *A. quercina* by Mörch is unknown, as is the location of the specimen figured by Lister (1691), and this name is therefore not based on a type specimen. The specimen in Linnaeus' collection in London, designated above as the lectotype of *M. scrobilator* and the neotype of *B. pesleonis*, is therefore also here designated the neotype of *Apollon quercina*.

Other material examined.—Almost all Recent material is from the Mediterranean Sea and West Africa, and is not listed here, apart from the four specimens seen from the **Azores Islands:** beach, Praia, Santa Maria Island, AGB, February 1998 (GNS WM15966, 1); dived, 10-20 m, Ponta Delgada, Sao Miguel Island, 9-15 July 1983 (MNHN, 1); rocks, 6 m, Vila do Porto, Santa Maria Island, June 1990 (MNHN, 1); infralittoral, 0-1 m, Ilheu de Vila Franca, São Miguel Island, July 1988 (MNHN, 1); Açores, coll. Drouët (MNHN, 1); Santa Clara (MNHN, 1). **Canary Islands:** Canaries (TFMC 1122, 1 good, "typical *scrobilator*" form); Canarias (TFMC 1565, 4 good, all "typical *scrobilator*" form); 20 m, Tenerife (GNS WM15185, 1); 5 m, Punta del Carmen, Lanzarote (GNS WM17413, 1).

Fossils: Atlantic Costa Rica: Latest Pliocene-Early Pleistocene, Limón (McNeill *et al.*, 2000): NMB 17789 (1); 17792 (3); 18113 (1); 18272 (2); 18273 (2); 18277 (1); 18278 (4); TU 954 = NMB 19026 (8); 1240 = NMB 19008 (36; 2 illustrated, Pl. 7, Figs 3-4, 6-7; NMB H 17899-17900; GNS WM16952, 14; WM18855, 20); 1307 = NMB 19015 (1); USGS 21035 (USNM, 1); Puerto Limón, coll. T. Kemperman, 1982 (ZMA, 1); Moín Fm, Limón, collection of Bernard Landau (12); Lomas del Mar reef member, Moín Fm (Late Pliocene), Lomas del Mar West, Puerto Limón (BMNH Palaeontology Department, 1). Recorded also from the Moín Fm by Robinson (1991, 1993). **Atlantic Panama: Pleistocene:** Swan Cay Fm: NMB 18372, 3 m-thick shelly sandstone, Swan Cay, N of Isla Colon, Bocas del Toro Basin (1 large). **Colombia: Pliocene(?):** 0.6 m band above limestone, Point Pua, Departamento de Bolívar (UCMP S-66, 1).

Distribution.—*Bursa scrobilator* lives today only in the Mediterranean Sea, along the coast of West Africa at least as far south as Ghana (southern limit not well established; recorded from Gabon by Bernard, 1984: 126, fig. 266), and at the Atlantic islands; it is recorded from the Azores (Ávila *et al.*, 1998), Canary and Cape Verde Islands and at Madeira. Fossil

specimens of *B. scrobilator* are recorded from a Pleistocene shellbed behind the beach at Praia, Santa Maria Island, Azores (Garcia-Talavera, 1990a), and were recollected by AGB and Bernard Landau during February 1998, from a Pleistocene shellbed ca. 2 m above sea level at Tenerife, Canary Islands (Garcia-Talavera *et al.*, 1978), and from a Pleistocene shellbed on Selvagem Pequenha Island, Selvagem Islands, off of West Africa (Garcia-Talavera, 2001). Meco *et al.* (2002: table 2) also recorded fossils from uplifted Pleistocene terraces at Arucas and Las Palmas, Canary Islands. Fossils also are widespread in the Miocene and Pliocene rocks of Europe and the Mediterranean region. Fossils of *B. scrobilator* in the Americas are limited to Pliocene and Early Pleistocene rocks along the Atlantic coasts of Costa Rica, Panama, and Colombia (the sole Colombian record possibly is as old as Late Miocene, but its age is poorly constrained).

***Bursa victrix* Dall, 1916**
Pl. 2, Fig. 5

Bursa victrix Dall, 1916: 507, pl. 88, fig. 10.

Remarks.—Although *Bursa victrix* is a very poorly known species, and is Oligocene in age, it is refigured here (apparently for the first time since its description) to show its similarity to *B. corrugata*, the moderately common, widespread species of the living fauna of western America and the eastern and western Atlantic. The fossil record of *B. corrugata* is so scanty — specimens are recorded above only from the Plio-Pleistocene of Mexico and the Galápagos Islands — as to suggest that it might have been a very recent arrival in the Americas, but the presence of *B. victrix* in the Oligocene rocks of Georgia, USA, shows this not to have been the case. The holotype of *B. victrix* is a natural mold of the exterior of only about a third of the surface of a shell; the illustration is of a silicone impression from the natural mold. The almost evenly inflated whorl profile, with a slightly protruding shoulder angle formed by a row of rounded nodules at approximately the upper third of the whorl height on the spire, the numerous lower rows of nodules or granules extending down over the anterior canal, the relatively short posterior canal (as far as can be seen), and the deeply buttressed abapertural face of the varix on the penultimate whorl are all characters in common with *B. corrugata*. Indeed, it is only because of the lack of enough critical characters for accurate comparison that this form is maintained as distinct from *B. corrugata*. Further material from the Flint River is needed to clarify the relationships of this species.

A possible earlier name for *Bursa victrix* is *Tritonium (Lagena) edentatum* Gabb (1877: 281). The holotype (ANSP. IP T.16887, from “Pataula Creek, Clay County, Georgia”) is a small *Bursa* species that seems to me to be indistinguish-

able from *B. corrugata*. Gemmate fine spiral cords on the early spire whorls are reduced on the last few intervariceal intervals to two peripheral rows of rounded nodules. The holotype has the aperture broken away, and so is difficult to compare with modern and Oligocene specimens. The type locality supposedly is in the Providence Sand, of Late Maastrichtian (Late Cretaceous) age (Warren Blow, USNM, pers. comm., 1987). Eargle (1955: 70, fig. 12) described and illustrated outcrops of Providence Sand, of which “very fossiliferous beds are at several localities in the valley of Pataula Creek and vicinity in northwestern Clay and southern Quitman Counties,” Georgia. The specimen almost certainly is mislocalized, because I am not aware of any other records of Bursidae older than Eocene, let alone Paleocene or Late Cretaceous. No species of Bursidae are present in the classical tropical Eocene faunas of the Paris Basin, India, or Indonesia. The significance of this name will not be clear unless the true locality can be determined or more material collected. If indeed it is a Cretaceous record of *Bursa*, it would be critically important for the phylogeny of the Bursidae, which otherwise have an apparently very late appearance on the geological scene, and highly mysterious origins.

Dimensions.—The very incomplete mold of the holotype of *Bursa victrix*: H 43, D 24 mm; *Tritonium edentatum*, holotype: H 33.3, D 21.6 mm.

Type material.—*Bursa victrix* holotype USNM 166728, from USGS 7079, Mascot Point, eastern bank of Flint River, below the mouth of Blue Spring, Decatur Co, Georgia, in chert blocks; only known specimen. Assigned by Dall (1916: table p. 489) to the “upper beds” at Flint River, considered by Dall (1916: 487–488) and by Vaughan (cited by Dall) to be equivalent to the *Orthaulax pugnax* zone of Florida, of Late Oligocene age; stated by MacNeil & Dockery (1984: 103) to be included in the Flint River Fm, considered by them to be an erosional remnant of Byram, Chickasawhay, and possibly Marianna limestones.

Genus ***ASPA*** H. & A. Adams, 1853

Aspa H. & A. Adams, 1853 (in 1853–1858): 106. Type species (by monotypy): *Ranella laevigata* Lamarck, 1822 (= *Buccinum marginatum* Gmelin, 1791), Miocene to Recent, Mediterranean and West Africa; Late Pliocene–Early Pleistocene, Costa Rica.

Remarks.—I pointed out (Beu, 2005: 8) that what previously had been considered the single genus *Bufonaria* Schumacher, 1817, actually comprises two genera on the basis of the opercular nucleus position. *Bufonaria* species have the nucleus half way along the columellar (left) margin, a fan-shaped outline formed by the two straight margins above and below the nucleus, and an evenly curved right margin. It is therefore

similar to that of all taxa of the cassid subfamily Phaliinae. Another group of species has the nucleus a little posterior to the anterior end and situated a little toward the right from the midline, as in the bursid genus *Tutufa* Jousseaume, 1881, and for this, I concluded that the earliest name is *Bursina* Oyama, 1964 (Beu, 2005: 24). Species of *Bursa* and *Marsupina* have an anterior terminal opercular nucleus. The species that I identify as *Aspa marginata*, discussed below, also has an anterior terminal nucleus, as in *Bursa* and *Marsupina* species. I have previously ranked *Aspa* as a subgenus of *Bufonaria*, based on the similarity of the teleoconch of European Early Miocene fossils of this species group to Indo-West Pacific *Bufonaria* species. However, the opercular evidence suggests that *Aspa* is just as likely to be related phylogenetically to *Bursina*, and as with the former subgenera of *Cymatium* (see below), it seems preferable to avoid untestable phylogenetic hypotheses by classifying *Aspa* as a separate genus.

***Aspa marginata* (Gmelin, 1791)**

Pl. 7, Fig. 2, Pl. 11, Fig. 3, Pl. 51, Figs 1-3

- Buccinum marginatum* Gmelin, 1791: 3486; Brocchi, 1814: 332, pl. 4, fig. 17.
Cassis marginata. Borson, 1821: 228, pl. 1, fig. 19.
Ranella laevigata Lamarck, 1822: 154; G. B. Sowerby II, 1835: pl. 89, fig. 15; Gray, 1839: 110, pl. 36, fig. 18; Kiener, 1841: 34, pl. 13, fig. 2; Deshayes, 1843: 550; Philippi, 1844: 183; Reeve, 1844b: pl. 8, fig. 50; Michelotti, 1847: 254; D'Ancona, 1872: 176, pl. 8, figs 3-4; Martens, 1877: 236.
Ranella marginata. J. Sowerby & G. B. Sowerby I, 1824: pl. 233, fig. 2; de Serres, 1829: 114; Locard, 1897: 298.
Eione inflata Risso, 1826b: 172; Arnaud, 1977: 120, pl. 4, fig. 52.
Ranella brocchii Bronn, 1828: 533.
Buccinum pleurotoma Calcare, 1841: 61, pl. 2, fig. 6.
Ranella (Aspa) laevigata. H. & A. Adams, 1852: 106; Chenu, 1859: 156, fig. 721; Coulon, 1933: 139.
Aspa laevigata. Rochebrune, 1881: 303.
Ranella (Aspa) marginata. Bellardi, 1873: 243; Tryon, 1880: 42, pl. 23, fig. 52; Dautzenberg, 1891: 23; Sacco, 1904: 40, pl. 11, figs 13-14; Cossmann & Peyrot, 1924: 315.
Ranella (Lampas) cruentata. Gabb, 1881: 353 (not *Ranella cruentata* G. B. Sowerby II, 1835).
Apollon marginatus. Cossmann, 1903: 118.
Bursa (Aspa) marginata. Thiele, 1929: 284; Settepassi, 1970: Cymatiidae xviii, pl. 10, figs 29a-b, 30a-b, with var. *tuberculata*, appendix p. xi, illus. (with further synonymy).
Bursa marginata. Nicklès, 1950: 88, fig. 136; Bernard, 1984: 64, pl. 52, fig. 103; Gofas *et al.*, 1984: 132.
Gyrineum (Aspa) marginatum. Malatesta, 1974: 273, pl. 23, figs 6a-d (with long synonymy); Nordsieck & Garcia-Talavera, 1979: 127, pl. 28, fig. 6.
Bufonaria (Aspa) marginata. Beu, 1985: 65, fig. 51; Robinson, 1991: 340, pl. 14, figs 11-12; Cossignani, 1994: 12; Giannuzzi-Savelli *et al.*, 1997: 242, figs 905a-b, 906; Guerreiro & Reiner, 2000: 122; Landau *et al.* 2004: 69, pl. 5, figs 6-7, pl. 10, fig. 2.

Bufonaria marginata. Warén & Bouchet, 1990: 80, figs 113-114; Gofas & Beu, 2002: 102; Ardevini & Cossignani, 2004: 132, upper left 2 figs; Chirli, 2007: 105, pl. 38, figs 5-16 (with long synonymy).

Remarks.—*Aspa marginata* is the most readily recognized of all Bursidae, because of its extremely short spire, its very low, wide varices, and its inflated form with an almost smooth surface and no nodules at all. *Aspa marginata* is extremely well known in the Pliocene to Recent fauna of Europe and West Africa, and nothing even vaguely resembling it ever has been reported from the Americas. It was a surprise, then, to recognize a single half-grown specimen of *A. marginata* in the latest Pliocene-Early Pleistocene fauna of the Moín Fm at Limón, Costa Rica, in the extremely large and diverse collection made by Emily and Harold Vokes. Robinson (1991, 1993) previously recorded *A. marginata* from the Moín Fm, on the basis of four further specimens collected subsequently by Emily and Harold Vokes.

Cossmann & Peyrot (1924: 313-317), in a long discussion of the characters of fossil ancestors of *Aspa marginata* in Europe, distinguished a series of species in an evolutionary lineage, and this was discussed again by Landau *et al.* (2004: 70-71). Material from many localities in the Aquitaine Basin, France, in MNHN (shown to me by Pierre Lozouet) and in Université Bordeaux-1 in Talence and several private collections in and near Bordeaux (shown to me by Bruno Cahuzac, Alain Clouzaud, and Jean-François Lesport), and more from Le Peloua, Saucats, Aquitaine Basin (5 specimens; Burdigalian, Early Miocene) and Termotura strata, Baldissero, Turin Hills, Italy (4 specimens; also Burdigalian), in the collection of Bernard Landau, demonstrate that early forms are consistently distinct from the Recent species. The earliest specimen of *Aspa* from Europe of which I am aware, from the Early Miocene (Aquitainian; Pierre Lozouet, MNHN, pers. comm., 2003) locality of Gaas, Landes, in the Aquitaine Basin of France, has a surprisingly tall spire and resembles the Indo-West Pacific species *Bufonaria margaritula* (Deshayes, 1832) (SMF, one specimen). The valid name for this earliest member of the lineage is *A. subgranulata* (d'Orbigny, 1852). It differs from *A. marginata* in having a higher spire, coarser sculpture of even granules, a row of nodules at the shoulder persisting onto the last whorl and an obsolescent lower row of nodules, and larger nodules inside the outer lip than in *A. marginata*. This apparently ancestral species therefore resembles the Indo-West Pacific species of *Bufonaria* and *Bursina* much more closely than does *A. marginata*. Cossmann & Peyrot (1924: 316-317) recognized an intermediate species, *A. depressa* (Grateloup, 1833), from Middle and Late Miocene rocks of Europe, but Landau *et al.* (2004: 70) regarded this as varying greatly enough to be considered a synonym of *A. marginata*. Hoernes & Aiunger's (1879) material from Lapugy,

western Roumania (Badenian, Middle Miocene), examined at NMHV, also seems best included in *A. marginata*.

The little-known name *Buccinum pleurotoma* was based on material from the Pleistocene of Altavilla, Palermo, Sicily, and, although the location of Calcara's specimens is not known to me, his drawing leaves no doubt that this name is a synonym of *Aspa marginata*.

Many recent European authors have credited the authorship of the name *Murex marginata* to "Martin," 1773, but as pointed out by Landau *et al.* (2004), this is an error for Martini (*in* Martini & Chemnitz, 1769-1795), a non-binominal work. The earliest available publication of this species name was by Gmelin (1791: 3486).

Dimensions.—TU 1240 = NMB 19008, Moín, Costa Rica: H 21.4, D 15.5 mm; Grund, Vienna Basin, Badenian (Middle Miocene; GNS WM5392): H 48.2, D 31.2 mm; Recent, 40 m, Tenerife, Canary Islands (GNS WM15205): H 29.2, D 23.3 mm; neotype of *Buccinum marginatum*, BMNH GG9183a: H 39.6, D 29.0 mm.

Types.—Gmelin (1791: 3486) cited only the figures by Martini (1777: pl. 120, figs 1101-1102) to illustrate *Buccinum marginatum*. As with all of Martini's material, the location of this specimen is unknown. Gmelin stated the locality as "Habitat – hactenus modo fossile repertum in Pedemontio." *Ranella laevigata* was also based on fossil specimens; Lamarck (1822: 154) gave the locality as "Habite ... Fossile de Piémont. Mon cabinet." However, no type material is present in either the zoological or paleontological collections in MHNG (Y. Finet, pers. comm., 1999); four Recent specimens of *Aspa marginata* in the Delessert collection (MHNG 27998) were not part of Lamarck's collection, and are not type material. Also, Lamarck type material in MNHN does not include any possible types of *Ranella laevigata* (examined, AGB, October 2004). *Eione inflata*, type material "presumed lost" (Arnaud, 1977: 120). Arnaud's publication of Risso's (1826b) plates leaves no doubt that this name is a synonym of *A. marginata*. Orlando *et al.* (1994) listed the types of 13 taxa described by Calcara, stored in the Museo dell'Istituto di Zoologia dell'Università di Palermo, but did not include *B. pleurotoma*, and its location is not known to me. However, it remains possible that this specimen exists in an Italian museum. Therefore, I am not aware of the location of *any* type material of *A. marginata* or any of its synonyms. A specimen in the Department of Palaeontology, BMNH, from the classical northern Italian Pliocene locality of Asti, is here designated the neotype of *Buccinum marginatum* Gmelin, 1791, the neotype of *Ranella laevigata* Lamarck, 1822, and the neotype of *Eione inflata* Risso, 1826. The neotype (BMNH Palaeontology Department, GG9183a; Pl. 51, Figs 1-3) is from the Asti sand beds at Valle Andona, near Torino, Italy, obtained by exchange with G. Pavia. Specimens from this lo-

cality are all a little abraded and incomplete, and the neotype has a small area of the outer lip missing at the anterior, but is chosen from here because it is thought to be the most likely source of northern Italian specimens of *A. marginata* during the 17th and 18th centuries. Pedriali & Robba (2005: 178, loc. 12) identified the age of this locality as late Zanclean to early Piacenzian, Early to "middle" Pliocene.

Other material examined.—**Recent:** The huge collections in museums of Miocene to Pleistocene material of *Aspa marginata* from central and southern Europe and of Recent material from the Ibero-Moroccan Gulf and West Africa are not listed here.

Fossils: Atlantic Costa Rica: Latest Pliocene-Early Pleistocene: Limón (McNeill *et al.*, 2000): NMB 19008 = TU 1240 (1, immature specimen; illustrated, NMB H 17901; Pl. 7, Fig. 2, Pl. 11, Fig. 3); 1240 (1 juvenile, illustrated by Robinson, 1991: pl. 14, fig. 11; and 1 other specimen); 1489 (1 large adult, illustrated by Robinson, 1991: pl. 14, fig. 12). Robinson (1991: 340) also pointed out that the large specimen collected by Gabb and misidentified by him (Gabb, 1881: 353) as *Bursa cruentata* is still present in ANSP (ANSP.IP 3391), and is another large Limón specimen of *A. marginata*.

Distribution.—*Aspa marginata* lives today in the Ibero-Moroccan Gulf and down the coast of West Africa from southern Spain to Angola (Gofas *et al.*, 1984: 132), and at the Canary and Cape Verde Islands and at Madeira. A single juvenile specimen was recorded from Seine Bank, Lusitanian seamounts, eastern Atlantic, Seamount 1 cruise, sta. DW78, 33°49'N, 14°23'W, in 235 m, by Gofas & Beu (1993: 102). The first Recent specimen seems to have been recorded by von Martens (1877: 236), who gave a description of a specimen taken off of the Cape Verde Islands (16°40'N, 23°11'W, 86 m, SM Corvette "Gazelle," 25 July 1874), pointed out that Gmelin's name *Buccinum marginatum* was the earliest for the species, and commented at length on Brocchi's (1814) "sub-appennine" fossils found living off of West Africa, but *not* in the Mediterranean. Records of Recent specimens from the western Mediterranean need confirmation; in the opinion of Serge Gofas (University of Malaga, pers. comm., 1992), there are no authentic Recent records of *A. marginata* from the Mediterranean Sea. Settepassi (1970: appendix, p. xi) illustrated an immature specimen ("var. *tuberculata*") collected on a beach at "an island of the Greek Archipelago," but suggested that it is a young fossil. Di Natale (1982) reported a Recent specimen from the southern coast of Sicily, but Gofas & Beu (2002: 102-104) suggested that this was dropped from fishing boats. Fossils occur widely in central and southern Europe in Miocene and Pliocene rocks of suitable shallow offshore facies. The southernmost specimen of which I am aware is a Pleistocene fossil from the "12.7 feet [3.8 m] beach," 55

km north of Swakopmund, Namibia (NMP 7868, 1 abraded specimen). In the Americas, the one fossil record is in the latest Pliocene-earliest Pleistocene Moín Fm at Limón, Costa Rica, where a total of 5 specimens is recorded at present. The occurrence of this very distinctive, now strictly West African species in Atlantic Costa Rica highlights the many changes that have occurred in the geographical ranges of tonnoideans during the Neogene.

Genus **CROSSATA** Jousseaume, 1881

Crossata Jousseaume, 1881: 175. Type species (by original designation): *Ranella ventricosa* Broderip, 1833, Pliocene to Recent, southern California to Peru.

Remarks.—*Crossata* is a distinctive genus of Bursidae containing (according to my interpretation) only one western American species of large size and of unusually short, wide shape for a bursid, although its spire is not as extremely short and wide as in *Aspa marginata*. The posterior siphonal canal is particularly widely open but shallowly excavated into the top of the outer lip, and the aperture is large and rounded with widely flared lips but little armature, other than 5 or 6 low, wide folds in the outer part of the outer lip. The varices are relatively low, and become quite ill-defined to almost obsolete on the last one or two whorls of many large specimens; they are aligned down opposing sides of the spire on small shells, but become significantly offset as the shell grows. The rest of the external sculpture also is weak, and consists of very low, weakly defined spiral cords and 4 slightly more prominent, widely spaced major cords, the upper 2 or 3 of which bear low nodules on most specimens, and the uppermost, at the shoulder angle, bears low to quite prominent, narrowly rounded nodules on most specimens. The operculum is evenly oval, rather than having a pointed anterior as in *Bursa*, with its nucleus a little to the right of the anterior end. *Crossata ventricosa* (below) reaches approximately 140 mm in height, and so is second only to the species of *Tutufa* in size in the Bursidae.

Crossata ventricosa (Broderip, 1833)

Pl. 7, Figs 1, 5, Pl. 8, Figs 1-7, Pl. 9, Fig. 2, Pl. 51, Fig. 7

Ranella ventricosa Broderip, 1833: 178; G. B. Sowerby II, 1836: pl. 92, fig. 16; d'Orbigny, 1841b: 451, pl. 62, figs 11-12; Kiener, 1842: pl. 14, fig. 2; Deshayes, 1843: 555; Reeve, 1844b: pl. 2, fig. 6; Hupé, 1854: 184; Tapparone-Canefri, 1876a: 118; Küster & Kobelt, 1871: 140, pl. 38a, figs 3-4.

Ranella tenuis Potiez & Michaud, 1838: 426, pl. 34, figs 1-2.

Ranella californica Hinds, 1843: 255 [April]; Reeve, 1844b: pl. 2, figs 9a-b [July]; Hinds, 1844b: 12, pl. 2, fig. 4 [October]; Küster & Kobelt, 1871: 141, pl. 39, fig. 5; Arnold, 1903: 287.

Ranella (Lampas) californica. Tryon, 1880: 40, pl. 22, fig. 42.

Ranella (Lampas) ventricosa. Tryon, 1880: 40, pl. 20, figs 16-18.

Crossata ventricosa. Jousseaume, 1881: 175 (reprint: 4); Beu, 1985: 66; Parth, 1996a: 135; Cossignani, 1994: 95; Beu, 2001: 711, fig. 1.8.

Crossata californica. Jousseaume, 1881: 175 (reprint: 4); Beu, 1988: 74; Albi, 2002: 33, figs 2-5, 7 (lower row), 8 (lower), 9 (lower row).

Bursa (Lampadopsis) calcipicta Dall, 1908: 320.

Bursa ventricosa. Dall, 1909b: 226; Basly Santa Maria, 1983: 19, pl. 5, fig. 43.

Bursa (Bufonaria) californica. Dall, 1921: 141; Oldroyd, 1927: 241, pl. 33, figs 7-8.

Bursa californica. Jordan, 1924: 149; 1926: 246; 1936: 113; Oldroyd, 1927: 241, pl. 33, figs 7-8; Grant & Gale, 1931: 731; Durham, 1950: 115, pl. 35, fig. 10; Keen, 1958: 348; McLean, 1978: 40, fig. 21.1.

Bursa (Crossata) ventricosa. Olsson, 1932: 186, pl. 21, fig. 1; Pilsbry & Olsson, 1941: 39; Ramírez, 1987: 150, fig. 186; Guzmán *et al.*, 1998: 46, illus.

Ranella (Lampas) ventricosa. Coulon, 1933: 138.

Bursa (Crossata) californica. Abbott, 1954: 199, pl. 20r; Abbott, 1974: 167, pl. 7, fig. 1783.

Bursa californica sonorana Berry, 1960: 118; Hertz, 1984: 24, fig. 50.

Bursa calcipicta. Keen, 1958: 348, fig. 328; 1971: 508, fig. 965 (in part, = *Ranella rugosa* G. B. Sowerby II, 1835).

Bursa sonorana. Keen, 1971: 509, fig. 967.

Crossata californica californica. Beu, 1985: 66; Cossignani, 1994: 91-92.

Crossata californica sonorana. Beu, 1985: 66, fig. 52; Cossignani, 1994: 93-94; Schneider, 1999: table 1.

Remarks.—The large, short, wide, robust shell identified here as *Crossata ventricosa* has little sculpture other than the one peripheral row of large, low nodes, and has a uniquely wide and shallow posterior canal for a bursid. It is common in shallow water (ca. 8-100 m) off of southern California, from approximately Monterey to the southern Gulf of California. There are few records of adult specimens from south of the gulf, until *C. ventricosa* becomes common again in Ecuador to Peru, but small specimens identified previously as *Bursa calcipicta* occur in ca. 10-120 m off of Costa Rica to northern Ecuador, and are concluded to be immature specimens of *C. ventricosa* linking the two adult populations. Parth (1996b) previously has pointed out the overlap in morphology between the supposed "species" *C. californica* and *C. ventricosa*, and suggested that these are part of the variation of one species, and I agree with this suggestion. Many of the southern, Peruvian specimens of *C. ventricosa* are plain dull cream, weakly nodulose shells that do not particularly resemble Californian specimens, but many other southern specimens are paler cream with narrow, medium-to-dark brown spiral bands around the nodule rows and prominent, narrow nodules, and closely resemble the southern, "*sonorana*" form of the northern population, previ-

ously known as *C. californica*. Northern specimens certainly reach a significantly larger size than specimens from south of the equator, but all other supposed differences intergrade, and in my opinion this is one species, with two main adult populations, north and south of the warmest tropical area, linked by the larval population and the few immature benthic specimens that manage to survive and grow in the intervening area. However, a molecular study is needed to confirm the suggested relationship. Hinds (1843: 256) himself realized that *Ranella californica* is very similar to *C. ventricosa*, and commented: "There is some chance that this shell may be confounded with *R. ventricosa*, as the more prominent features of both have only comparative value. This, however, is a much larger shell, is without any disposition to tuberculation near the suture, the varices are much bolder and cavernous, the tubercles on the spire fewer and larger, and the pillar lip is set with many small transverse ridges."

"*Bursa calcipicta*" is the most poorly known of western American Bursidae. This is partly because Dall (1908) did not illustrate this species when he named it, and partly because Keen (1971: 508) confused the real, offshore "*B. calcipicta*" (= juvenile *Crossata ventricosa*, in my interpretation) with another, more robustly sculptured *Bursa* species that lives commonly in the intertidal zone of rocky shores from Panama and the Galápagos Islands to Peru. I show above that the correct name for this common Panamic intertidal species is *B. rugosa*. The specimen illustrated by Keen (1971: fig. 965) is the holotype of *B. calcipicta* (USNM 123027; Pl. 8, Figs 3-4). Other relatively small (ca. 20-40 mm H) specimens agreeing with the holotype are present in LACM and USNM from relatively shallow offshore waters (8-120 m) from off of Cape San Lucas, Baja California Sur, and from Costa Rica to Ecuador (listed below). These specimens all are characterized (a) by a prominent, thick, finely reticulate intritacalx, forming a cream-colored layer over the pale brown teleoconch, (b) by a relatively thin, light-weight teleoconch, (c) by an only weakly curved siphonal fasciole, (d) by a deep, wide, and relatively long posterior siphonal canal (which, however, does not protrude beyond the whorl surface to form a semitubular spine, as it does in the robust, shallow-water species of *Bursa*, including *B. rugosa*), (e) by the low, strictly aligned varices, (f) by the subdued external sculpture, the spiral row of low, rounded nodules at the shoulder angle being the only prominent sculpture, and (g) by the widely open, weakly flared, and only weakly armed aperture. These characters are shared with *C. ventricosa*, and demonstrate that "*B. calcipicta*" was based on tall-spined, immature, deep-water specimens of *C. ventricosa*. The varices are strictly aligned in these small specimens of *C. ventricosa*, but gradually become a little further offset down the shell, to be offset about 20° in some large adult specimens.

The name *Bursa californica sonorana* (holotype illustrated by Hertz, 1984: fig. 50) was based on specimens dredged in the Gulf of California by commercial shrimpers. The shell is a little taller and narrower and the peripheral nodules of most specimens a little larger and sharper than on most specimens from San Diego and farther north. The large LACM collections include a few lots of this form from the northern Gulf of California, but again all taken by shrimp boats. A few specimens of the "*sonorana*" form also are present in the LACM collection from well north of the Gulf of California (LACM 70-28, 27 m, near W end of Catalina Island, California, 33°28.2'N, coll. J. H. McLean, 14 June 1970; 1 tall, with large nodules). In contrast, several lots at the LACM collection are "typical *C. californica*" from south of the supposed range of the "*sonorana*" form (e.g., LACM-AHF 974-39, 30-50 m, off of Isla Isabel, W Mexico, 21°54'10"N; 1 large, short-spined, with small nodules, and a heavily callused, subcircular aperture). It appears that the specimens of the "*sonorana*" form might all have been collected in deeper water than the other, shorter specimens, and so exhibit the usual ranellid and bursid progression into a taller and narrower form in deeper water. In any case, their ranges overlap and the "*sonorana*" form cannot be a subspecies of *C. californica*. In my opinion the "*sonorana*" form is merely a variant of no taxonomic significance in the clinal variation displayed by the single species *C. ventricosa*.

In the north of the species' range, fossils are recorded from the Pliocene of Los Angeles and the San Diego area (Arnold, 1903; Grant & Gale, 1931: 732; Albi, 2002) and from Pleistocene terrace faunas from Pacific Beach, San Diego, California, and in the lower Gulf of California and the Mexican coast just to the south (Jordan, 1924, 1926, 1936; Grant & Gale, 1931: 732; Durham, 1950: 115). A small Pliocene specimen is recorded here from Valiente Peninsula, Bocas del Toro Basin, on the Atlantic coast of Panama. The specimen has been identified as *Crossata ventricosa* because of its very weak spiral sculpture, its large peripheral nodules, its widely open posterior canal, and its deeply excavated columella. Other fossils are recorded from the Miocene(?) Tumbes Fm in Peru (Olsson, 1932: pl. 21, fig. 1), the Pliocene Canoa Fm in Ecuador (Pilsbry & Olsson, 1941: 39), basal shell ledges of the Late Pliocene(?) Golf Course Member of the Taime Fm at Bahia Taime, northwestern Peru (DeVries, 1988: 129), and the Pliocene Onzole Fm in Ecuador (below).

Dimensions.—Lectotype of *Ranella ventricosa*: H 81.3, D 55.4 mm; paralectotypes: H. 67.5, D 46.4 mm, and H 61.5, D 45.0 mm; holotype of *Bursa californica sonorana*: H 98.8, D 62.2 mm; *R. californica*, neotype: H 90.4, D 66.3 mm; Recent, LACM-AHF 1025-39, intertidal, Horse Cove, near Pyramid Cove, San Clemente Island, California: H 137, D 92 mm (largest seen); southernmost large, typical "*californica*" form, LACM-AHF 974-39, 30-50 m, off of Isla Isabela, W

Mexico, 21°54'10"N: H 76.0, D 53.8 mm; LACM 35-24, 16-18 m, Bahia Independencia, Peru: H 63.5, D 43.0 mm, and H 48.1, D 33.1 mm; holotype of *B. calcipicta*: H 44, D 25 mm (Dall, 1908: 320); other specimens identified as *B. calcipicta*: LACM-AHF 863-83, Bahia Honda, Panama: H 42.8, D 27.8 mm; LACM-AHF 212-34, off of La Plata Island, Ecuador: H 41.4, D 29.8 mm; fossils: USNM 645258, Onzole Fm (Early Pliocene), Punta Gorda, Ecuador: H 64.2, D 46.9 mm; figured specimen, NMB H 17902, from NMB 17854, Valiente Peninsula, Atlantic coast of Panama: H 45.0, D 30.8 mm.

Types.—*Ranella ventricosa*, three syntypes BMNH 1950.11.28.1-3, from "Bay of Callao, Peru." The largest specimen, marked "holotype," is the syntype figured by Reeve (1844b: pl. 2, fig. 6), and is here designated the lectotype (Pl. 8, Figs 1-2; one paralectotype also illustrated, Pl. 8, Fig. 6). *Ranella tenuis*, type material originally in the Muséum de Douai, northern France, but destroyed during World War II (P. Bouchet, MNHN, pers. comm., 2001); the lectotype of *R. ventricosa*, BMNH 1950.11.28.1, is therefore here also designated the neotype of *R. tenuis*. *Ranella californica*, type material [*i.e.*, specimen(s?) illustrated by Hinds and Reeve] not present in BMNH; Cossignani (1994) stated that Hinds' (1844b) figured specimen is in the USNM, but this assumption is incorrect, and apparently the figured specimen was (as with *Triton vestitum* Hinds, 1844) among the type material from the *Sulphur* voyage sold by Captain Sir Edward Belcher (Keen, 1966). A specimen in BMNH, no. 1842.1.22.634, is labelled "*californica*, Hinds" and "California, R. B. Hinds, esq." and, although this is a shorter and much plainer, medium brown shell, and not that illustrated by Hinds (1844b: pl. 2, fig. 4) or Reeve (1844b: pl. 2, fig. 6), there is no doubt that it is an authentic specimen collected during the *Sulphur* voyage, and so possibly a syntype. This specimen (Pl. 8, Fig. 7) therefore is here designated the neotype of *R. californica*. The type locality is San Diego, California, USA, the locality stated by Hinds (1843, 1844b). *Bursa (Lampadopsis) calcipicta*, holotype USNM 123027 (Pl. 8, Figs 3-4), from USS *Albatross* sta. 3368, near Cocos Island, Gulf of Panama, in 120 m. *Bursa sonorana*, holotype CASIZ 43931 (*ex* Stanford University collection, SU 9510), from near Guaymas, Sonora, Mexico (*i.e.*, presumably from Guaymas shrimpers); with one paratype, SDNHM 42802 (Hertz, 1984: 24).

Other material examined.—**Recent:** *Crossata californica* form, LACM collection: northernmost record is 20-25 m, on sand, near mouth of Salinas River, Monterey Bay, California, 36°44'30"N, 121°49'30"W (LACM-AHF 888-38, 6 large specimens). Other lots are from southern California (128 lots), outer coast of northern Baja California (30 lots), outer coast of central Baja California (38 lots), outer coast of Baja California Sur (6 lots), Gulf of California (9 lots), southern Mexico (1

small specimen, LACM-AHF 485-35, 12 m, Tenacatita Bay, Jalisco, 15 February 1935, 19°18'N, 104°50'W; H 31.2, D 22.0 mm), Costa Rica (3 lots, each of 1 small juvenile), Panama (2 lots, again each of one juvenile), Colombia (1 juvenile only), and Ecuador (3 lots, again each of 1 juvenile or small shell only). Typical, large southern specimens of *C. ventricosa* in the LACM collection are nearly all from off of Peru (the northernmost is the single Ecuador record of large specimens: LACM-AHF 398-35, 6 m on sand, off of Salango Island, Ecuador, 1°35'15"S, 80°52'52"W, 18 January 1935, 2 specimens); the other 35 lots are from Peru (from LACM 66-129, 118-133 m, W of Paita, 4°57'-5°01'S, 81°23'W, *Anton Bruun* cruise 16, sta. 625A, 2 June 1966, 4 specimens; south to LACM-AHF 824-38, 20-40 m, on sand and shell, San Juan Bay, Peru, 15°20'30"S, 75°10'07"W, 7 February 1938, 21 specimens; LACM 385-24, Bahia Independencia, Peru, 2 immature specimens illustrated, Pl. 8, Fig. 5, Pl. 9, Fig. 2). *Crossata ventricosa* evidently is common off of Peru, because several LACM lots have many specimens (*e.g.*, LACM 66-135, NW of Isla Lobos de Tierra, 146 m, 46 specimens; LACM 66-146, W of Isla Macabi, 170 m, 29 specimens). **The "*calcipicta*" form:** U.S. Fish Commission sta. 2758, 40 m, SE of Cape San Lucas, Baja California, *Albatross*, 22°52'N (USNM 125665, 1; resembles holotype of *B. calcipicta*); 8-14 m, N side of Isla del Caño, Puntarenas Province, Costa Rica, *Searcher* sta. 471-474, 14-19 March 1972 (LACM 72-63, 1); 60-100 m, off of Bahia Honda, Panama, 1 March 1938 (LACM-AHF 863-83, 1); 60-70 m, off of Medidor Island, Bahia Honda, Panama, 28 March 1939 (LACM-AHF 948-39, 1); 90 m, off of Port Utria, Colombia, 24 January 1935 (LACM-AHF 415-35, 1); 90 m, Tagus Cove, Albermarle Island, Galápagos Islands, 10 December 1934 (LACM-AHF 324-35, 1); 16-20 m, off of Bahia Santa Elena, Ecuador, 9 February 1934 (LACM-AHF 209-34, 1); and 90-110 m, off of La Plata Island, Ecuador, 10 February 1934 (LACM-AHF 212-34, 1).

Fossils: **California: Pliocene:** LACMIP loc. 305, San Diego Fm, K Ranch, hills south of Tijuana River, San Diego Co (*ca.* 80 specimens). **Early Pleistocene:** Santa Barbara Fm, Rincon Hill, Santa Barbara Co, collection of Bernard Landau (1). **W Mexico: Pleistocene:** Bahia de Santa Inés, near Mulegé, Baja California Sur, Mulegé Terrace cover deposit (oxygen isotope stage 5e), collection of Bernard Landau (2). **Atlantic Panama: Early Pliocene:** Shark Hole Point Fm: NMB 17854, Shark Hole Point, Valiente Peninsula, Bocas del Toro Basin (1, small; illustrated, NMB H 17902; Pl. 7, Figs 1, 5). **Ecuador: Pliocene:** USGS 23479, Onzole Fm, Punta Gorda (1); NMB 19141, Onzole Fm (1, frag); loc. CRB 291, Onzole Fm, Quebrada Camarones, 0°59'N, 79°34'W, 20 km E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town (BMNH Palaeontology Department,

1 small, short-spined, with very prominent varices; Pl. 51, Fig. 7). **Peru: Miocene:** PRI 2310, Tumbes Fm, Quebrada Tucillal, Zorritos (1; specimen figured by Olsson, 1932: pl. 21, fig. 1).

Distribution.—*Crossata ventricosa* occurs as large adults in relatively shallow water (ca. 8–100 m) from Monterey, California, USA, south to the Gulf of California (Keen, 1971); smaller specimens seem to link the two populations of larger adults, as well as occurring at the Galápagos Islands, and then it occurs again as relatively shallow-water adults from southern Ecuador to Peru. This, then, appears to be a single clinally varying species with adults in relatively cool northern and southern waters, linked through the tropical eastern Pacific by planktonic larvae and a few small specimens that manage to survive in offshore waters, although apparently not reaching breeding size. Large, typical specimens of the *californica* form are commonly collected by scuba divers or dredged off of southern California, from Santa Barbara to San Diego and at the Channel Islands (Jim McLean, LACM, and the late Bob Foster and Charles Glass, pers. comm., both 1979), whereas specimens from the Gulf of California appear to be collected only in deeper water by shrimp trawlers. Similarly, specimens from Peru and southern Ecuador were obtained from fishermen's nets, or dredged in ca. 6–170 m. Fossils are recorded from Pliocene rocks around Los Angeles and San Diego, from Pleistocene terraces of San Diego and Baja California (e.g., Emerson *et al.*, 1981: 111; Turtle Bay, Baja California Sur), from the Pliocene of the Bocas del Toro Basin on the Atlantic coast of Panama (demonstrating that the Panama Isthmus had not been elevated at that time), and from the Miocene(?) Tumbes Fm of Peru and the Pliocene Onzole and Canoa Formations of Ecuador.

Genus **MARSUPINA** Dall, 1904

Buffo Montfort, 1810: 574 (*nomen oblitum*). Type species (by monotypy): *Buffo spadiceus* Montfort, 1810 (= *Murex bufo* Bruguière, 1792), Pliocene to Recent, western Atlantic.

Marsupina Dall, 1904: 118 (*nomen protectum*). Replacement name for *Buffo* Montfort, 1810, supposedly a junior homonym of *Buffo* Lacépède, 1788 (Amphibia; rejected by ICZN Opinion 2104, 2005).

Bechthelia Emerson & Hertlein, 1964: 360. Type species (by original designation): *Gyrineum strongi* Jordan, 1936, Pleistocene, Gulf of California.

Remarks.—*Buffo* Montfort, 1810, has been rejected in the past (following Dall, 1904) as supposedly a junior homonym of *Buffo* Lacépède, 1788 (Amphibia). I am grateful to Philippe Bouchet (MNHN, pers. comm., February 2009) for pointing out that Lacépède's (1788) work has been ruled nonbinominal and placed on the Official Index of Rejected and Invalid

Works in Zoological Nomenclature by ICZN Opinion 2104 (2005), and the valid amphibian name is *Bufo* Laurenti, 1768. Adoption of the generic name *Buffo* would make the correct name for the type species *Buffo bufo* (Bruguière, 1792), because *Murex bufo* Bruguière is a senior synonym of *Buffo spadiceus*. This would be confused forever with the name of the European toad, *Bufo bufo* (Linnaeus, 1758), so rejection of *Buffo* Montfort is exceedingly desirable. Because *Marsupina* has been used as a valid generic or subgeneric name at least 25 times by at least ten authors over the last 50 years, and *Buffo* Montfort has not been used as a valid name after 1899 (indeed, I am not aware of any usages as a valid name after it was proposed), *Marsupina* is here declared a *nomen protectum* under ICZN Article 23.9.1. It is mandatory to adopt *Marsupina* Dall, 1904, instead of *Buffo* Montfort, 1810. Clarification of the type species is needed, however, because Montfort (1810: 573) provided a clear woodcut of the species here identified as *M. bufo* (Bruguière, 1792), but added (Montfort, 1810: 574) a reference to a figure by “Martin. 4” (i.e., Chemnitz, 1780: pl. 128, figs 1233–1234). This is a rather poor drawing of *Gyrineum gyrinum* (Linnaeus, 1758), presumably the illustration that Montfort thought showed the nearest resemblance to *M. bufo* of those of which he was aware. As first reviser, I select the specimen illustrated by Montfort (1810: 573) as the lectotype of *Buffo spadiceus*.

The required list of 25 usages of the name *Marsupina* as a valid genus or subgenus during the last 50 years is as follows: (1) Jung (1969: 487); (2) Coelho & Matthews (1971: 55); (3) E. Vokes (1973: 100); (4) Abbott (1974: 167); (5) Rios (1975: 82); (6) Petuch (1982: 301); (7) Beu (1985: 65); (8) Rios (1985: 80); (9) Vaught (1989: 37); (10) Rios (1994: 93); (11) Cossignani (1994: 39–40); (12) Petuch (1994: pl. 39, figs D–E); (13) Petuch (1997: 223); (14) Landa-Jaime & Arciniega-Flores (1998: 161); (15) Lindner (1999: 89); (16) Macsotay & Campos Villarroel (2001: 70); (17) Beu (2001: 711); (18) López de la Fuente & Ramos (2004: 86); (19) Beu (2005: 8); (20) Cantalamessa *et al.* (2005: 6); (21) Vermeij (2005: 641); (22) Landau *et al.* (2007: 54); (23) Petuch & Roberts (2007: 104); (24) Landau *et al.* (2008: 457); (25) Robin (2008: 150). The name *Marsupina* also appears as a valid genus-group name in several “official” on-line catalogs, such as the Panama Paleontology Project catalog of genera (Todd, 2000) and the Paleobiology Database, and in a huge number of club and dealer webpages.

Marsupina is treated here as a restricted American genus with a dorsoventrally compressed, finely granulose shell, agreeing with the Indo-West Pacific genus *Bufo* in most characters, but having an anterior opercular nucleus as in *Bursa*, rather than one with the nucleus in the center of the left (columnellar) edge, as in *Bufo*. Species of *Marsupina* have an evenly biconic shape brought about by the envelopment of

preceding whorls up to the edge of the sutural ramp by the succeeding whorl, and by the joining of posterior siphonal canals (at least partly) into semicylindrical gutters extending up the opposing sides of the spire. Varices are strictly aligned up opposing sides of the spire in all species, probably necessitated by the style of posterior siphonal canal. Recognition (Beu, 2005: 24) of the separate genus *Bursina* Oyama, 1964, for Indo-West Pacific shells with a teleoconch similar to that of *Bufonaria* (although with finer surface granules, lower nodules and, in several species, longer posterior siphonal canals), but with an operculum with an anterior terminal nucleus as in *Bursa* and *Marsupina*, suggests the possibility that *Marsupina* and *Bursina* are sister taxa. Because *Marsupina* has been discrete in the Americas since at least Eocene time [*M. chira* and *M. yasila* of Olsson (1930), Eocene and Oligocene of Peru] but no species of *Bursina* have been recognized in the Indo-West Pacific before Miocene time, *Marsupina* is here maintained as a separate genus. Further studies of its relationships are obviously warranted, and this is an example of the sort of biogeographical question that will be best solved by a molecular phylogeny. A single species lives on each side of tropical America at present [*M. bufo* (Bruguière, 1792) in the western Atlantic; *M. nana* (Broderip & Sowerby, 1829) in the eastern Pacific], but the genus was a little more diverse in western tropical and South America previously.

***Marsupina bufo* (Bruguière, 1792)**

Pl. 9, Figs 1, 3-15, Pl. 10, Figs 1-3, 5

Murex bufo Bruguière, 1792b: 126.

Bursa gibbosa Röding, 1798: 128.

Buffo spadiceus Montfort, 1810: 575.

Ranella granulata Lamarck, 1816: pl. 412, fig. 4, "Liste des objets": 4; Lamarck, 1822: 152; Kiener, 1841: 18, pl. 12, fig. 1; Deshayes, 1843: 547.

Murex crassus Dillwyn, 1817: 692.

Ranella crassa. d'Orbigny, 1841a: 134; Reeve, 1844b: pl. 4, figs 18a-b; Krebs, 1864: 25; Guppy, 1866: 288, pl. 18, fig. 9; 1874: 438; 1876: 522; Tryon, 1880: 38, pl. 19, fig. 10.

Bursa crassa. Gabb, 1873: 212; Maury, 1917a: 108, pl. 17, figs 6-7; Olsson, 1922: 306, pl. 15, fig. 19; Maury, 1925: 217; M. Smith, 1948: 24, pl. 9, fig. 8.

Ranella spadicea. Mörch, 1877: 23.

?*Bursa nana*. Gabb, 1881: 353 (not *Ranella nana* Broderip & Sowerby, 1829).

Gyrineum crassum. Dall, 1903a: 1584.

Bursa crassa proavus Pilsbry, 1922: 360, pl. 29, figs 4-5.

Bursa crassa bowdenensis Pilsbry, 1922: 360, pl. 29, fig. 8.

Bursa (Marsupina) proavus bowdenensis. Woodring, 1928: 303, pl. 19, fig. 4.

Bursa crassa colombiana Weisbord, 1929: 41, pl. 8, figs 1-2.

Bursa spadicea. McGinty, 1940: 71; 1962: 41; van Regteren Altena, 1975: 38, pl. 6, figs 8-9; Diaz & Götting, 1988: 156; Diaz & Puyana, 1994: 174, fig. 651.

Bursa crassa caribbaea M. Smith, 1948: 25, pl. 9, fig. 10.

Bursa (Bufonaria) spadicea. Morrison, 1949: 11; Abbott, 1954: 198, pl. 25, fig. p; Warmke & Abbott, 1962: 103, pl. 18, fig. l; Humfrey, 1975: 127, pl. 14, figs 7-7a; Rios, 1970: 75, pl. 18, lower left fig.

Bursa (Marsupina) bufo. Jung, 1969: 487, pl. 49, figs 3-6; Abbott, 1974: 167, pl. 7, fig. 1782; Rios, 1975: 82, pl. 23, fig. 333; 1994: 93, pl. 31, fig. 367; Macsotay & Campos Villarroel, 2001: 70.

Bursa (Marsupina) spadicea. Coelho & Matthews, 1971: 55, figs 16-17.

Marsupina bufo. E. Vokes, 1973: 100; Beu, 2001: 711.

Bursa amphitrites. E. Vokes, 1973: 100 (in part not *Bursa amphitrites* Maury, 1917).

Bursa bufo. Finlay, 1978: 150; Princz & Pacheco, 1981: table; Cosel, 1986: 241, fig. 155; Lipe & Abbott, 1991: 14, illus.

Bursa (Colubrellina) bufo. Okutani, 1983: 263, illus.

Bufonaria (Marsupina) bufo. Beu, 1985: 65, fig. 48; Rios, 1985: 80, pl. 28, fig. 350; Cossignani, 1994: 39-40.

Bufonaria bufo. Calvo, 1987: fig. 84 (radula).

Bursa proavus. Petuch, 1992: 108, fig. 3H.

Bursa (Marsupina) proavus. Petuch, 1994: pl. 39, figs D-E; 1997: 223.

Remarks. — The living population of *Marsupina bufo* is variable in a large range of characters, demonstrating that related fossil species need to be interpreted with care. Recent specimens reach quite a large size (up to at least 70 mm H) and are tall and narrow, dorsoventrally compressed, moderately to weakly granulose all over most specimens, conspicuously biconic because of their combination of a rather long, gradually tapered last whorl and neck with an equally tall spire made straight-sided by the enclosure of earlier whorls up to the shoulder of the sutural ramp by succeeding whorls, and have an elongate-oval aperture with prominent transverse ridges on the interior of both lips, and a tall, deep, widely open posterior canal that, in most specimens, does not protrude as a spine above the varix, but extends up the surface of the whorl to fuse (or nearly so) with the canal of the previous whorl. The varices of the last few whorls are low, wide, and strictly aligned. Many specimens have a fairly coarsely nodulose early spire, but the granulose sculpture becomes progressively weaker over the last few whorls so that, on many but by no means all specimens, the last whorl is smooth or only faintly nodulose and quite highly polished. An excellent color illustration by Okutani (1983: 263) clearly shows the rich red-brown coloration and highly polished, yet still weakly granulose, surface of a moderately large but rather short specimen, which is a little unusual in that the posterior canals of the last whorl form short spines. It is important for understanding the variation of fossils to note that small (young) specimens in the same samples as living specimens differ from the adults in having a shorter and wider shape, with a more sharply contracted neck,

much more prominent varices, and consistently coarse granulate sculpture, with small rounded granules over the entire teleoconch surface, and a row of small to moderately large, conspicuous nodules around the shoulder angle. Some weakly sculptured adult specimens bear prominent nodules in a row around the shoulder angle, whereas others have at most very weak nodules and the shoulder angle weakly expressed. A few of the weakly sculptured adults have a single large, rounded nodule on the shoulder angle midway between the varices, a character not observed on any fossils. The slope of the sutural ramp increases with growth in some specimens also, so not only do some juvenile specimens have proportionally shorter spires than adults, but also the spire outline of many specimens is weakly convex. The protoconchs of the juvenile specimen in MCZ 274189 (*ca.* 100 km N of Georgetown, British Guiana) and of the abundant RMNH material from off of Suriname are similar in shape to the low-turbineform ones seen in most other Bursidae, but are only half the size of those of other bursids, and are distinctive in having elaborate cancellate sculpture over the entire surface.

The interpretation of fossils is made difficult because most are small (*i.e.*, young) specimens, still relatively robustly sculptured (*e.g.*, Vokes, 1973: figs 1a-b), with prominent varices and a sharply contracted neck. The living population demonstrates that these characters result mainly from the small fossils being immature; they are closely similar to Recent juveniles. The relatively few large adult specimens (identified by being at least 50–60 mm H) available from Miocene and Early Pliocene rocks show that these early specimens of the *Marsupina bufo* group differ from Recent ones in consistently being coarsely granulate over the entire teleoconch surface, and in having moderately to very conspicuous nodules around the well-marked shoulder angle. The difficulty with the taxonomy of this species complex is that the change from coarsely granulate adults to variable but mostly weakly sculptured adults seems to have taken place very gradually. It is a gradual, anagenetic change, rather than an abrupt speciation event. In this situation, although evolution definitely has occurred, there is no point at which the complex can be subdivided into species in any unambiguous way. I have therefore adopted the treatment of this same species complex arrived at previously by Morrison (1949) and Jung (1969: 417–418), who regarded all Miocene to Recent taxa proposed in this complex as part of the single species, *M. bufo*.

Dimensions.—*Murex bufo*, neotype, and lectotype of *Ranella granulata*: H 58.3, D 29.5 mm; *Bursa crassa bowdenensis*, holotype: H 49.1, D 28.9 mm; *B. c. proavus*, holotype: H 25.3, D 19.5 mm; USGS 23741, Bowden, Jamaica: H 27.5, D 19.4 mm; *B. c. colombiana*, holotype: H 34.8, D 22.9 mm; Recent, AMNH 190116, off N coast of Brazil: H 63.0, D 36.2 mm; USNM 369464, Woodring's (1928) figured speci-

men, Bowden: H 67.8, D 37.1 mm; NMB H 15150, hypotype of Jung (1969: pl. 49, figs 5–6), Talparo Fm, Matura, Trinidad: H 74.7, D 44.9 mm.

Types.—No original material remains in MNHN or MHNG of *Murex bufo*. As pointed out by Lamy (1930: 54–55), Bruguière's collection was purchased by the Ministre de l'Intérieur, France, in 1799 for FF 6,000, and incorporated into MNHN. There, however, it seems to have been at least partially "acquired" by Lamarck; virtually no original Bruguière material is identifiable now in MNHN, but a few specimens are recognizable in Lamarck's collection in MHNG. This does not include *M. bufo*, however, and because it was described from material "sent from Cayenne, to the Société d'Histoire Naturelle de Paris," the original material possibly belonged to the Society rather than to Bruguière. The location of any type material is unknown. Also, no original material is known for the names proposed by Röding (1798). The lectotype (designated above) of *Buffo spadiceus* is, of course, also long lost. *Ranella granulata*, 2 syntypes MHNG 1098/84 and 1098/85, without locality; the type locality is here designated as off of Cayenne, Guiana. The specimens are conspecific; the larger one closely matches the illustrations by Lamarck (1816: pl. 412, fig. 4) and Kiener (1841: pl. 12, fig. 1). The larger syntype of *R. granulata*, MHNG 1098/84 (Pl. 10, Figs 1–2), is here designated as the lectotype of *R. granulata*, as well as the neotype of *Murex bufo* Bruguière, 1792, the neotype of *Bursa gibbosa* Röding, 1798, the neotype of *Buffo spadiceus* Montfort, 1810, and the neotype of *Murex crassus* Dillwyn, 1817. Dean (1936: 231) discussed the material remaining in Dillwyn's collection in the National Museum of Wales, Cardiff, and identified four species represented by lectotypes. One is present for *Murex mulus* Dillwyn, 1817 [= *Distorsio reticularis* (Linnaeus, 1758)] but none is present for any other tonnoidean, including *Murex crassus*. *Bursa crassa proavus*, holotype ANSP/IP 3227 (Pl. 9, Fig. 14), Late Miocene–Early Pliocene, Dominican Republic, *ex* Gabb collection [the specific epithet is a noun in apposition (Latin, grandfather) and should not be declined]. *Bursa c. bowdenensis*, holotype ANSP/IP 3747, from Bowden shellbed, Jamaica, Late Pliocene. The specimen in ANSP illustrated by Pilsbry (1922: pl. 19, fig. 8) is labelled "syntype," but Pilsbry (1922: 360) expressly stated "Type no. 3747 ANSP," so this specimen is the holotype (Pl. 9, Figs 7–8). *Bursa c. colombiana*, holotype PRI 22964 (Pl. 9, Figs 3, 5), from near Tuhera Cedral, Morro Hermoso, Departamento de Atlantico, Colombia, "Middle Miocene." *Bursa c. caribbaea*, type material not seen, location not known to me, presumably originally in the private collection of M. Smith.

Other material examined.—**Recent:** **Florida:** 300 m, S of Key West (AMNH 154660, 3); off of Dry Tortugas (DMNH 107676, 1). **Atlantic Honduras:** 40 m, off of Honduras (AMNH 120905, 1; GNS WM13601, 3). **Atlantic Panama:**

3 km N of Colon, in 20 m (MCZ, 3); E Panama (AMNH 48094, 2; LACM-A. 1463, 1); Colon (USNM 589555, 1). **Cuba:** Matanzas Bay (AMNH 84362, 1); shallow water at low tide, Matanzas Bay (ANSP 315431, 1). **Trinidad:** *R/V Chain* cruise 35, sta. 44, dredged in 30 m, 16 km S of Moruga Pt, S Trinidad (MCZ 274315, 2); Manzanilla Bay (AMNH 190492, 1); Gulf of Paria, dredged, C. J. Finlay collection (now at FAU, 1); Gulf of Paria (USNM 432407, 1). **Antillean islands:** "West Indies" (ANSP 36913, 4); Barbados (AMNH 190493, 10; AMNH 136208, 1; AMNH 141822, 5; C. J. Finlay collection, now at FAU, 1). **Colombia:** R. von Cosel's material in SMF: 18 lots from shrimp boats, offshore along the entire Colombian coastline; westernmost: 6-7 m, off of Punta Caribana, entrance to Gulf of Uraba (1); easternmost: 40-45 m, SE of Punta Espada, Goajira Peninsula (1). **Venezuela** (at NMB, J. & W. Gibson-Smith collection): Laguna la Reina, Estado Miranda (NMB 17687, 2); Adicora, Paraguaná Peninsula, Falcón (NMB 17666, 16); La Vela de Coro, base of Paraguaná Peninsula, Falcón (NMB 17668, 17); Puerto Cumarebo, Estado Falcón (NMB 17669, 5); RV *La Salle* sta. 13A, Orinoco Delta, September 1971 (NMB 17734, 1); Juan Griego, Isla Margarita (NMB 17696, 1). Other localities: coast at Coro (ANSP 42577, 1); 40-60 m, on mud, 5 km N of Coche Island (LACM-AHF. A.33-39, 3). **Guiana:** 118 lots (more than 500 specimens, most juvenile) dredged from Suriname shelf examined at RMNH, from *Coquette*, *Luymes*, *Snellius*, etc. expeditions; *R/V Chain* cruise 35, sta. 40, ca. 100 km N of Georgetown (MCZ 274289, 1 juvenile); 60 m, off of Suriname (AMNH 125516, 2); trawled between Georgetown and Paramaribo, *Amazon* (AMNH 142276, 1); 40-60 m, off of French Guiana (GNS WM17388, 9); Suriname (ANSP 246576, 1); off of Paramaribo, Suriname, *Coquette* sta. 166 (USNM 670449, 2); mouth of Mattippicca Canal, Suriname (USNM 635255, 2). **Brazil:** shrimpers off N coast of Brazil (AMNH 190116, 11); dredged, 40 m, off of Cabo Maguari, Ilha Marajo, N Brazil (AMNH 140141, 2; 140143, 2); *R/V Oregon II* cruise 58, sta. BBC-1602, 70-80 m, off of Calcoene, Guiana Basin, Brazil (USNM 767410, 1); 112 m, on mud, off of Amalpa (LACM 55550, 2); 32 m, off of Cossiporé, Amalpa, *N/O Almirante Saldanha* (GNS WM14011, 2).

Fossils: **Florida: Middle Miocene:** TU 69a, Shoal River Fm, Shoal River, first ravine upstream from Shell Bluff, Florida (USNM 647109, 1 juvenile; specimen figured by Vokes, 1973: figs 1a-b) as *Bursa amphitrites*; Pl. 9, Fig. 6). Petuch (1994: pl. 39, figs D-E) also illustrated a specimen from the middle Pliocene (late Piacenzian, Petuch, 1994: 19; middle Pliocene, Vermeij, 2005: 628) Pinecrest fauna, Tamiami Fm at "Bird Road dig," Miami. **Jamaica: Late Pliocene,** Bowden: USNM 115480 (1); USGS 24743 (3); 2580 (8); USNM 339464 (1; specimen figured by Woodring, 1928: pl. 19, fig. 4; illustrated here, Pl. 9, Figs 1, 4); NMB

11146 (1; illustrated, Pl. 9, Figs 10-11); NMB 10651 (1); BMNH Palaeontology Department, G64025 (2; specimens recorded by Guppy, 1866: 288); BMNH Palaeontology Department, G64073 (1, specimen figured by Guppy, 1866: pl. 18, fig. 9); BMNH Palaeontology Department, GG3860 (1); UCMP S-2 (1). **Dominican Republic: Late Miocene:** Cercado Fm: NMB 16982 (1); Cercado Fm, Río Cana, collection of Bernard Landau (1); Gurabo Fm: TU 1449 (GNS WM18856, 1). **Late Miocene/Early Pliocene:** Gurabo Fm: NMB 16821 (1); TU 1451 (GNS WM16946, 1); "Río Cana?" (PRI 28761, 1; specimen figured by Maury, 1917a: pl. 17, figs 6-7). **Early Pliocene:** Mao Fm: NMB 15833 (1). **Trinidad: Pleistocene,** Matura: USGS 19860, USGS 18204, and USNM 645672 (7); NMB H 15150 (1, specimen figured by Jung, 1969: pl. 49, figs 5, 6; illustrated here, Pl. 9, Fig. 12); NMB H 15151 (1; specimen figured by Jung, 1969: pl. 49, figs 3-4); NMB H 15149 (1). **Pacific Costa Rica: Pleistocene:** USGS 24792, stream courses including Río Vaca, crossed by Progreso-Largato trail, Puntarenas Province. (1). **Atlantic Costa Rica: Pliocene,** Banáno Fm: NMB 17446 (1); 17448 (1); 17450 (3); 18096 (3); 18100 (1); TU 589 = NMB 19024 (3). **Latest Pliocene-Early Pleistocene,** Limón: USGS 8343 (4); TU 954 (GNS WM18857, 1 frag from a large shell); basal Moín Fm mudstone (late Pliocene), Rte. 32, 3 km W of Puerto Limón, coll. J. A. Todd, February 1998 (1, BMNH Palaeontology Department). Robinson (1991) also recorded this species from Limón, on the basis of one specimen collected by Gabb (ANSP.IP 3404). **Atlantic Panama: Pliocene:** Escudo de Veraguas Fm: NMB 17622 (1); 17849 (1); 18668 (1); Cayo Agua Fm: NMB 17812 (2); 17822 (1); 17827 (1); 18373 (1); 18720 (1); 18772 (1); apparently Fish Hole Reef Member of Shark Hole Point Fm (see Appendix 3); USGS 8307 (1). **Colombia: Miocene/Pliocene:** USGS 11356 (1); Arroyo Grande, 500 m NW of Megua, Departamento de Atlantico (UCMP S-8007, 1); lowermost sandstone, Point Canoas, Departamento de Bolivar (UCMP S-70, 4 large); *Turritella* bed above S-70 (UCMP S-71, 3); Arroyo Dorrera, W of Usiacuri, Departamento de Atlantico (UCMP S-7374, 1); as above (UCMP S-7385, 1); head of Arroyo Grande, Usiacuri, Departamento de Atlantico (UCMP S-7607, 1); Arroyo Mons near Boca de Arroyo Mons, Departamento de Atlantico (UCMP S-7511, 3); "Miocene, Colombia" (UCMP S-168, 1; C-9295, 1; C-12470, 3 large). **Pliocene:** USGS 11335 (1); Juan de Acosta (BMNH Palaeontology Department, G35044, 1). **Pleistocene:** USGS 8734 (1); 11010 (1); 11012 (1). **Venezuela: Pliocene:** NMB 12045 (1); 12892 (1); 13339, Cubagua Fm, Cerro Negro Member, Cañon de las Calderas, Cubagua Island (9; 2 illustrated, NMB H 18055, H 18056; Pl. 9, Figs 13, 15); same as last, collection of Bernard Landau, many (GNS WM17697, 9, pres. B. Landau); NMB 17512 (1); 17515 (1); 17531 (1); USGS

24564 (17); USNM, A. A. Olsson loc. 210, same as last (6); PRI loc. 1729, same as last (5); Cubagua Island, S of Isla Margarita (BMNH Palaeontology Department, G64569, 1); 400 m SW of house at Las Calderas, Cubagua Island, Nueva Esparta (UCMP S-122, 100+); Punta Gavilán, collection of Bernard Landau (1). **Pleistocene:** NMB 17607 (2).

Distribution.—*Marsupina bufo* is dredged commonly on the shelf in ca. 30–200 m at the present day, from southeastern Florida (McGinty, 1940; Abbott, 1974: 167), USA, south to Bahia, Brazil (Rios, 1994). Specimens are abundant in relatively shallow water along the northern coast of Venezuela, Suriname, and Guiana. Fossils are common at a few Miocene to Pleistocene localities, notably in the Early Pliocene of Cubagua Island, Venezuela, but are uncommon to rare at other localities, or somewhat surprisingly absent at still others. Specimens are rare in Dominican Republic localities. The specimens recorded by Gabb (1881: 353) from Limón, Costa Rica, as *Bursa nana* seem likely to refer to *Marsupina bufo*, because there are several other records of *M. bufo* from Limón. Rutten (1931: 664) recorded fossils [as *Bursa (M.) crassa*] from Pleistocene localities in Suriname, citing four earlier publications that I have not seen. All fossil localities where *M. bufo* has been collected are either on the Caribbean islands or on the Atlantic coasts of Florida (rare), Costa Rica, Panama, Colombia, Venezuela, and Suriname; there are virtually no records from the Pacific coast of western America. The one exception is a specimen from the Río Vaca (Plio-Pleistocene?), Puntarenas Province, Costa Rica. This again provides valuable evidence that the Central American seaway was not yet closed.

Marsupina freya (Olsson, 1932)

Pl. 10, Figs 6, 8–9

Bursa (Marsupina) freya Olsson, 1932: 187, pl. 21, figs 3, 4–6.

Bursa aff. *B. (Marsupina) freya*. Marks, 1951: 378.

Remarks.—*Marsupina freya* is a highly distinctive species differing from the living *M. bufo* and *M. nana* in its (a) much shorter and wider form, (b) much finer, closer, and more even, more uniform granulation of the whole teleoconch surface on all specimens, (c) markedly lower spire, and (d) proportionally larger but shorter aperture and long, widely open posterior siphonal canals extending up the spire. The shell as a whole is markedly dorsoventrally compressed, and much more closely resembles *M. bufo* than any other American Bursidae. This species also resembles the Indo-West Pacific species of *Bufonaria*, and particularly such short, wide species as *B. margaritula*. However, *M. freya* is similar in shape to *M. chira* and *M. yasila* (Olsson, 1930: 62–63) from the Oligocene and Eocene, respectively, of Peru, and this record indicates a long

evolutionary history in South America, rather than *M. freya* being a relatively recent arrival from the western Pacific.

The specimens described by Olsson (1932) had only two large, rounded nodules in each intervariceal interval on the obscurely defined shoulder angle, but it is clear that his specimens had a more finely nodulose periphery on spire whorls, and the degree to which the shoulder nodules are reduced on the last whorl should be expected to vary. The specimens identified by Marks (1951: 378) as “*Bursa* aff. *B. (Marsupina) freya*” differ from Olsson’s material only in having “three small, pointed nodes” in each intervariceal interval at the periphery, and clearly are conspecific. Twelve rather poor specimens (calcite neomorphs in hard, lime-cemented sandstone) from Malpais, Nicoya Peninsula, Costa Rica, appear to represent *M. freya*, and the best of them (Pl. 10, Fig. 9) agrees with the type material in all characters, including having only two peripheral nodules in each intervariceal interval, except that the granulose sculpture over the exterior surface is a little coarser than on the specimens illustrated by Olsson (1932: pl. 21, figs 3–4, 6).

Dimensions.—*Marsupina freya*, holotype: H 23.1, D 16.5 mm; NMB 17474, Nicoya Peninsula, Costa Rica: H 24.8, D 17.3 mm.

Types.—*Bursa (Marsupina) freya*, holotype PRI 2312 (Pl. 10, Figs 6, 8), with two paratypes 2313 and 2315 (specimens illustrated by Olsson, 1932: pl. 21, fig. 4 and pl. 26, fig. 6, respectively), from “Zorritos Miocene,” divide between Quebrada Conchudo Bravo and Quebrada Seca, Mancora, Peru (10 specimens; Olsson, 1932: 188).

Other material examined.—**Fossils: Pacific Costa Rica: Late Oligocene–Early Miocene:** NMB 17474, sandstone 2 km N of village at Malpais, SW coast of Nicoya Peninsula (12; 1 illustrated, NMB H 17903; Pl. 10, Fig. 9). **Ecuador: Miocene:** PRI loc. 11202, loc. 676 of Marks (1951), Subibaya Fm, Progreso Basin, SW Ecuador (PRI 4207C, 1).

Distribution.—*Marsupina freya* has been recorded previously only from the Miocene of Ecuador and Peru, and the range is extended a long way northward here, to the Nicoya Peninsula, Costa Rica. All three localities apparently are Miocene, and all lie along the Pacific coast of tropical America.

Marsupina judensis n. sp.

Pl. 10, Figs 4, 7, 10

?*Bursa (Colubrellina) caelata amphitrites*. Aguilar, appendix in Seyfried et al., 1985: 64 (not *Bursa amphitrites* Maury, 1917).

Description.—Shell of moderate size for genus (54 mm H), short, wide and solid, prominently angled at periphery, particularly on varices, with spire one quarter of height and height 1.4 times width, with very wide, very thick varices for genus, and with weak sculpture. Protoconch and first intervariceal

interval of teleoconch abraded; first visible well-preserved teleoconch sculpture (apparently on second intervariceal interval) of regular, small, closely spaced nodules, at junctions of 5 evenly spaced, low, narrow spiral cords, the central one at periphery, and 11-12 low, narrow axial ridges of same size and spacing as spiral cords. Peripheral and subsutural cords increasing in prominence and all other cords decreasing in prominence on succeeding intervariceal intervals, therefore over intervariceal intervals 4-8, a prominent subsutural row and a prominent suprasutural row of 8-10 small nodules, on a wide, moderately prominent spiral cord, are separated by a prominent, wide, median peripheral cord bearing 3-6 large, rounded nodules (decreasing in number and increasing in size down the shell), by 3 very low, narrow, widely spaced, weakly granulose threads on weakly concave sutural ramp, and by one narrow, almost-smooth spiral thread between peripheral and suprasutural cords. Over last 3 intervariceal intervals, all spiral cords and nodules decreasing in prominence; sculpture of last 2 intervals consisting of 3 wide, low, rounded, faintly nodulose to smooth, lightly polished spiral cords, with smooth, polished interspaces each approximately equal to one cord in width. Spiral cords remaining prominent, weakly granulose and with 3-4 narrow, weakly granulose threads on uppermost spiral interspace, and 1-2 in all lower interspaces over varices onto last whorl, and 4 major spiral cords strongly elevated to form prominent buttressing ridges across both faces of all varices. Anterior siphonal canal very wide, extremely prominent, strongly curving to left and then to right, forming exceedingly prominent fasciole with central hollow filled by inner lip callus, its exterior bearing 7 narrow, weakly but obviously granulose spiral cords. Posterior siphonal canals forming tall, rather thin-walled, deeply excavated channels of semicircular section, on last three varices extending up to periphery of previous whorl, shorter (or broken) on earlier whorls. Inner lip strongly thickened, moderately widely spread over previous whorl, particularly in parietal area and over anterior siphonal fasciole, bearing many prominent, rounded, widely spaced, slightly irregular transverse ridges over its entire height. Interior of outer lip bearing 10-11 short, narrow, very prominent transverse ridges, arranged in pairs with slightly wider interspaces than between members of one pair, with outer margin of lip flange strongly fluted by a shallow channel between each pair of ridges; ridges protruding strongly anteriorly (in direction of spiral growth) to digitate outer lip margin prominently.

Dimensions.—Holotype (the one complete specimen seen): H 54.0, D 37.4 mm.

Types.—Holotype NMB H 18308 (Pl. 10, Figs 4, 7, 10), from Punta Judas, 40 km WNW of Quepos, Pacific coast of Costa Rica, Late Miocene, coll. and pres. Bernard Landau; NMB 17753, locality as for holotype (2 incomplete para-

types); NMB 17754, locality as for holotype (3 incomplete paratypes); NMB 17755, locality as for holotype (1 incomplete paratype); NMB 17757, Punta Judas (1 frag, assigned tentatively); NMB 17758, Punta Judas (1 frag, assigned tentatively). The NMB localities are in stratigraphical succession around Punta Judas; the higher ones are shown on the map by Jung (1995: fig. 1). I have seen only the type material. Jung (1995) described the type locality in some detail when he described the new buccinid genus *Judaphos* from the same locality, and Seyfried *et al.* (1985) described the facies and stratigraphy of the section in detail.

Remarks.—This possibly is the form intended to bear the name *Bursa nana jamanensis* Pilsbry & Olsson, 1941, but this is a *nomen nudum* at the two places where it has been published (Pilsbry & Olsson, 1941: 8; Olsson, 1942: 170) and specimens that I have seen from the Jama Formation (Pliocene) are fairly typical specimens of *Marsupina nana*. *Marsupina judensis* n. sp. resembles *M. nana* in most characters, and particularly in the smooth, polished appearance of adult specimens and in the style, the range of variation, and the decrease in prominence down the teleoconch of its intervariceal sculpture. It is readily differentiated from *M. nana* by its much wider and thicker varices and its wider, lower shape and overall much more squat, solid appearance. It seems likely that *M. judensis* n. sp. was directly ancestral to *M. nana*, to judge from the morphological similarity and age relationships. The only other Oligocene-Early Miocene *Marsupina* species known so far from the Pacific coast of the Americas is *M. freya*, discussed above. *Marsupina judensis* n. sp. is readily distinguished from *M. freya* by its larger size, its markedly taller spire and its smoother sculpture, particularly on the varices. It is a pleasure to record that, once again, the excellent holotype was collected by and was contributed generously to this project by Bernard Landau.

Distribution.—I have seen definite material of *Marsupina judensis* n. sp. only from Punta Judas, Pacific coast of Costa Rica. It seems likely to occur widely in Miocene rocks of the Pacific coast of tropical and northern South America.

Etymology.—The specific name ("from [Punta] Judas") refers to the type locality.

Marsupina nana (Broderip & G. B. Sowerby I, 1829)

Pl. 10, Figs 11-12, Pl. 11, Figs 1-2, 5, 7-8

Ranella nana Broderip & G. B. Sowerby I, 1829: 376; G. B. Sowerby II, 1835, "small sheet": caption to pl. 85, fig. 6; 1841b: 51; Kiener, 1841: 21, pl. 9, fig. 2; Reeve, 1844b: pl. 6, fig. 29; Menke, 1850: 189; C. B. Adams, 1852: 119; Stearns, 1894: 188.

Ranella pulchra G. B. Sowerby II, 1835, "small sheet": caption to pl. 89, fig. 14 (senior primary homonym of *R. pulchra* G. B. Sowerby II, 1836, "small sheet": caption to pl. 93, fig. 19).

- Ranella albofasciata* G. B. Sowerby II, 1841a: unpaginated catalog of *Ranella* species; 1841b: 52.
Ranella albifasciata (sic). Reeve, 1844b: pl. 6, fig. 27; Tryon, 1880: 38, pl. 19, fig. 9.
Bursa nana. Pilsbry & Olsson, 1941: 39, pl. 5, fig. 6; Keen, 1971: 509, fig. 966.
 ?*Bursa nana jamanensis* Pilsbry & Olsson, 1941: 8; Olsson, 1942: 170 (nomen nudum).
Bursa (*Colubrellina*) *nana albofasciata*. Hertlein & Strong, 1955b: 264.
Bufonaria (*Marsupina*) *nana*. Beu, 1985: 65, fig. 50; Cossignani, 1994: 41.
Bursa (*Colubrellina*) *caelata amphitrites*. Aguilar & Fischer, 1986: 223, pl. 2, fig. 7 (not *Bursa amphitrites* Maury, 1917).
Marsupina nana. López de la Fuente & Ramos, 2004: 86.

Remarks.—*Marsupina nana* has been mentioned and discussed in the literature surprisingly few times, considering that it is one of the most common offshore bursids along the western coast of America from Coronado Island, outer coast of Baja California Peninsula, and from Guaymas, Sonora, Mexico, to off of Tumbes, northern Peru (3°28'S) (LACM material listed below). Much live-collected material is available in museums, showing clearly that the operculum has an anterior terminal nucleus. The shell is of moderate size (to ca. 60 mm H, but most up to 50 mm), with its varices quite low and subdued in adults and strictly aligned, with a steeply sloping sutural ramp that clasps the previous whorl to a little below the shoulder. In many specimens, the sutural ramp is a little more concave than in *M. bufo*, with a widely open, tall posterior siphonal canal linked up the spire to the previous canals, at least on some specimens, and with a prominent siphonal fasciole in adults, formed by the anterior canal being strongly deviated to the left and then recurved to the right. *Marsupina nana* is therefore clearly related to *M. bufo* in a close phylogenetic sense, and appears to be the eastern Pacific cognate of the western Atlantic *M. bufo*. All small juvenile specimens of *M. nana*, many half-grown shells, and a few adult specimens have quite coarse granulose sculpture or rows of more obvious, small, subrectangular nodules, and many have more prominent varices than in adults; this is the form named *Ranella albofasciata* by G. B. Sowerby II (1841a, b). However, virtually all large adults and a range of medium-sized to moderately large specimens in all collections examined have an almost completely smooth, highly polished shell surface on the last whorl or two, apart from a weak shoulder angulation bearing a few low, smoothly rounded nodules. There is no doubt that the form *albofasciata* was based on coarsely granulose immature specimens of *M. nana*, and that this species undergoes the same sculptural change with growth as *M. bufo*, except that most specimens reduce the granulose sculpture even further than does *M. bufo*, and are completely smooth on the last whorl or two. In Recent material, *M. nana* is also easily dis-

tinguished from *M. bufo* by its dark purplish brown (rather than pale to medium red-brown) coloration; *M. nana* also has some paler spiral banding, white on some specimens, and a bright white aperture and anterior canal, standing out in more marked contrast than in *M. bufo*.

R. E. Petit (North Myrtle Beach, South Carolina, pers. comm., 13 February 2008) pointed out an unfortunate nomenclatural complication with the names *Ranella pulchra* and *R. albofasciata* of G. B. Sowerby II (1835-1836, 1841a, b). Sowerby (1835: pl. 89, fig. 14), in the temporary "small list" captions for plates 89 and 90 issued with this part of "The conchological illustrations," initially identified the *albofasciata* form of *Marsupina nana* by the name *R. pulchra*. Soon afterward, he (Sowerby, 1836: "small sheet" caption to pl. 93, fig. 19; copy of original figure published by me (Beu, 1998b: 30, fig. 4f) used this manuscript name of Gray's again for a *Biplex* species, the smaller western Pacific species for which I (Beu 1998b: 32) adopted the name *B. pulchra*. Purchasers were instructed by Sowerby (in "instructions to the binder" at the end of the book) to discard these temporary caption lists when the more final catalogs of species were issued and the whole work bound – in this case, the *Ranella* catalog was issued in 1841 – and so most bound copies of this work do not contain the "small sheet" lists. By the time the complete catalog was issued, Sowerby (1841a) presumably realized that he had used the same name for two species, and the name *R. albofasciata* was adopted for the earlier of the two usages of *R. pulchra*. *Ranella albofasciata* was also formally described as new by Sowerby (1841b: 52). Because the name *R. pulchra* G. B. Sowerby II, 1836, has been used as the valid name for the small western Pacific *Biplex* species in only a few works since 1998 (I am aware of five), and not earlier, it is not possible to preserve it under ICZN Article 23.9.1, and it must remain a junior primary homonym of *R. pulchra* G. B. Sowerby II, 1835. This, in turn, is a junior synonym of *R. nana* Broderip & Sowerby, 1829. For the smaller western Pacific *Biplex* species for which I (Beu, 1998b: 32) adopted the name *B. pulchra* (G. B. Sowerby II, 1836), the next-youngest name must now be adopted: *B. aculeata* (Schepman, 1909: 115, pl. 10, figs 1a-c; lectotype and paralectotype: Beu, 1998b: 33, figs 5d-e).

Dimensions.—*Ranella nana*, lectotype: H 56.4, D 32.3 mm; paralectotypes: H 49.8, D 30.7 mm, and H 54.3, D 34.0 mm; *Ranella albofasciata*, lectotype: H 46.0, D 30.4 mm; paralectotypes: H 46.6, D 30.4 mm, and H 24.3, D 16.7 mm; figured specimen, NMB H 17905, from NMB 17471, Playa Cocalito, Nicoya Peninsula, Costa Rica: H 49.8, D 28.9 mm; figured specimen, NMB H 17904, from NMB 18161, locality same as last: H 34.4, D 23.1 mm.

Types.—*Ranella nana*, 3 "probable" syntypes BMNH 1950.11.28.14-16, labeled "Panama, coarse sand, 10 fathoms" [18 m]; in the absence of any other possible type mate-

rial, these are accepted as the syntypes of *R. nana*. The largest syntype, BMNH 1950.11.28.14, most nearly resembles the illustration by G. B. Sowerby II (1835: pl. 85, fig. 6), although it is a little paler and wider than the shell in the figure, and is here designated the lectotype of *R. nana*. There is no separate type material labeled *R. pulchra* that applies to the present species. *Ranella albofasciata*, 3 syntypes BMNH 1950.11.28.20-22, with identical locality label to that of the syntypes of *R. nana* (there is little doubt that Hugh Cuming subdivided an originally single population into more finely and more coarsely sculptured specimens); the intermediate-sized syntype (Pl. 11, Figs 1-2) matches the illustrations by both G. B. Sowerby II (1835: pl. 89, fig. 14) and Reeve (1844b: pl. 6, fig. 27) and is here designated the lectotype of *R. albofasciata*. *Ranella nana* originally was published without locality; G. B. Sowerby II (1835: caption to *Ranella* plates) originally stated the locality of *R. albofasciata* as "Panama, of the Philippines" (quoting the highly unreliable memory of Hugh Cuming), and Hertlein & Strong (1955b: 264) designated the type locality as Panama Bay, in 18 m.

Other material examined.—Recent: 98 lots examined at AMNH, GNS, LACM, ZMC, ZMF; from W Mexico (northernmost: 28 m, on sand, 8 km E of South Coronado Island, outer coast of Baja California, 32°24'N, 117°09'15"W, LACM-AHF 871-38, 1), W Guatemala, El Salvador, W Costa Rica, W Panama (including under rocks at low tide, Venado Island, GNS WM13915; 1), W Colombia, Ecuador, and Peru (southernmost: 10-40 m, off of Tumbes, between Caleta La Cruz and Puerto Pizarro, 3°28'S, 80°36'W, shrimp boat, LACM 72-170, 1).

Fossils: Pacific Costa Rica: Pliocene: NMB 18037 (1); 18039 (3); 18043 (1); 18047 (1); 18049 (3); 18052 (1); 18053 (1); 18054 (1); 18055 (3); 18056 (4); 18057 (1); 18293 (1); 18295 (1); Charco Azul Group, Penita Fm, Quebrada La Penita, Burica Peninsula, collection of Bernard Landau (4); A. A. Olsson's loc. 116, mouth of Quebrada La Penita (USNM, 3). **Pleistocene:** NMB 17471 (41; 1 illustrated, H 17905; Pl. 11, Figs 5, 7-8); 17767 (32); 17799 (4); 18116 (9); 18160 (2); 18161 (6; 1 illustrated, NMB H 17904; Pl. 10, Figs 11-12); 18284 (1); 18285 (1); 18303 (1); USGS 24792, stream courses including Río la Vaca, crossed by Progreso-Lagarto trail, Puntarenas Prov. (4); Montezuma Fm, Playa Cocalito, Nicoya Peninsula, collection of Bernard Landau (29). **Pacific Panama: Pliocene:** NMB 18068 (1). **Pleistocene:** NMB 17443 (1); 18066 (2); 18069 (2); 18070 (52); 18076 (2); A. A. Olsson's loc. 125, Burica Peninsula (USNM, 1); A. A. Olsson's loc. 130, Burica Peninsula (USNM, 1). **Panama, Darien: Late Miocene:** NMB 18517 (1). **Ecuador: Pliocene:** NMB 19142 (1); 19152 (1); 19153 (1, large); USGS 23478, Jama Bay S to Punta Barrocho, A. A. Olsson (6); 23507, *Loripes* zone, Punta Blanca, A. A. Olsson (2).

Distribution.—*Marsupina nana* lives today in the eastern Pacific from the outer coast of Baja California Peninsula (32°24'N) throughout the Gulf of California and along the western coast of tropical America, southward to northern Peru (to at least 3°28'S). Specimens have been collected alive from the shallow subtidal to a depth of ca. 100 m. Fossil specimens are recorded from Pliocene and Pleistocene rocks along the western coasts of Costa Rica and Panama, well within the living range.

***Marsupina strongi* (Jordan, 1936)**

Pl. 11, Figs 4, 6

Gyrineum strongi Jordan, 1936: 160, pl. 18, fig. 10; Durham, 1950: 28, 115, pl. 29, figs 19, 22; Schneider, 1999: fig. 10.

Gyrineum (*Bechtelia*) *strongi*. Emerson & Hertlein, 1964: 360, fig. 5g.

Remarks.—I reviewed (Beu, 1998b) the species of *Gyrineum*, and showed that it is a uniform genus of small, solid, robustly and consistently sculptured species, limited to the Indo-West Pacific province during Miocene to Recent times, apart from a few species in Miocene and Pliocene rocks of Europe and southern Australia. No American species are correctly referred to the genus. It was traditional during the first half of the 20th century to refer most fossil Ranellidae of western North America to *Gyrineum*, but these species are not congeneric with the living Indo-West Pacific type species, *G. gyrinum* (Linnaeus, 1758). J. T. Smith (1970) and I (Beu, 1988) removed most western North American fossil species to other genera; most belong in *Ameranella* Beu, 1988, *Argobuccinum* Herrmannsen, 1846, *Cymatium* Röding, 1798, *Fusitriton* Cossmann, 1903, or *Ranella* Lamarck, 1816.

A final, highly unusual species, *Gyrineum strongi* Jordan, 1936, has remained in a subgenus *Gyrineum* (*Bechtelia*) since the subgenus was proposed by Emerson & Hertlein (1964), but this species also shares very few characters with *G. gyrinum*. The one character in common is the varices being aligned up the opposing sides of the teleoconch, but this is an unreliable guide to relationships, because it occurs in both Bursidae and Ranellidae: Ranellinae. The varices are unusually low and wide in *G. strongi*, and the combination of low varices with moderately large size [holotype 46.8 mm H, with much of the spire apex missing; the excellent specimen illustrated by Schneider (1999: fig. 10) originally was about 60 mm high] and an unusual, tall, steep, weakly concave sutural ramp extending to just below the periphery of the previous whorl produces a unique fusiform shape, more nearly resembling that of *Charonia* than any other tonnoidean. However, the aperture has a tall but rather shallow posterior siphonal notch, the interior of both the inner and outer lips bears numerous small rounded nodules, and the outer lip flange outside the

terminal varix is quite strongly digitate. The posterior sinus is a character found only in the Bursidae, and nodules on the apertural lips and a digitate outer lip are much more common in Bursidae than in Ranellidae. *Gyrineum strongi* therefore should be referred to family Bursidae. The strictly aligned varices, the digitate outer lip margin, the weak teleoconch external sculpture, the extension of the sutural ramp up to just below the peripheral nodules of the previous whorl, and the elongate shape indicate that *G. "(Bechtelia)" strongi* probably is most closely related to the living species *Marsupina nana*, and it seems likely that *Bechtelia* was based on an unusual species of *Marsupina*, although it must be admitted that the taxonomic position is uncertain. The taller spire, the taller, more steeply inclined, only weakly concave sutural ramp, and the reduction of teleoconch intervariceal sculpture (at least over the last 3.5 whorls, all that is known of this species) to very fine, low, close spiral cords and a row of low, rounded peripheral nodules distinguish *M. strongi* readily from the shorter and more coarsely sculptured species *M. nana*.

The really unusual thing about *Marsupina strongi* is that it is recorded only from late Middle Pleistocene (Last Interglacial, oxygen isotope stage 5e, ca. 125,000-130,000 years old; Emerson *et al.*, 1981; Ashby & Minch, 1987; Ashby *et al.*, 1987) terrace faunas of Baja California Sur, Mexico. That a species should be limited to such a small area and to such a short time range is almost unique in the Tonnoidea, and perhaps indicates that *M. strongi* might still be found living in tropical western America. It also suggests that this species had lecithotrophic development, although because the spire apex seems consistently to be decollate on all specimens, the protoconch is unknown. Decollation of the spire apex is a character that I have not otherwise observed in the Tonnoidea, so it will be particularly interesting if this is indeed a consistent character of *M. strongi*. It is conceivable that further study of a larger range of material will demonstrate that a subgenus *Marsupina* (*Bechtelia*) is useful to contain this unusual species.

Dimensions.—Holotype: H 46.8 mm (spire apex missing), D 30.0 mm; specimen figured by Durham (1950: pl. 29, figs 19, 22): H 50.3 (spire apex missing), D 29.2 mm; specimen figured by Schneider (1999, fig. 10): H 51.5 (spire apex missing), D 30.3 mm; Bahia de Santa Inés, collection of Bernard Landau: H 40.0 (spire apex missing), D 24.6 mm.

Types.—*Gyrineum strongi*, holotype CAS 5480, with one paratype CAS 5481, from late Pleistocene terrace (presumably coeval with Mulegé Terrace, oxygen isotope stage 5e), beach south of village, Bahia Magdalena, Baja California Sur, Mexico; cast pres. L. G. Hertlein (GNS WM11282).

Other material examined.—**Fossils:** **W Mexico:** **Late Middle Pleistocene**, oxygen isotope stage 5e: UCMP A-3550, Isla Coronado, Baja California (1, specimen recorded by Durham, 1950, pl. 29, figs 19, 22); UCMP A3598, Bahia

Concepción, Baja California Sur (1); uplifted terrace, Bahia de Santa Inés, near Mulegé, Baja California Sur, collection of Bernard Landau (1), pres. B. Landau (GNS WM17430, 1).

Distribution.—*Marsupina strongi* is recorded only from late Middle Pleistocene (Last Interglacial period, oxygen isotope stage 5e, ca. 125,000-130,000 years old) terrace faunas of Isla Coronado, northern Mexico, and Isla Monserrate and Isla San Diego in the southwestern Gulf of California (Emerson & Hertlein, 1964), from the mainland coast of western Mexico at Bahia Magdalena (Jordan, 1936), on the inner coast of Baja California Peninsula at Bahia Concepción and in the Santa Rosalia area (Durham, 1950) and at three localities in Mulegé Terrace cover beds near Punta Chivato, south of Santa Rosalia (Schneider: 1999: table 1; at Punta Gallito, sea cliffs northwest of Punta Prieta, and northern end of Punta Santa Inés).

FAMILY PERSONIDAE Gray, 1854

Genus *DISTORSIO* Röding, 1798

Distorsio Röding, 1798: 133. Type species (by subsequent designation, Pilsbry, 1922: 347): *Murex anus* Linnaeus, 1758, Pliocene to Recent, Indo-West Pacific.

Distortrix Link, 1807: 122. Type species (by subsequent designation, Dall, 1904: 133): *Distortrix anus* Link, 1807 (= *Murex anus* Linnaeus, 1758).

Persona Montfort, 1810: 603. Type species (by monotypy): *Persona anus* Montfort, 1810 (= *Murex anus* Linnaeus, 1758).

Distorta Perry, 1811: caption to pl. 2. Type species (by subsequent designation, Emerson & Puffer, 1953: 96): *Distorta rotunda* Perry, 1811 (= *Murex anus* Linnaeus, 1758).

Calcarella Souleyet, 1850: 247. Type species (by monotypy): *Calcarella spinosa* Souleyet, 1850 (= larval shell of *Distorsio* sp.; Warén & Bouchet, 1990: 94).

Rhysema Clench & Turner, 1957: 236. Type species (by original designation): *Triton clathratum* Lamarck, 1816, Late Miocene to Recent, western Atlantic.

Remarks.—*Distorsio anus* (Linnaeus, 1758), the type species of *Distorsio*, is an extremely distorted species, with a very widely expanded apertural shield that masks the rest of the shell, except for the spire tip, in adult specimens in conventional apertural view, and with its anterior siphonal canal bent toward the dorsum at right angles to the coiling axis and the plane of the aperture. Clench & Turner (1957: 236) proposed the subgenus *Distorsio* (*Rhysema*) for all the other *Distorsio* species, which are less distorted, have a smaller apertural shield and have a less strongly twisted anterior canal than *D. anus*. When Lewis (1972) described the endemic Hawaiian species *D. burgessi*, which has several characters intermediate between those of *D. anus* and the species that had been included in *D. (Rhysema)*, he suggested that there was little point in maintaining a separate subgenus *Rhysema*. Most later workers have agreed, and *Rhysema* has not been recognized in the sub-

stantial reviews of *Distorsio* by Henning & Hemmen (1993), Kronenberg (1994), and me (Beu, 1998b). I continue to regard *Distorsio* as a single indivisible genus.

Many authors over the years have debated the identity of the western Atlantic *Distorsio* species, and the fossil species of the Caribbean region have provided just as many difficulties as the living ones. Since the recognition of two living Caribbean species (Dall, 1889: 222; Olsson & McGinty, 1951; Puffer, 1953; Emerson & Puffer, 1953) and the addition of a third by Lewis (1972), it gradually has been realized that, especially in the Indo-West Pacific, there is a large number of closely similar and, in many cases, syntopic species of *Distorsio* (reviewed by Kronenberg, 1994). Nine species are recorded from both the Philippine Islands and New Caledonia (although only eight are common to both island groups) so it is not surprising that four species are now recognized in the present fauna of tropical western America: *D. constricta* (Broderip, 1833), *D. decussata* (Valenciennes, 1832), *D. jenniernestae* Emerson & Piech, 1992, and *D. minoruohnishii* Parth, 1989. Along with the three western Atlantic species, *D. clathrata* (Lamarck, 1816), *D. mcgintyi* Emerson & Puffer, 1953, and *D. perdistorta* Fulton, 1938 (although the last is not known as a fossil within the study area), a few additional taxa are known only as fossils in the area studied here. The interplay of biogeographical changes of all of these species through the Panama seaway has produced a complex picture. Most of the early taxonomic revisions are now seen to have been too conservative (for example, three rather than two species of *Distorsio* occur in the Late Pliocene Bowden shellbed in Jamaica) and further taxa might well be distinguished in the future.

***Distorsio biangulata* n. sp.**

Pl. 22, Figs 4, 7; Pl. 51, Figs 4-5

Description.—Shell moderately large for genus (to 75 mm H), relatively wide, with wide, gently sloping, weakly convex to weakly concave sutural ramp, producing strongly gradate outline that increases in prominence of stepping as shell grows; extremely prominent, narrow, nodulose peripheral keel protruding strongly over earlier two-thirds of each intervariceal interval but more weakly over final third of each interval; unusually wide, weakly sculptured, anteriorly tapering interval below peripheral carina; moderately prominent second angulation formed by protruding peribasal spiral cord; spiral sculpture of 12-14 moderately prominent cords over base and canal; moderately long, almost straight anterior siphonal canal inclined to left and curved slightly toward dorsum. Sculpture commencing on early spire whorls as two narrow peripheral cords crossed by 10-11 narrow, sharp-crested axial ridges per intervariceal interval; from fifth whorl, upper spiral cord increasing in prominence and lower cord decreasing, to

form single prominent peripheral carina on sixth and seventh whorls; axial ridges weakening, decreasing in number to 9 and eventually 7-8 per intervariceal interval on last whorl, and becoming much more widely spaced, to form low, narrow, clearly defined axial ridges with weakly concave interspaces over last whorl, forming small, sharply rounded nodules at peripheral carina. Surface of sutural ramp and peripheral depressed interval bearing numerous, closely spaced, fine spiral cords of several orders of magnitude, all crossed by extremely close, fine axial ridgelets. Suture well above peribasal angulation on early spire whorls; as distortion of coiling increases with growth, more of depressed peripheral band becomes revealed progressively until, on whorl six, peribasal angling ridge revealed over early, most inflated half of penultimate intervariceal interval. Aperture standard for genus, with deeply embayed columella, flared outer lip (mostly broken off in both available specimens), inner lip shield a relatively narrow, thin smear over previous whorl, and siphonal canal edge of lower columella elevated into very prominent, hollow, long ridge parallel to canal, bearing numerous low, narrow, short transverse ridges; left edge of row of transverse ridges sharply defined; area between row of transverse ridges and previous shell whorl smooth, concave. Inner lip bearing one low, narrow parietal ridge, numerous low, weakly defined transverse ridges lower down columella (corresponding to spiral cords on previous whorl), and irregular, wide, low, flat-crested, anastomosing transverse ridges over outer area of lower third to half of inner lip shield. Inner edge of outer lip bearing wide, prominent transverse ridges of rounded section, third ridge from posterior end larger than others (in paratype); central and lower part of outer lip missing from both specimens. Protoconch not seen.

Dimensions.—Holotype: H (incomplete) 73.5, D (incomplete) 40.0 mm; paratype: H (incomplete) 71.0, D (incomplete) 46.0 mm.

Type material.—Holotype UCMP50022 (Pl. 22, Figs 4, 7), from loc. UCMP S-8360, lower Cantaure shellbed (late Early Miocene), "approximately 300 m south of Casa Cantaure, which is about 10 km west of Pueblo Nuevo, near San José," Paraguaná Peninsula, Estado Falcón, Venezuela; one paratype, from lower Cantaure shellbed (late Early Miocene) at the same locality, collection of Bernard Landau (Pl. 51, Figs 4-5).

Distribution.—Known only by the holotype and paratype. This species is evidently rare at Cantaure, because most collections from there, including the huge collection in NMB made by Win and Jack Gibson-Smith, do not include this species.

Remarks.—*Distorsio biangulata* n. sp. is the most distinctive new species in the genus to come to light in recent years. Its strongly biangled last whorl, brought about by the wide, weakly sculptured, concave interval between the very narrow peripheral keel and the peribasal angulation, is unique among

American *Distorsio* species. For many years, I had seen only the holotype, and it seemed possible that this specimen was a highly aberrant individual of *D. jungi* n. sp. (the common species in the Cantaure Fm) in which the sculpture weakens down the shell, apart from an abnormal strengthening of the peripheral cord and widening of the interval between the two angulations. However, the recent collection of an almost identical specimen by Bernard Landau indicates that this is a distinct, unnamed species. The only other species of *Distorsio* with a wide, depressed, weakly sculptured peripheral band similar to that of *D. biangulata* n. sp. is the Recent West African species *D. smithi* (von Maltzan, 1884) (see below; Pl. 22, Figs 3, 5), but *D. smithi* differs greatly from the new species in its narrower sutural ramp, its much wider (anteroposteriorly), more strongly sculptured, and less protruding peripheral sculptured band, contrasting strongly with the narrow, protruding, nodulose to almost spinose keel of *D. biangulata* n. sp., and in its still wider but more nearly vertical, peripheral depressed, weakly sculptured band. A close phylogenetic relationship between *D. biangulata* n. sp. and *D. smithi* seems very unlikely; it is more likely that *D. biangulata* n. sp. is another member of the *D. decussata* species group (see below, under *D. decussata*). All other American *Distorsio* species differ greatly from *D. biangulata* n. sp. in their narrower shape, narrower sutural ramp, wider peripheral keel or ridge, and more closely spaced peripheral and peribasal spiral cords, without the depressed, weakly sculptured, wide peripheral zone of *D. biangulata* n. sp.

Etymology.—The specific epithet (intended to mean “two-angled”) refers to the distinctive shape of the outline of the last whorl.

***Distorsio clathrata* (Lamarck, 1816)**

Pl. 12, Figs 1-10

?*Distorsio clatrata* Röding, 1798: 133 (*nomen nudum*).

Triton clathratum Lamarck, 1816: pl. 413, figs 4a-b, “Liste des objets”: 4; Lamarck, 1822: 186; Kiener, 1842: 21, pl. 14, fig. 1; Deshayes, 1843: 637.

Triton ridens Reeve, 1844a: pl. 12, fig. 46 (in part); Reeve, 1844c: 115; Küster & Kobelt, 1872: 202, pl. 58, fig. 4; Kiliass, 1973: 207 (in part).

Persona clathrata. Chenu, 1859: 155, fig. 707.

Tritonium reticulare. Krebs, 1864: 24 (not *Murex reticularis* Linnaeus, 1758).

Persona simillima. Guppy, 1866: 288, pl. 17, fig. 13; 1867: 158; 1874: 439 (in part not *Triton simillimus* G. B. Sowerby I, 1850).

Distorsio acuta occidentalis Mörch, 1877: 34 (*nomen nudum*).

Distorsio cancellina. Tryon, 1880: 35, pl. 17, fig. 177 (not *Murex cancellinus* de Roissy, 1805, an incorrect usage of *Triton cancel-*

linus Lamarck, 1803; Beu, 1998b: 199; Landau *et al.*, 2004: 71-73, neotype).

Distortrix reticulata var. *reticulata*. Dall, 1889: 221; Morretes, 1954: 53 (not *Distorsio reticulata* Röding, 1798, = *Murex reticularis* Linnaeus, 1758).

Distortrix reticulata var. *clathrata*. Dall & Simpson, 1901: 416.

Distortrix simillima. Dall, 1903a: 1584 (in part not *Triton simillimus* G. B. Sowerby I, 1850).

Distortrix reticulare. Dall, 1903b: 132.

Distortio (sic) *reticulatus* var. *clathratus*. Maury, 1922: 115.

Distorsio (*Distorsio*) *clathratus gatunensis*. Woodring, 1928: 300, pl. 19, figs 2-3; Weisbord, 1929: 41, pl. 8, fig. 3 (not *Distorsio gatunensis* Toulou, 1909, = *Tritonium decussatum* Valenciennes, 1832).

Distorsio clathratus. Rutsch, 1930: 607, pl. 17, figs 5-6; 1934: 28; M. Smith, 1948: 22, pl. 8, figs 6, 12.

Distorsio clathrata. Pilsbry, 1922: 359; Puffer, 1953: 110; Emerson & Puffer, 1953: 97; Abbott, 1954: 196, pl. 25, fig. AA; 1974: 165, pl. 7, fig. 1770; Olsson & McGinty, 1958: 15; Warmke & Abbott, 1961: 102, pl. 18, fig. d; Lewis, 1972: fig. 35; Rios, 1975: 80, pl. 22, fig. 327; 1984: 78, pl. 27, fig. 340; 1994: 91, pl. 30, fig. 358; Laursen, 1981: 27, fig. 42; Okutani, 1983: 260, illus.; H. & E. Vokes, 1983: 23, pl. 11, fig. 12; Bandel, 1984: 97, fig. 163, pl. 8, fig. 6; Cosel, 1986: 240, fig. 154; de Jong & Coomans, 1988: 70; Diaz, 1990: 19; Warén & Bouchet, 1990: figs 146-147; Emerson & Sage, 1990a: 131, figs 1-9; 1990b: 108, figs 1-2; Parth, 1991a: 11, illus.; Lipe & Abbott, 1991: 14, illus.; Henning & Hemmen, 1993: 137, pl. 29, figs 1-3; Diaz & Puyana, 1994: 173, fig. 647; Kronenberg, 1994: 66, text-fig. 8, pl. 1, figs 5a-f, 7, pl. 2, figs 1-3, pl. 4, figs 1a-b, 2; Piech, 1995: 20; Macsotay & Campos Villarroel, 2001: 68; Beu, 2001: 711.

Cancellaria (*Cancellaria*) *cossmanni*. Oinomikado, 1939: 623, pl. 29, fig. 17 (not *Cancellaria cossmanni* Olsson, 1922).

Personella floridana. Alencástor-Ibarra, 1950: 578, fig. 26; Perrilliat, 1960: 20, pl. 3, figs 8-9 (not *Personella floridana* Gardner, 1947).

Distorsio (*Rhysema*) *clathrata*. Clench & Turner, 1957: 236, pl. 131, pl. 132, figs 2-8, pl. 133; Pflug, 1961: 41, pl. 9, figs 1-2 only (in part not *Triton clathratum* Lamarck, 1816); Weisbord, 1962: 267, pl. 25, figs 12-16; Olsson, 1964: 174, pl. 30, figs 1-1b; Andrews, 1971: 107, illus.; Kiliass, 1973: 200, fig. 143; van Regteren Altena, 1975: 37, pl. 2, figs 6-7; Andrews, 1977: 134, illus.; Coelho *et al.*, 1981: 131, fig. 13; Petuch, 1987: pl. 11, figs 5-6; 1994: pl. 39, figs J, N; Petuch, 1997: 279, fig. 115A.

Distorsio (*Rhysema*) *floridana*. Perrilliat, 1972: 75, pl. 37, figs 6-11 (not *Personella floridana* Gardner, 1947).

Distorsio (*Distorsio*) *clathrata*. Beu, 1985: 62; Emerson & Piech, 1992: figs 9-12.

Distorsio (*Rhysema*) *robinsoni* Petuch, 1987: 64, pl. 11, figs 3-4; Kalafut, 1991: 13.

Distorsio clathrata f. *robinsoni*. Parth, 1989a: 52, top right fig.

Remarks.—*Distorsio clathrata* is the common *Distorsio* species in relatively shallow water in the western Atlantic at present. Although it is highly variable in shape, size, and coloration, it is nevertheless one of the most distinctive of *Distorsio* species, as it is the only one in the study area with an evenly convex shell wall between the varices, and with its prominent, narrow, widely spaced spiral cords completely evenly spaced. All other species of *Distorsio* (other than the much smaller *D. parvimpedita* Beu, 1998, endemic to New Caledonia) have markedly humped growth between the varices, an obvious shoulder angle defining a weakly concave sutural ramp, and two or more spiral cords more closely spaced than the others and situated on the shoulder angle.

The range of variation in teleoconch height is a surprising aspect of *Distorsio clathrata*. Large samples from the Pliocene Agueguexquite Fm in the Isthmus of Tehuantepec, Mexico, collected by Emily and Harold Vokes, consist entirely of tiny (ca. 20 mm H), short and wide, almost spherical specimens of *D. clathrata*. This form was identified as *Personella floridana* Gardner, 1947, and *D. (Rhysema) floridana* by Perrilliat (1960, 1972). However, a few of the largest specimens (to ca. 35 mm H) are a little more elongate than the others, and it is clear that this species varies through these near-spherical dwarfs and such short modern specimens as the type material of *D. robinsoni* Petuch, 1987, to relatively tall, large adults. Kalafut (1991) illustrated specimens of the forms known as “typical” *D. clathrata* and as *D. robinsoni*, and distinguished them by the length and density of periostracal bristles, *D. clathrata* supposedly having sparse, long bristles and *D. robinsoni* supposedly having a short-bristled, velvety periostracum with closely spaced bristles. However, it seems unlikely that the periostracum has any taxonomic significance, because markedly different periostracal bristles in different specimens have long been known for other *Distorsio* species (e.g., *D. perdistorta*; Lewis, 1972: figs 26-34). There is little doubt that the differences between *D. clathrata* and *D. robinsoni* are trivial.

The very distinctive protoconch of *Distorsio clathrata*, with two prominently spinose spiral ridges on the periostracum, was illustrated excellently by Laursen (1981: fig. 42). This provided an identification for the “unusual veliger, ... found only once in the outside waters” of Bermuda, illustrated by Lebour (1945: fig. 25) as “undetermined larva,” and stated to have a radula “of *Cymatium* type.” This elaborately spinose larva was also made the type of the genus *Calcarella* by Souleyet (1850). The protoconch usually seen on specimens without periostracum, and on fossils, is also distinctive because it is larger and wider (lower-spired) than in all other *Distorsio* species in the study area, and its coiling is parallel to that of the teleoconch.

The specimen illustrated under the name *Cancellaria coss-manni* by Oinomikado (1939: 623, pl. 29, fig. 17) is a juvenile

specimen of a species of *Distorsio*, apparently *D. clathrata*.

Dimensions.—USNM 597527, 30 m, off of Tortugas, Florida: H 81.7, D 45.8 mm (largest seen); GNS WM18113, 30 m, off of Fort Myers, Florida: H 75.9, D 41.4 mm; figured specimens, NMB 19020 (TU 1046), Agueguexquite Fm, Mexico; NMB H 17906: H 37.9, D 24.5 mm; NMB H 17907: H 27.8, D 19.9 mm.

Types.—*Triton clathratum*, lectotype designated by Kronenberg (1994: 66) MHNG 1100/11, with three paralectotypes MHNG 1100/10/1-3 (paralectotype 1100/10/2 is a specimen of *D. reticularis*) (Kronenberg, 1994: 66); from “Mers de l’Amérique méridionale”; type locality restricted by Clench & Turner (1957: 239) to Bay of Campeche, E Mexico. *Triton ridens*, lectotype (designated by Lewis, 1972: 48) AMNH 6369; three paralectotypes BMNH 1967630, one paralectotype MCZ 186600. *Distorsio (Rhysema) robinsoni*, holotype USNM 859832 (not seen), from Oak Ridge, Roatan Island, Honduras.

Other material examined.—**Recent:** 124 lots at GNS, LACM, NMB, SMF, USNM; from North Carolina (northernmost: 22 km WSW of Diamond Shoal, USNM 596994, 3; scallop dredgers off of Beaufort, GNS WM16594, 1), Georgia, Florida, Gulf of Mexico, E Mexico, Haiti, Puerto Rico, Antillean islands (Tortola, Montserrat, Barbados), Colombia, Venezuela, Surinam, and Brazil (southernmost: Maceio, Alagoas, LACM 35499, 2; 5 m, off of Praia Barra Sirinhaém, Pernambuco, GNS WM18117, 2).

Fossils: Louisiana: Late Pleistocene or Holocene, from Mississippi delta “mudlumps”: USGS 26949 (3); 26471 (1). **Florida:** The only fossils from Florida of which I am aware are the Holocene specimens illustrated by Petuch (1994: pl. 39, figs J, N) from Capeletti Brothers pit, Miami. **Mexico: Pliocene:** USGS 12084 (1); 12086 (5); 22279 (9); TU 638 = NMB 19031 (210, of which 4 are in NMB; GNS WM16957 + WM 18818, 206); 1025, Concepción Fm, road cut, Veracruz (GNS WM18815, 1); 1046 = NMB 19020, Agueguexquite Fm, Perrilliat’s loc., cutting on Mexico Hwy 180, Isthmus of Tehuantepec (74; 2 illustrated, NMB H 17906, H 17907, Pl. 12, Figs 2, 9; GNS WM16958, 18; WM18817, 54); 1318 = NMB 19016, Lower Concepción Fm (Pliocene), NE of Campo El Chapo, Nueva Teapa, Veracruz (24; 1 illustrated, NMB H 18066; Pl. 12, Fig. 8); Pena Madama Brea, on Río Coatzacoalcas, Veracruz (UCMP S-8393, 3); Texistepec, Veracruz (UCMP S-2646, 2); “Pliocene, Mexico” (UCMP S-155, many small); Veronica, Veracruz (UCMP S-4153, 9 small); Arroyo Agueguexquite, Veracruz, as USGS 12086 and TU 1046 (UCMP S-4140, 1); San Eulalio, Veracruz (UCMP S-4054, 20); second arroyo ca. 1 km N of trig. station, Veronica, southern Veracruz (UCMP S-200, 3); arroyo 150 m NW of trig station, Veronica, 6 km SE of Puerto Mexico (= Coatzacoalcas), southern Veracruz (UCMP S-201, 1).

Jamaica: Late Pliocene, Bowden: NMB 10651 (1); USNM 115512 (3; largest shell is Woodring's (1928: pl. 18, figs 7-8) illustrated specimen of *D. decussata*, other 2 are *D. clathrata*); USNM 369463 (1, Woodring's (1928: pl. 19, figs 2-3) illustrated specimen of "*D. clathrata gatunensis*"); USNM 559570 (2); A. A. Olsson collection, USNM (1); USGS 2374 (6); 2580 (8); 18205 (1); 61537 (1); UCMP S-2 (4); BMNH Palaeontology Department, GG3849 (1); BMNH Palaeontology Department, G64072 (1; specimen illustrated as *D. simillima* by Guppy, 1866: 288, pl. 17, fig. 13; Pflug, 1961: pl. 9, figs 1-2); "Cumaná," Guppy collection (= Bowden) (USNM 115511, 1). **Dominican Republic: Early Pliocene**: Gurabo Fm: USGS 8544 (1, illustrated, Pl. 12, Figs 1, 5); TU 1214, Gurabo Fm, Río Gurabo, collection of Bernard Landau (1 large, illustrated, Pl. 12, Figs 3-4). **Carriacou**: Grenadine Islands: **Middle Miocene**: NMB 10709 (2; possibly n. sp. aff. *D. clathrata*, as have large shoulder nodules not seen on any Pliocene-Recent shells); NMB 13759 (1). **Atlantic Costa Rica: Pliocene**, Banáno Fm: NMB 17450 (1); 17453 (2); 17477 (1); 17774 (2); 17784 (1); 18095 (2); 18264 (1); TU 589 = NMB 19024 (2); USGS 5882h (1). **Latest Pliocene-Early Pleistocene**, Limón: NMB 18272 (1); NMB 18278 (2); TU 954 (2); 956 (GNS WM18814, 1); USGS 20468 (1); 21035 (2); basal Moin Fm mudstone (Late Pliocene), Rte. 32, 3 km W of Puerto Limón, coll. J. A. Todd, February 1998 (BMNH Palaeontology Department, 1); Moin Fm, Puerto Limón (ZMA, 2). Robinson (1991) also recorded one specimen from the Moin Fm at Limón in TU 1240. **Atlantic Panama: Late Miocene**: Gatun Fm: TU 962 (1); Chagres Fm: NMB 18987 (1); Valiente Fm: NMB 18375 (1); NMB 18771 (3). **Pliocene**: Escudo de Veraguas Fm: NMB 17622 (1); 17847 (1); 18668 (8); 18669 (1); 18670 (3); 18671 (2); 18681 (10); 18682 (4); 18683 (2); 18685 (2 juveniles); 18686 (1); Shark Hole Point Fm: NMB 18387 (1); 18388 (1); 18976 (2); apparently Fish Hole Reef Member of Shark Hole Point Fm (see Appendix 3): USGS 8307 (1). **Colombia: Pliocene**: USGS 11520 (2); Arroyo Grande, 500 m NW of Megua, Departamento de Atlantico (UCMP S-8007, 1); Upper Cibarco Fm, Tubará, Departamento de Atlantico (UCMP S-8008, 4 large); 1200 m SW of Tubará, Departamento de Atlantico (UCMP S-8010, 1); Puerto Colombia, Departamento de Atlantico (UCMP S-8012, 6); type locality of Tubará Fm, Tubará, Departamento de Atlantico (UCMP 19158, 2); lowermost sandstone at Point Canoas, Departamento de Bolívar (UCMP S-70, 7); *Turritella* bed above S-70 (UCMP S-71, 3); 400 m W of Bonza de la Quenta, NW of Usiacuri, Departamento de Atlantico (UCMP S-7425, 1); head of Arroyo Grande, Usiacuri, Departamento de Atlantico (UCMP S-7607, 2); Piojo-Usiacuri Road, 200 m NE of Agua Viva, W of Usiacuri, Departamento de Atlantico (UCMP S-7507, 1); CAS loc. 267E, Tubará Hill, N end of Tubará (1);

CAS loc. 267R, Tubará Village, locality same as above (2); Zapó (BMNH Palaeontology Department, G35198, 1); W of jetty, Puerto Colombia (BMNH Palaeontology Department, GG12160, 1); Arroyo Juan de Acosta (BMNH Palaeontology Department, G35046-7, 2); USGS 11325 (1); USGS 11344 (1); Fault Peak, 3 km SE of Agua Viva, N of Usiacuri, Departamento de Atlantico (UCMP S-7396, 1); CAS loc. 325A, section between Chorrera and Cibarco (2); CAS loc. 351, Punta Pua, 32 km N of Cartagena (2). **Venezuela: Late Miocene**: NMB 13388 (1); 13640 (2); 13641 (1). **Pliocene**: NMB 12045 (8); 12865 (2); 12887 (6); 12892 (7); 12898 (1 large); 13349 (5); 13357 (1); 17512 (30); 17531 (8); 17532 (6); Punta Gavilán (NMB H 1867, 1; specimen illustrated by Rutsch, 1930: pl. 17, figs 4-5); same as last (NMB H 1868/1-3, 3; 1 illustrated, Pl. 12, Fig. 6); locality same as last, collection of Bernard Landau (8); same as last (NMB H 11475, 1; specimen identified as that illustrated by Rutsch "1930: pl. 17, fig. 4," but see NMB H 1867 above); USGS 18252 (1); 18253 (1); 24564 (1); A. A. Olsson's loc. 210, same as last (USNM, 1); same as last, collection of Bernard Landau (1); loc. J248a, Mare Fm, W of Quebrada Mare Abajo, Cabo Blanco (PRI 26196, 1; specimen illustrated by Weisbord, 1963: pl. 25, figs 12-13); loc. T248a, 250 m W of Quebrada Los Pailas, upper Mare Fm (PRI 26197, 1; specimen illustrated by Weisbord, 1962: pl. 25, figs 14-16); Cubagua Fm, 400 m SW of house at Las Calderas, Cubagua Island, Nueva Esparta (UCMP S-122, 4); same as last (UCMP S-155, 1); Cumaná Fm, 2.5 km NE of "Castillo" of Cumaná, N slope of Cumaná Hills, Departamento de Sucre (UCMP S-110, 2); 6 km E of "Castillo" of Cumaná, same as above (UCMP S-112, 1); CAS, unreg., Mare Fm, Cabo Blanco (1 large); Punta Gavilán beds, Punta Gavilán (BMNH Palaeontology Department, G57827, 1). **Pleistocene**: NMB 17607 (1); USGS 18410 (1). **Ecuador: Middle-Late Miocene**: NMB 12816, Borbón Fm, first cliff E of Punta Same, Esmeraldas (1). **Pliocene**: NMB 12822, Onzole Fm, artificial outcrop on hilltop, km 493.05 on Trans-Ecuadorian pipeline, 10 km S of Esmeraldas (2).

Distribution.—In the living fauna, *Distorsio clathrata* is restricted to the western Atlantic (despite the planktotrophic larva illustrated by Laursen, 1981: 27, fig. 42, pl. 2, fig. 5), where it is recorded from North Carolina (Merrill & Petit, 1969), USA, and Bermuda south to Sergipe, Brazil (Coelho *et al.*, 1981). Fossils are recorded widely in the Caribbean region from Miocene (rarely) and Pliocene-Pleistocene rocks, and from the Pleistocene (and possibly latest Pliocene) of Atlantic Panama. Earlier confusion between the species on the eastern and western sides of the Atlantic is discussed below under *D. smithi*.

Rather surprisingly, three specimens are recorded here from the Miocene Borbón Fm and Pliocene Onzole Fm of

Esmeraldas Province, Ecuador, on the *western* coast of tropical America, where *Distorsio clathrata* is not living at present. However, Olsson (1964: 174, pl. 30, figs 1-1b) previously recorded and illustrated two typical specimens of *D. clathrata* from the Onzole Fm at Punta Gorda, Ecuador, and commented that "It seems remarkable that this *Distorsio* from Ecuador should belong to the West Indian-Caribbean *D. clathrata*, rather than to the Pacific group of *D. decussata*." It should be pointed out, though, that *D. decussata* does occur in the Late Miocene of Ecuador; Olsson's (1964: 174, pl. 30, figs 2-2b) specimens identified as *D. gatunensis* from the Angostura Fm at Cueva de Angostura, Rio Santiago, are reidentified here as *D. decussata*.

***Distorsio constricta* (Broderip, 1833)**

Pl. 13, Figs 4-5, 9

Triton constrictus Broderip, 1833: 5; Reeve, 1844a: pl. 12, fig. 41; C. B. Adams, 1852: 116 (in part).

Distorsio constrictus. Tryon, 1880: 35, pl. 17, fig. 176 only; Bosworth, 1922: pl. 26, fig. 16; Pilsbry & Olsson, 1941: 40, pl. 5, fig. 12; Kilias, 1973: 203, fig. 145 (in part not *Triton constrictus* Broderip, 1833).

?*Distortio simillimus*. Gabb, 1881: 353 (not *Distorsio simillima* G. B. Sowerby I, 1850).

?*Distortrix gatunensis*. Li, 1931: 269; Pilsbry, 1931: 433 (either this species or *D. decussata*).

Distorsio (Rhysema) decussata gatunensis. Aguilar & Fischer, 1986: 223, pl. 2, figs 13-14 (not *Distorsio gatunensis* Toulou, 1909).

Distorsio constricta. Emerson & Puffer, 1953: 98; Kilias, 1973: 203, fig. 145 (in part); Parth, 1989b: 9, lowest central fig.; 1991: text-fig. 8; Finet, 1991: 270; Emerson & Piech, 1992: 109, figs 1-4, 23; Henning & Hemmen, 1993: 138, pl. 28, fig. 3.

Distorsio (Rhysema) constricta. Kilias, 1973: 203, fig. 145; Powell, 1988: 17 (list).

Distorsio (Distorsio) constricta constricta. Beu, 1985: 62; Piech, 1995: 20.

Distorsio constricta constricta. Emerson, 1991: 71; Kronenberg, 1994: 68, fig. 9, pl. 1, fig. 2, pl. 2, fig. 6.

Distorsio (Distorsio) constricta. López de la Fuente & Ramos, 2004: 86.

Remarks.—With the recognition by Parth (1989) that two species previously had been confused under the name *Distorsio constricta*, and were sympatric with *D. decussata* in western America, and the further recognition by Emerson & Piech (1992) that still a fourth species, *D. jenniernestae*, is sympatric with all of these in the same area, the distinction between undoubted living species has become so subtle that it proves difficult to recognize some of them as fossils. Add to this the possibility of their occurrence alongside such apparently ex-

tinct species as *D. simillima* (G. B. Sowerby I, 1850), the occurrence of *D. clathrata* at a few fossil localities in Ecuador (see above) and the difficulty of distinguishing even fresh, colored, Recent specimens of some of these species in the juvenile state, and it becomes apparent that not all the fossils encountered in this work have been identified as certainly as I would have preferred.

A summary is provided here of the main points distinguishing the four eastern Pacific living species, based on Emerson & Piech (1986: table 1), emphasizing characters that should be useful in the identification of fossil specimens:

(1) *Distorsio constricta*: shell of medium size (up to *ca.* 60 mm H), but most smaller, the most strongly distorted of the four living eastern Pacific species; with only two closely spaced spiral cords around the shoulder angle, in some specimens with a weakly defined median cord between the two obvious ones; axial costae prominent, forming several rows of small, obvious, rounded nodules behind the terminal varix, but little different from the sculpture of *D. minoruohnishii*; inner lip shield widely spread, but only little, if at all, free from previous whorl along its lower left edge, the most heavily sculptured shield of those of all of these species, with prominent beads and ridges over most of its surface; anterior siphonal canal the shortest of the four species, fairly straight in apertural view, bent toward the dorsum; third tooth (from posterior end of aperture, in conventional view) inside the outer lip enlarged only a little more than its neighbors; outer lip straight in lateral view (*i.e.*, without the deep depression characterizing *D. jenniernestae*). The outer lip is also unique in having an almost straight upper (posterior) portion directed inward from the protruding lower margin to the top of the aperture, revealing more of the shoulder of the terminal varix in conventional apertural view than in any other *Distorsio* species.

(2) *Distorsio decussata*: shell much the largest of the four living eastern Pacific species (up to *ca.* 85 mm H), markedly taller and narrower than the others, the least strongly distorted of the four; with only two, prominent, closely spaced cords around the shoulder angle; axial costae and spiral cords narrow and widely spaced, with particularly widely spaced axial ridges, nodules more weakly developed than in the other three species; inner lip shield less widely spread than in *D. constricta*, but forming a well-raised free collar over the neck of the canal; anterior canal straight, narrow, the longest of the four species; third tooth inside the outer lip greatly enlarged, narrow; outer lip straight in lateral view. Pilsbry & Olsson (1941: 40) also pointed out that most specimens of *D. decussata* and all very closely related species have *two* long parietal callus ridges, bordering the posterior apertural notch, whereas all the other species considered here have only one ridge.

Initially, I regarded all specimens from the study area that fall within the above diagnosis as belonging to the single spe-

cies *D. decussata*. However, more careful comparison of secondary spiral sculpture and protoconchs of the huge collection of material of this species group available in NMB demonstrated that it is preferable, and biogeographically valuable, to recognize three species within what I initially identified as *D. decussata*:

(a) *Distorsio decussata* (*sensu stricto*) (= *gatunensis*), the large, Miocene to Recent species with very weak interstitial spiral sculpture and a moderately large protoconch with its coiling axis tilted at an obvious angle to that of the teleoconch, living only in the eastern Pacific but with many records from Miocene and Pliocene rocks on both coasts of tropical America;

(b) *Distorsio simillima*, the large Caribbean fossil species with a few narrow, prominent secondary spiral cords between the major ones, particularly on the sutural ramp, with a tall, narrowly conical protoconch with its coiling axis parallel to that of the teleoconch; and

(c) *Distorsio jungi* n. sp., a smaller species than the above two, although with similar or, in some specimens, narrower proportions and similar sculpture to those of *D. decussata*, but with slightly more distorted coiling, with a much smaller, tilted protoconch, occurring only in the Early Miocene Cantaure Fm and La Candelaria beds in Venezuela (and possibly in the coeval Chipola Fm, Florida).

(3) *Distorsio jenniernestae*: shell moderately large (to ca. 65 mm H), a little taller, narrower, and less strongly distorted than *D. constricta* and *D. minoruohnishii*, but markedly shorter, wider, and more strongly distorted than *D. decussata*; with a group of 3–4 low, weakly defined spiral cords around a clearly defined, well-raised peripheral nodule row, separated from the next major cord below by an obvious spiral depression; axial costae prominent but widely spaced, minor surface nodules less obvious than in *D. constricta* and *D. minoruohnishii*; inner lip shield widely spread, with well-raised free collar over neck of canal, thick and rather smooth, giving the aperture a more regularly oval appearance than in the other three living eastern Pacific species; anterior canal moderately long, straight or (in most specimens) inclined to the right and toward the dorsum; third tooth inside the outer lip greatly enlarged, wide in many specimens; outer lip, in lateral view, with a deep depression (notch), unique to this species, between enlarged third tooth and top of aperture.

(4) *Distorsio minoruohnishii*: the smallest of the four living eastern Pacific species (to ca. 50 mm H), most specimens short and wide, less distorted than *D. constricta* and *D. jenniernestae*; with only two closely spaced spiral cords around the shoulder angle; axial costae and minor surface nodulation similar to that of *D. constricta*; many specimens with a more prominent subsutural cord or band than in the other three species; inner lip shield widely spread, with a well-raised free

collar over the neck in some specimens, moderately thick and rather smooth to weakly nodulose, in some large specimens spreading further up onto the preceding whorl than in the other three species; anterior canal short to moderately long, curved to the right at the tip in many specimens, inclined toward the dorsum; third tooth inside the outer lip little enlarged, the smallest among the four species; outer lip flange wider over anterior half than posterior half in most specimens; outer lip straight in lateral view.

Recent specimens of *Distorsio constricta* can be distinguished from *D. minoruohnishii* very readily because of the dark red-brown lines between the nodules on the inner lip shield of *D. constricta*; the smoother shield of *D. minoruohnishii* is plain cream. However, without this character, it is clear that there is little to separate fossil specimens of *D. constricta* and *D. minoruohnishii*, unless they are excellently preserved.

A further species in this complex that is very significant for Panama Isthmus biogeography, and is just as difficult to distinguish as the four living eastern Pacific species distinguished above, is *Distorsio mcgintyi*. This species lives only in the western Atlantic at present, where it is sympatric with *D. clathrata*. Several specimens of *D. mcgintyi* have been collected from Pliocene rocks of Atlantic Panama, and it is the species that is most common in the Late Pliocene–Early Pleistocene rocks of Limón, Atlantic Costa Rica. Unfortunately, distinguishing these two species is just as difficult as distinguishing the three similar eastern Pacific species. Recent specimens are distinguished, again, from both *D. minoruohnishii* and *D. jenniernestae*, by the color pattern of red-brown lines between the obvious nodules and ridges on the inner lip shield. This pattern is similar to that of *D. constricta*, but in most specimens of *D. mcgintyi* is paler, a pale to medium tan rather than the dark red-brown of *D. constricta*, but it is distinctive in the tan lines being narrower than in *D. constricta*, and the nodules and ridges of the shield's surface are coarser but less regularly arranged than in *D. constricta*. Of course, the color pattern is again of no help for distinguishing fossils.

Distorsio mcgintyi shares some of the shell characters of both *D. constricta* and *D. jenniernestae*. Its most distinctive character is the wide peripheral spiral cord cluster, with three or, in most specimens, four narrow cords, to as many as six on large specimens, on the well-raised ridge around the periphery. The ridge is even wider than in *D. jenniernestae* and a little more prominent than in any of the other similar species, so that the sutural ramp is more strongly concave and the swollen left side of the shell, to the left of the penultimate varix in conventional apertural view, protrudes a little further to the left than in most specimens of any of the other similar species (although a few specimens of *D. constricta* have a similarly concave ramp). Also, as in *D. jenniernestae*, the third tooth

inside the outer lip is greatly enlarged, much more obviously than in *D. constricta* or *D. minoruohnishii*, and is quite wide in some specimens. The outer lip flange of most specimens is either equally expanded for its full height or curved outward to be widest near the center of the left margin, as in *D. jenniernestae*, rather than slightly narrower over the posterior (adapical) half as in most specimens of *D. constricta* and *D. minoruohnishii*. As in *D. constricta*, the inner lip shield adheres closely to the previous whorl, with its left margin slightly raised, at the most, and not raised into a free collar. Overall the shell is markedly shorter and wider than in *D. decussata* or most specimens of *D. clathrata*, but a little taller and narrower than any of the other three similar species, with small prominent nodules at the sculptural intersections over much of the exterior surface, and a moderately long and, in most specimens, fairly straight anterior canal turned slightly to the right and toward the dorsum. The outer lip lacks the deep depression that characterizes *D. jenniernestae*. *Distorsio mcgintyi* reaches a moderately large size (to ca. 60 mm H), comparable to that of *D. constricta*. In summary, *D. mcgintyi* resembles *D. constricta* most closely, but has a still more strongly angled left side in apertural view and has a particularly wide and prominent peripheral band bearing four or more spiral cords, rather than the two with, at most, a weak third between them in *D. constricta*, and the third tooth from the posterior end inside the outer lip is large, prominent and wide in *D. mcgintyi*, as in *D. jenniernestae*, whereas it is little raised above its neighbors in *D. constricta*. SEM examination of protoconchs showed that they are of only very subtly different shape in *D. constricta*, *D. mcgintyi*, and *D. minoruohnishii*. In all three species the protoconch is small, with coiling parallel to that of the teleoconch, unusually regularly conical in shape, and quite tall and narrow compared with other species examined.

Dimensions.—Lectotype: H 60.8, D 36.1 mm; paralectotypes: H 60.7, D 34.6 mm; H 54.7, D 31.1 mm (Emerson & Piech, 1992: 109); GNS WM18094, Recent, intertidal, Gobernadora Island, Panama Bay: H 41.8, D 24.6 mm.

Types.—*Triton constrictus*, lectotype BMNH 198016/1, designated by Emerson & Piech (1992: 109, figs 2-3), the specimen figured by Reeve (1844a: pl. 12, fig. 41), with two paralectotypes BMNH 198016/2-3; from “Monti Christi and Xipixapi.” The type locality was restricted by M. Smith (1944: 23) to St. Elena, Ecuador, which he apparently thought equivalent to “Xipixapi.” However, Jipijapa [= “Xipixapi”] and Montecristi [= Monti Christi] are inland towns close to Manta, which is 90 km north of Santa Elena (at Bahía de Santa Elena, W of Guayaquil). I am indebted to Emily Vokes for pointing out that Manta was the major port of the area at the time of Cuming’s collecting, important for shipping “Panama hats” (which are made in Jipijapa), and Cuming’s specimens, described by Broderip, undoubtedly would have

been obtained at Manta; the type locality is here corrected to Manta, Ecuador.

Other material examined.—**Recent:** Many lots at LACM, AMNH, ANSP, USNM, which however are not listed here because, when I examined them, the three similar eastern Pacific species *D. constricta*, *D. jenniernestae*, and *D. minoruohnishii* had not been distinguished; a selection of material was listed from 13 localities by Emerson & Piech (1992: 109); 5 lots at GNS. The northernmost record is off of Islas Murcielago, Guanacaste Province, Costa Rica (10°51.5’N), in 2.4-4 m; the southernmost that I have examined is from Peru (beach, between Mancora and Los Organos, 4°10’S, SMF 150628, 1).

Fossils: Pacific Costa Rica: Late Miocene: NMB 17753, Quepos, Punta Judas (1; very incomplete, with oyster in aperture, sculpture coarsely nodulose; referred here uncertainly). **Pacific Panama: Pleistocene:** A. A. Olsson’s loc. 452, Charco Azul Fm, Peninsula de Osa (USNM, 1).

Distribution.—*Distorsio constricta* lives now from Guanacaste Province, Costa Rica, at least as far south as 4°10’S in Peru, western America (Emerson & Piech, 1992; and data above). It was recorded from the Galápagos Islands by Finet (1985) and from both the Galápagos Islands and Cocos Island, Costa Rica, by Emerson (1991), but Emerson & Piech (1992) considered that the Galápagos record needs verifying in view of the other species now recognized in the eastern Pacific. Cosel (1984) recorded it from Gorgona Island, Colombia. Olsson (1924: 124) recorded it also from Salinas in Ecuador and from Mancora, Lobitos, and Negritos in Peru, although this could well include records based on *D. jenniernestae* and/or *D. minoruohnishii*. Besides the few fossils listed above, specimens illustrated by the following authors appear to represent *D. constricta*: Boswell (1922: pl. 26, fig. 16), as *Distorsio constrictus*, from Mancora uplifted terraces (“tablazos”), Pleistocene, in northwestern Peru; Aguilar & Fischer (1986: 223, pl. 2, figs 13-14), as *D. (Rhysema) decussata gatunensis*, from Montezuma Fm (Pleistocene), Nicoya Peninsula, Costa Rica; and Perrilliat (1992: 24, pl. 7, fig. 6), as *D. (Rhysema) decussata gatunensis*, from Ferrotepec Fm (Middle Miocene), Michoacan, West Mexico. Powell (1988: 17) recorded *D. constricta* also from the Imperial Fm (now Latrania Fm; Demere & Rugh, 2006), (Late Miocene?-Early Pliocene) of Imperial Co, California, USA, by far the northernmost record of *Distorsio* in the eastern Pacific, but I have not examined this material. Fossils therefore are recorded sparsely now from Middle Miocene to Pleistocene rocks of the Pacific coasts of California, Costa Rica, Panama, and Peru, although the Miocene record from Punta Judas, Costa Rica, is tentative; the only other Miocene record is Perrilliat’s (1992: 24, pl. 7, fig. 6) from Michoacan, West Mexico.

Distorsio decussata (Valenciennes, 1832)

Pl. 14, Figs 1-9; Pl. 15, Figs 1-5, 9

Tritonium decussatum Valenciennes, 1832: 306.*Triton ridens* Reeve, 1844a: pl. 12, fig. 46 (in part; not including lectotype).*Distorsio* (*Distortrix*, *Persona*) *gatunensis* Toula, 1909: 700, pl. 25, fig. 10.*Distorsio gatunensis*. Brown & Pilsbry, 1911: 356, pl. 26, fig. 8.*Distorsia* (*sic*) *constricta*. Pilsbry, 1922: 359 (in part not *Triton constrictus* Broderip, 1833).*Distortrix simillima*. Olsson, 1922: 305 (not *Triton simillimus* G. B. Sowerby I, 1850).*Distorsio decussatus gatunensis*. Rutsch, 1930: 609, pl. 17, fig. 6; Emerson & Puffer, 1953: 100.? *Distorsio gatunensis*. Li, 1931: 269; Pilsbry, 1931: 433 (either this species or *D. constricta*).*Distorsio decussatus*. Pilsbry & Olsson, 1941: 40, pl. 5, fig. 9; M. Smith, 1948: 22, pl. 8, fig. 13; Hertlein & Strong, 1955b: 265; Keen, 1958: 346, fig. 326.*Distorsio decussata*. Emerson & Puffer, 1953: 99; Lewis, 1972: 43, figs 36-37; Abbott, 1974: 166, fig. 1775; Parth, 1989a: 52, bottom left fig.; 1991: 11, 4 figs; Emerson & Sage, 1990a: figs 10-13; Henning & Hemmen, 1993: 139, pl. 29, fig. 5; Kronenberg, 1994: 73, text-fig. 12, pl. 1, figs 6, 11a-b, pl. 3, fig. 10; Piech, 1995: 20.*Distorsio* (*Rhysema*) *decussata gatunensis*. Woodring, 1959: 205, pl. 34, figs 7, 10, pl. 36, fig. 5.*Distorsio* (*Rhysema*) *decussata*. Emerson & Old, 1963a: 27, fig. 25; Keen, 1971: 508, fig. 963.*Distorsio* (*Rhysema*) *gatunensis*. Olsson, 1964: 174, pl. 30, figs 2-2b.*Distorsio* (*Distorsio*) *decussata*. Beu, 1985: 62; Emerson & Piech, 1992: 114, figs 21-22; López de la Fuente & Ramos, 2004: 86.*Distorsio ridens*. Parth, 1989a: 54 (not *Triton ridens* Reeve, 1844).

Remarks.—The characters separating *Distorsio decussata* from the other species living in the eastern Pacific are summarized above, under *D. constricta*. *Distorsio decussata* is highly distinctive in the living fauna because of its large size, its tall, narrow shape, its weak coiling distortion, its two narrow, closely spaced parietal spiral cords, and its long, nearly straight anterior siphonal canal. A more difficult problem in the tropical American fossil record is the question of whether *D. decussata* is a different taxon from *D. simillima* or *D. gatunensis*. The identity of these taxa has troubled all taxonomists since Woodring (1928: 300, pl. 18, figs 7-9, pl. 19, figs 1-3), in his very influential monograph of the Bowden fauna, confused the issue by illustrating both *D. mcgintyi* and what is here concluded to be *D. simillima* as “*Distorsio decussatus simillimus*,” and typical *D. clathrata* (Lamarck) as “*D. clathratus gatunensis*.” Of course, Woodring’s monograph was published long before the mysteries of western Atlantic *Distorsio* taxa were resolved by Olsson & McGinty (1951), Puffer (1953), and Emerson & Puffer (1953). *Distorsio gatunensis* is considered

here to be a synonym of *D. decussata*, whereas the distinct species *D. simillima* and *D. jungi* n. sp. are discussed separately below.

Woodring (1959: 206) further confused the recognition of species of *Distorsio* by describing incorrect protoconchs for several species. Assembling all the tropical American species together for comparison showed that a different combination of species actually exists from that recognized by Woodring.

(1) *Distorsio decussata*: In the relatively few available Recent eastern Pacific specimens with undamaged protoconchs (including several loaned by Gijs Kronenberg, Eindhoven), the protoconch is identical to that of Gatun Fm (Panama; Middle and Late Miocene) specimens identified by Woodring (1959) as *D. gatunensis*: moderately large, relatively low-spired (about equidimensional), and inclined at a slight but obvious angle to the coiling axis of the teleoconch. Woodring (1959: 206) described the protoconch of *D. decussata* as “small, high-spired, and not tilted.” This suggests that Woodring (1959) actually examined the protoconch of a specimen of *D. mcgintyi*, which his description matches exactly; this species has a taller and narrower protoconch than most other species seen, although it is also a description of that of *D. simillima*. I can find no consistent characters to distinguish Gatun Fm specimens from *D. decussata*, and in my opinion *D. gatunensis* is simply a synonym of *D. decussata*.

(2) *Distorsio jungi*: The specimens from the Cantaure Fm (late Early Miocene) of the Paraguaná Peninsula, Venezuela, identified by Jung (1965) as *D. gatunensis*, are described below as the new species *D. jungi*. The protoconch of this new species certainly is tilted at an angle to the teleoconch coiling axis, but the protoconch is significantly smaller and more strongly tilted than that of *D. decussata*. The teleoconch also is a little smaller and significantly taller and narrower than those of *D. decussata* and *D. simillima*.

(3) *Distorsio simillima*: Specimens assigned (on the basis of their large size and their prominent secondary spiral cords on the sutural ramp) to *D. simillima*, a species closely resembling *D. decussata* in all other characters, from both the Dominican Republic (Late Miocene-Early Pliocene) and from Panama (Early-Late Pliocene) and Limón, Costa Rica (latest Pliocene-Early Pleistocene), have a protoconch nearly identical to that of *D. constricta*, *D. mcgintyi*, and *D. minoruohnishii*: quite small, relatively tall and narrowly conical, and parallel to the teleoconch coiling axis. This character therefore strongly supports the separation of *D. simillima* from *D. decussata*.

The identity of specimens from the El Porvenir beds (late Early Miocene) near Buenevara, Paraguaná Peninsula, Venezuela, is difficult to resolve. Gibson-Smith & Gibson-Smith (1979) described the stratigraphy and ages of Paraguaná Peninsula localities, recognizing several faunas for the first time. The El Porvenir specimens are all calcite neomorphs,

most very incomplete, and many are encased in hard matrix. The two most complete specimens (Pl. 21, Figs 5, 7; Pl. 22, Figs 1-2) have been cleaned of matrix, and closely resemble Panama material referred here to *Distorsio decussata*. The largest and best-preserved (Pl. 21, Figs 5, 7) even has a partially preserved protoconch, which clearly is relatively large and tilted at an angle to the coiling axis of the teleoconch. This specimen is a little larger and more inflated than typical Panama specimens. These specimens also clearly bear the secondary and tertiary spiral threads on the sutural ramp that distinguish *D. simillima* from *D. decussata*. It is concluded that they are probably specimens of *D. simillima*, despite the evidence of the protoconch, although it seems possible that *D. simillima* and *D. decussata* were in the process of separating at this time. More well-preserved material from the El Porvenir beds would help the identification.

A particularly unusual lot of specimens from Ecuador deserves special mention: a large, narrow, slightly incomplete adult specimen (Pl. 53, Fig. 1; NMB H 18307) and three small, incomplete specimens from locality NMB 19084 (Onzole Fm?, Pliocene, downstream from Picaderos village, Río Santiago, Borbón, Esmeraldas Province, Ecuador). The largest specimen (NMB H 18307) has evenly rounded whorls and evenly spaced primary spiral cords (without a concave sutural ramp and two spiral cords more closely spaced than the others, angling the periphery, as in *Distorsio decussata*) and has a secondary spiral thread within each spiral interspace, and two or three tertiary threads in the two interspaces on the sutural ramp. The smaller specimens have secondary spiral threads, but have a narrow, weakly concave sutural ramp. They closely resemble one of the small, incomplete specimens assigned to *D. decussata* from locality NMB 19156 (Angostura Fm?, pueblito Marco, road to Santo Domingo, 20 km ENE of Flavio Alfaro, Manabí Province, Ecuador) and so it seems likely that these are highly aberrant specimens of *D. decussata*. However, it is possible that more material will demonstrate that this is yet another, unnamed species of *Distorsio*.

Dimensions.—Figured specimen, NMB H17908, from NMB 18289, Río La Vaca, Pacific Costa Rica: H 77.6, D 47.5 mm; Recent, LACM 59-11, shrimp boats out of Guaymas, Sinaloa, W Mexico, H 78.9, D 41.2 mm; Recent, R. von Cosel's material in SMF, *Cassique* cruise 69/10, sta. 229, off of Buenaventura, W Colombia: H 93.0, D 41.7 mm; lectotype of *D. gatunensis* Toulou: H 32.1, D 19.9 mm; paralectotype: H 28.7 (incomplete), D 19.3 mm; figured specimen, NMB H 17918, from NMB 18373, Panama: H 44.4, D 25.2 mm; figured specimen, NMB H 17917, from NMB 18510, Darien: H 33.6, D 21.9 mm.

Types.—*Tritonium decussatum*, no original Valenciennes material present in MNHN; neotype AMNH 85335, designated by Emerson & Piech (1992: 114, figs 21-22), from Arena

Bank, Baja California Sur, Mexico, 23°29'N, 109°25'W, in 82 m. *Distorsio* (*Distortrix*, *Persona*) *gatunensis*, two syntypes formerly in Sammlung Toulou, Technische Hochschule, Vienna (Rutsch, 1930: pl. 17, fig. 6), from Canal Zone, Panama; now NHMV 1933/18/188-189; Toulou's (1909: pl. 25, fig. 10) figured syntype (NHMV 1933/18/188) is a small, complete specimen of the species identified by this name by Woodring (1959), and here identified as *D. decussata*, with a large, tilted protoconch, and is here designated the lectotype of *D. gatunensis* Toulou, 1909. The unfigured paralectotype is incomplete, a little more distorted than the lectotype, and not certainly identifiable, and might not be conspecific with the lectotype. Both specimens have a matrix of rather coarse sandstone with clearly visible paler and darker sedimentary grains; many Gatun Fm specimens have a similar matrix.

Other material examined.—**Recent:** 89 lots, at LACM (mainly), GNS, SMF, and Kronenberg collection, from W Mexico (northernmost: 120 m, Puerto Refugia, Isla Angel de la Guardia, Gulf of California, LACM-AHF 708-37, 1), Nicaragua, Guatemala, W Costa Rica, W Panama, W Colombia, Ecuador, and Peru (southernmost: 32-74 m, S of Punta Pariñas, N of Paíta, *Anton Bruun* cruise 16, sta. 624-C, LACM 66-127, 1).

Fossils: Pacific Costa Rica: Pleistocene: NMB 17471 (1); 17736 (1); 17745 (8); 17752 (2); 17767 (2); 17799 (2); 18153 (1); 18161 (1); 18287 (1); 18289 (1, illustrated, NMB H 17908; Pl. 14, Figs 1-2, 5); USGS 24792 (4); Charco Azul Group, Penita Fm, Quebrada el Higo, Burica Peninsula, collection of Bernard Landau (5); Montezuma Fm, Playa Cocalito, Nicoya Peninsula, collection of Bernard Landau (1). **Atlantic Panama: Miocene:** Gatun Fm: NMB 17639 (1); 17643 (7); 17644 (14); 17645 (1); 17868 (5); 18258 (1); 18260 (3); 18261 (5); 18262 (9); 18308 (7); 18322 (1); 18324 (1); 18326 (3); 18360 (1); 18389 (1); 18390 (1); 18391 (1); 18392 (2); 18662 (5); 18663 (2); TU 958 = NMB 19028 (GNS WM16955 + WM18905, 36); 959 (GNS WM18906, 5); 962, as last (GNS WM18907, 1); USGS 5854 (1); 5899 (1); 8375 (1); 8383 (1); 8409 (2); 8410 (1); 8487 (1); 8488 (1); 16949 (2); 21956 (22); 22016 (4); 22018 (5); 23663 (4); 24173 (1); 25278 (1); 25281 (1); USNM 113689, Mt. Hope, Gatun (2); 562607, Stanford University loc. 2653, Gatun third locks (1; specimen illustrated by Woodring, 1959: pl. 34, figs 8-9); CAS loc. 2611, Gatun third locks, Gatun Fm (2); CAS loc. 2653, same as last (1); CAS loc. 2707, drainage ditch 160 m W of French canal and 1 km SW of Mindi Dock, Canal Zone (1); CAS loc. 323, near spillway, Gatun Locks (2); CAS loc. 60303, park at refinery 3 km N of Cativa, Gatun Fm (1); TU 961, Gatun Fm, Cativa, Colon, collection of Bernard Landau (8); Middle Gatun Fm (Messinian), Los Lomos storage facility, Cativa, Colon, Panama, coll. J. A. Todd, January 1998 (BMNH Palaeontology Department,

1); lower Gatun Fm, bed 1 of Todd, quarry floor, Los Lomos Suites, Cativa, Colon (BMNH Palaeontology Department, GG 22588-22592, 5); lower Gatun Fm, surface-picked, Los Lomos quarry, Cativa, Colon, P. Jeffery, August 1998 (BMNH Palaeontology Department, GG 22599-22607, 9); lower Gatun Fm, Fabrica de Colchones, Cativa, Colon (BMNH Palaeontology Department, GG 22609, 1); lower Gatun Fm, bed 6 of Todd, quarry floor, Los Lomos Suites, Cativa, Colon (BMNH Palaeontology Department, GG 22595-6; 2); lower Gatun Fm, bed 8 of Todd, quarry floor, Los Lomos Suites, Cativa, Colon (BMNH Palaeontology Department, GG 22598; 1); lower Gatun Fm, bed 9 of Todd, quarry floor, Los Lomos Suites, Cativa, Colon (BMNH Palaeontology Department, GG 22593-4, 2); lower Gatun Fm, *ex situ*, ?beds 6-10 of Todd, quarry floor, Los Lomos Suites, Cativa, Colon (BMNH Palaeontology Department, GG 22597, 1); lower Gatun Fm, *ex situ*, Fabrica de Colchones, Cativa, Colon (BMNH Palaeontology Department, GG 22608, 1); Chagres Fm: NMB 18989 (1); Valiente Fm: NMB 17629 (8); NMB 17824 (5); NMB 18711 (4); NMB 18769 (1, juvenile, identity uncertain); USGS 8326 (1); Nancy Point Fm: NMB 18768 (3). **Pliocene:** Escudo de Veraguas Fm: NMB 17622 (1 large); NMB 17628 (1 juvenile, illustrated, Pl. 14, Fig. 8); NMB 17840 (4; 1 juvenile illustrated, Pl. 14, Figs 7, 9); Cayo Agua Fm: NMB 17816 (1); 17823 (1); 18373 (2; one illustrated, H 17918; Pl. 15, Figs 1-2); 18719 (2); 18734 (2); Shark Hole Point Fm: NMB 18705 (5); 18716 (2). **Pacific Panama: Pleistocene:** NMB 17442, (1); 17443 (2); 18066 (2); 18071 (1); Armuelles Fm, Río Rabo de Puerto, Burica Peninsula, collection of Bernard Landau (1). **Panama, Darien: Middle-Late Miocene:** NMB 18510 (2; one illustrated, NMB H 17917; Pl. 15, Figs 3-4); 18657 (1); USGS 8477 (1). **Ecuador: Miocene:** NMB 19078 (6); 19125 (7); 19126 (8); 19156 (2 poor, fragmentary); USGS 23487 (4; including USNM 644044, USNM 652257, the 2 specimens illustrated by Olsson (1964: pl. 30, figs 2-2b) as *D. gatunensis*). **Pliocene:** NMB 12825 (2; unusually finely sculptured); 19151 (1, incomplete); 19154 (1, incomplete); USGS 23478 (1).

Distribution.—*Distorsio decussata* has been reported previously as living from the Gulf of California south to Manta, Ecuador (Hertlein & Strong, 1955b; Emerson & Piech, 1992), and the material listed above shows that it reaches at least as far south as Tumbes, northern Peru. Peña (1970) also recorded it from off of Tumbes. Fossils are abundant in Pliocene rocks of the Atlantic coasts of both Costa Rica and Panama, in the Middle to Late Miocene Gatun Fm in Panama, and in Miocene to Pleistocene rocks of Pacific Costa Rica and Panama, and a few specimens are known from the Pliocene rocks of Ecuador.

***Distorsio floridana* (Gardner, 1947).**

Pl. 15, Figs 6-8, 10-12

Personella floridana Gardner, 1947: 535, pl. 53, fig. 8.

Distorsio floridana. Emerson & Puffer, 1953: 99; Kronenberg, 1994: pl. 4, figs 9-10.

Remarks.—*Distorsio floridana* is a poorly known species, apparently largely limited in Florida to the Shoal River Fm, Alum Bluff Group, Miocene, although a single, small, fragmentary specimen is listed below from the Chipola Fm that tentatively is assigned to *D. floridana*. Gardner's (1947: pl. 53, fig. 8) holotype is a small, immature specimen (Pl. 15, Figs 6-7), and several other specimens from the Shoal River Fm in the USGS collections, USNM, show that the adult (Pl. 15, Figs 10-11) is a distinctive form, perhaps most nearly similar to *D. clathrata* in most characters, but easily distinguished from *D. clathrata* by its much shorter and wider shape, its less prominent axial and spiral sculpture, its more strongly inflated intervariceal area after each varix, and in having a single narrow secondary spiral thread halfway between the subsutural and peripheral cords on the weakly developed, narrow, slightly concave sutural ramp. The ramp is similar in *D. clathrata*, but most specimens lack the central thread. Two specimens (Pl. 15, Figs 8, 12) in collections from the Pliocene Charco Azul Fm of the Burica Peninsula, Pacific Costa Rica, agree with the Florida shells in most characters, including the fine thread on the sutural ramp, although the axial costae are more prominent than in the larger Florida specimens. The Costa Rican specimens are, however, a little smaller than the largest Florida ones, and the holotype has similar axial costae to the Panama shells, so possibly the prominent costae merely reflect the immaturity of these specimens. The prominent costae of the Costa Rican shells introduce a similarity to immature specimens of *D. constricta* and *D. mcgintyi*, indicating that it is quite likely that the Costa Rican specimens represent another, as yet poorly known species, as is also suggested by their much younger age than the Florida specimens. The identity of the Costa Rican shells will remain uncertain until more specimens are available. The relationships of *D. floridana* are still unclear.

Dimensions.—Holotype of *Personella floridana*: H 23.1, D 16.9 mm; USGS 10603, Shoal River Fm (late Middle Miocene), ca. 2.5 km SE of Eucheeanna, Walton Co, below Shell Bluff, Shoal River, largest and most complete known (Pl. 15, Figs 10-11): H 50.5, D 32.3 mm; figured specimen, NMB H 17916, from NMB 18055, Penita Fm (Pliocene), Burica Peninsula, Costa Rica: H 33.5, D 23.1 mm.

Types.—*Personella floridana*, holotype USNM 371879 (Pl. 15, Figs 6-7), from USGS 3742, Shoal River Fm (Miocene), Shell Bluff, WNW of Mossy Head, Florida, USA.

Other material examined.—**Fossils: Florida: Late Early Miocene,** Chipola Fm: TU 830, Tenmile Creek, Chipola

River, coll. & pres. E. H. Vokes (1 small, fragmentary, more inflated than the specimens of *D. jungi* n. sp. recorded below; but too small for certain identification). **Middle Miocene**, Shoal River Fm: USGS 3742 (USNM 351478, 1); 3856 (USNM 351477, 1); 5184 (USNM 351479, 1); 5195 (USNM 351480, 1); 10603 (1, illustrated, Pl. 15, Figs 10-11); "*D. floridana* n. sp.," Shoal River (USNM, 1). **Pacific Costa Rica: Pliocene**: NMB 18054, Chaco Azul Group, Penita Fm, near waterfall, Quebrada la Penita, Burica Peninsula (1, referred with hesitation); NMB 18055, 100 m upstream from NMB 18054 (1, referred with hesitation; illustrated, NMB H 17916; Pl. 15, Figs 8, 12).

Distribution.—*Distorsio floridana* is recorded only from the Middle Miocene Shoal River Fm of Florida, USA, and (tentatively) from the late Early Miocene Chipola Fm of Florida and the Pliocene Charco Azul Fm of Burica Peninsula, Pacific coast of Costa Rica. The Charco Azul Fm specimens likely represent another, apparently unnamed species, but more, better material is required to evaluate this form.

***Distorsio jenniernestae* Emerson & Piech, 1992**

Pl. 17, Figs 1-3

Distorsio (Rhysema) constricta. Emerson & Old, 1963a: 26, fig. 24 (in part); Keen, 1971: 508, fig. 962 (in part); Lewis, 1972: 45, fig. 41 (in part); Kerstich, 1989: 45, fig. 89 (in part not *Triton constrictus* Broderip, 1833).

Distorsio ridens. Parth, 1991: 8, 10, top 4 figs (in part not *Triton ridens* Reeve, 1844).

Distorsio jenniernestae Emerson & Piech, 1992: 111, figs 5-8, 16-18, 24; Chaney, 1992: 89, fig. 9; Henning & Hemmen, 1993: 142, pl. 29, fig. 4; Kronenberg, 1994: 83, text-fig. 16, pl. 2, fig. 9; Piech, 1995: 21.

Distorsio (Distorsio) jenniernestae. Kaiser, 1997: 32.

Remarks.—*Distorsio jenniernestae* is distinguished above from the sympatric western American species *D. constricta*, *D. decussata*, and *D. minoruohnishii*. It is particularly easily recognized by the deep depression (seen in lateral view) in the upper part of the outer lip of adult specimens, but has other distinctive characters such as the three closely spaced cords around the peripheral raised band; all other western American species have only two cords on this raised area.

Dimensions.—Holotype of *Distorsio jenniernestae*: H 59.9, D 32.3 mm (Emerson & Piech, 1992: 113); figured specimen, NMB H 17919, Río la Vaca, Pacific Costa Rica: H 45.2, D 28.2 mm.

Types.—*Distorsio jenniernestae*, holotype AMNH 232214, paratypes: AMNH 232215 (4), USNM 860245 (2, none of them seen), GNS WM15345 (1), B. J. Piech collection (10, not seen), all from between Isla Cébarco and Isla Coiba, off Pacific coast of Veraguas, Panama, in 73 m, collected by J.

Ernest, 1991.

Other material examined.—**Recent**: Specimens were listed from 14 Recent localities by Emerson & Piech (1992). These range from off of Isla Tiburón, Gulf of California (AMNH 77066) to the type locality, in the Gulf of Panama, and to the Galápagos Islands (LACM.AHF 38-48). **W Mexico**: dredged, 50 m, off of Isla Macapule, Sinaloa (GNS WM18091, 1). **Pacific Panama**: low tide, Venado Island (GNS WM18090, 1). **Pacific Colombia**: R. von Cosel's material in SMF: shrimp boat, 50 m, NE of Isla Gorgona (1); *Cassique* haul 18, off of Buenaventura (1); *Cassique*, 50 m, near the last, N of Isla Gorgona (1).

Fossils. Pacific Costa Rica: Pleistocene: NMB 18288, Armuelles Fm, lower course of Río La Vaca, Golfo Dulce (one, illustrated, NMB H 17919; Pl. 17, Figs 1-3).

Distribution.—Recent specimens of *Distorsio jenniernestae* were recorded by Emerson & Piech (1992: 113) only from the Gulf of California, the Pacific coast of Costa Rica, the Gulf of Panama, and the Galápagos Islands, in depths from the intertidal zone to 137 m. It possibly ranges more widely, but earlier records of *D. constricta* in western America need reevaluation to establish the ranges of *D. jenniernestae* and *D. minoruohnishii*. It was recorded from Cocos Island, Costa Rica, by Chaney (1992; Skoglund, 1992). The single fossil specimen seen in this survey, from Pleistocene rocks on the Pacific coast of Costa Rica, is moderately large (H 45.2 mm) and agrees with the Recent ones in all characters.

***Distorsio jungi* n. sp.**

Pl. 16, Figs 1-11; ?Pl. 17, Figs 4-5, 7

Distorsio (Rhysema) decussata gatunensis. Jung, 1965: 512, pl. 68, figs 9-11 (not *Distorsio gatunensis* Toulou, 1909, = *Tritonium decussatum* Valenciennes, 1832).

Description.—Shell small for genus (to 57 mm H, but few specimens exceeding 50 mm), tall and narrow, with tall, narrow spire, moderately long, narrow anterior siphonal canal with straight left edge (inner lip extension), low, narrow varices at each two-thirds of a whorl down entire teleoconch, a narrow peripheral angulation formed by two closely spaced, narrow spiral cords, and weakly distorted coiling. Protoconch of 3.5 smooth, strongly inflated whorls with deeply impressed sutures (as in other *Distorsio* species), low-turbiniiform, small for genus, obviously tilted at an angle of ca. 10° to coiling axis of teleoconch. Teleoconch sculpture commencing as 4 equal, evenly spaced spiral cords crossed by low, narrow axial costae similar in size and spacing to spiral cords, forming low, regular nodules at sculptural intersections; interval between subsutural and next lowest cord widening gradually and becoming weakly concave down shell to form sutural ramp, which varies in width around each intervariceal interval in conformity with

eccentric coiling; 2 spiral cords below sutural ramp maintaining their close spacing to form bi-angled peripheral cord down entire teleoconch; one major, high, narrow, flat-topped spiral cord below periphery on inflated parts of intervariceal intervals on spire and 5 on last whorl, separated by flat interspaces each about twice the width of one cord; *ca.* 8-10 further low, narrow, widely spaced cords on base and anterior canal. Axial costae on last 2-3 intervariceal intervals widely spaced, 10-12 on last interval of holotype, prominent and widely spaced on early, inflated part of each intervariceal interval, but becoming progressively lower, narrower, and more closely spaced over each interval as inflation decreases; small nodules at sculptural intersections correspondingly larger and more widely spaced over early, inflated part of each interval, gradually weakening and then obsolescent over later part of each interval. Interstitial sculpture of faint, low, widely spaced spiral threads only, apart from one low, inconspicuous, narrow secondary spiral cord near center of sutural ramp of many specimens. Aperture typical of genus, similar to that of *D. decussata*, with very thin, moderately wide inner lip shield spreading only to a short distance above periphery and across penultimate varix, sculptured by ridges of previous whorl clearly visible through callus, with 2 prominent, very oblique, callous ridges on parietal area, several prominent, long, transverse ridges on lower, outer part of outer lip, and diagnostic *Distorsio* raised ridge on columellar base bearing 10-12 short, very prominent transverse ridges, decreasing regularly in size down left margin of straight siphonal canal. Outer lip with rather narrow, flat anterior flange, normal to coiling direction, bearing 8 short, narrow, prominent transverse ridges on its inner edge, third from posterior (upper) end much the largest, and another row of 10 short, prominent transverse ridges along outer margin of lip; central third of lip flange smooth.

Dimensions.—Holotype: H 55.8, D 30.7 mm; largest paratype, NMB H 18331 (Pl. 16, Figs 5, 8): H 56.6, D 34.1 mm; wide, strongly distorted paratype, NMB H 18332 (Pl. 16, Fig. 3): H 49.0, D 29.7 mm; small, wide paratype resembling *Distorsio minoruohnishii*, NMB H 18333 (Pl. 16, Figs 4, 7): H 43.3, D 26.8 mm; very small, narrow paratype, NMB H 18334: H 33.5, D 17.3 mm; small, weakly distorted paratype, NMB H13697, illustrated by Jung (1965: pl. 68, figs 9, 11; Pl. 16, Fig. 6): H 44.3, D 25.0 mm.

Types.—Holotype NMB H 18330 (Pl. 16, Figs 1-2), from NMB17516, lower shellbed, Cantaure Fm (late Early Miocene), *ca.* 300 m S of Casa Cantaure, *ca.* 10 km W of Pueblo Nuevo, near San José, central Paraguaná Peninsula, Falcón, Venezuela, collected by Jack and Win Gibson-Smith (one of 100 specimens in this lot); 4 illustrated paratypes from this same lot, NMB H 18331-18334, Pl. 16, Figs 3-5, 7-8; 1 paratype from this lot studied by SEM, NMB H 18061, Pl. 16, Figs 9-11); 3 paratypes from this lot, GNS WM16893;

one paratype, NMB H13697, from an earlier collection from the type locality (specimen figured by Jung, 1965: pl. 68, figs 9, 11; illustrated, Pl. 16, Fig. 6); 4 paratypes GNS WM17446, from the type locality, coll. and pres. Bernard Landau, March 2003.

Other material examined.—**Fossils:** **Florida: late Early Miocene:** NMB 19030 = TU 459, Chipola Fm, E bank Chipola River, Calhoun Co (1 frag with tall spire and two closely spaced spiral cords on shoulder, referred here with some hesitation, NMB H 17914; illustrated, Pl. 17, Fig. 7; 1 small frag, GNS WM18904); TU 820, Chipola Fm (late early Miocene), Farley Creek at bridge of Florida Highway 275, Chipola River, Calhoun Co, Florida, coll. S. Hoerle (USNM, unreg., one incomplete; Pl. 17, Figs 4-5). **Venezuela: Late Early Miocene,** Cantaure: NMB 12842 (8); 17240 (2); 17516 (95; with 1 specimen of *D. mcgintyi*); 17517 (3); 17518 (3); 17519 (12); 17520 (8); type locality, collection of Bernard Landau (12); USNM 645525, Cantaure, Paraguaná Peninsula (1); NMB 17521, La Candelaria beds (late Early Miocene), Paraguaná Peninsula (30, poorly preserved, probably *D. jungi* n. sp.).

Distribution.—*Distorsio jungi* n. sp. is known at present with certainty only from the Cantaure Fm and La Candelaria beds (both late Early Miocene) on Paraguaná Peninsula, Venezuela. However, the two poor specimens of the *D. decussata* species group that I have seen from the coeval Chipola Fm of Florida, USA, probably also belong to *D. jungi*. These are the earliest records of the *D. decussata* species group from the western Atlantic region, and the small, relatively gracile *D. jungi* is strongly distinct from the coeval, robust, coarsely sculptured species *D. ringens* (Philippi, 1887) in Chile. This implies a complex biogeographical history for this species group, rather than the pan-tropical American distribution that might have been expected at this time before any sign of closure of the CAI.

Remarks.—*Distorsio jungi* n. sp. is easily distinguished from the other species resembling *D. decussata* by its consistently small size, by most specimens having a gracile, weakly sculptured, narrowly elongate shape, by the lack of obvious secondary spiral cords, other than one narrow, thread-like secondary cord on the sutural ramp on some specimens, and by its unusually small, equidimensional protoconch tilted at an obvious angle to the axis of the teleoconch. Most specimens also are a little more distorted than either *D. decussata* or *D. simillima*, having the early part of each intervariceal interval expanded and protruding more than in other, closely related species. The coeval to markedly younger species *D. simillima* is the equivalent species of the *D. decussata* species group in the late Early Miocene to Early Pliocene of the Dominican Republic and the late Pliocene-Early Pleistocene of Panama, of Limón, Costa Rica, and of Bowden, Jamaica. It differs from

D. jungi n. sp. in reaching a markedly larger size, in having a slightly larger, taller, and narrower protoconch that is not tilted at an angle to the axis of coiling of the teleoconch, and in having much more prominent secondary spiral sculpture, particularly on the sutural ramp. The living eastern Pacific species *D. decussata* is closely similar to *D. simillima* in all characters, except that it lacks all sign of secondary spiral sculpture, has a shorter, tilted protoconch, and does not reach quite as large a maximum size.

Several paratypes of *Distorsio jungi* are illustrated to show the range of variation. The majority of specimens resembles the holotype and the largest paratype (Pl. 16, Figs 5, 8) in sculpture and shape, but many specimens are a little wider and more strongly distorted than these (Pl. 16, Fig. 3). Some of the narrower paratypes are similar to specimens of *D. decussata* and *D. simillima* in shape (Pl. 16, Fig. 6), whereas a few are more extremely distorted than most other specimens of species of the *D. decussata* group, other than *D. ringens*. One small, wide, rather weakly distorted paratype has the sutural ramp ascending almost to the periphery of the previous whorl, and is interesting in resembling the eastern Pacific species *D. minoruohnishii* (Pl. 16, Figs 4, 7), suggesting the possibility that *D. minoruohnishii* evolved from this or a similar species of the *D. decussata* species group. The most extremely narrow, small paratype (NMB H 18061) is narrower than any specimens seen of other closely related species; its excellently preserved, small, tilted protoconch is illustrated (Pl. 16, Figs 9-11).

Etymology.—It is a great pleasure to name this species in honor of Peter Jung, formerly Director, Naturhistorisches Museum Basel, to recognize his excellent monograph of the Cantaure fauna, his numerous other contributions to tropical American Cenozoic molluscan paleontology, and his fostering of the paleontology of the region by long-continued support of the Dominican Republic and Panama Paleontology Projects.

***Distorsio mcgintyi* Emerson & Puffer, 1953**

Pl. 13, Figs 2-3, 6-8; Pl. 17, Figs 6, 8; Pl. 18, Figs 1-2, 4-5, 7-9; Pl. 19, Figs 1, 4

Distortrix reticulata var. *clathrata*. Dall, 1889: 221 (not *Triton clathratum* Lamarck, 1816).

Distortrix reticulata. Dall & Simpson, 1901: 416 (not *Distorsio reticulata* Röding, 1798, = *Murex reticularis* Linnaeus, 1758).

?*Distortio* (sic) *reticulatus*. Maury, 1922: 115 [not *Distorsio reticulata* Röding, 1798, = *Murex reticularis* (Linnaeus, 1758)].

Distorsio constricta floridana Olsson & McGinty, 1951: 27, pl. 1, figs 5-6, 9 (junior secondary homonym of *Personella floridana* Gardner, 1947, transferred to *Distorsio* by Emerson & Puffer, 1953).

Distorsio mcgintyi Emerson & Puffer, 1953: 101 (replacement

name for *D. floridana* Olsson & McGinty, 1951, preoccupied); Warmke & Abbott, 1961: 103, pl. 18, fig. c; Humfrey, 1975: 125, pl. 14, figs 2-2a; de Jong & Coomans, 1988: 70; Diaz & Puyana, 1994: 172, fig. 648.

Distorsio constricta mcgintyi. Abbott, 1954: 197, pl. 25, fig. Z; 1974: 165, fig. 1771; Lewis, 1972: fig. 40; Rios, 1975: 80, pl. 22, fig. 328; 1984: 78, pl. 28, fig. 341; 1994: 91, pl. 30, fig. 359; Laursen, 1981: 27, fig. 43; Parth, 1989a: 52, center right fig.; Emerson, 1991: 68, 74; Kronenberg, 1994: 70, text-fig. 10, pl. 1, fig. 3, pl. 2, fig. 7.

Distorsio (Rhysema) mcgintyi. Clench & Turner, 1957: 240, pl. 132, figs 9-10, pl. 134, figs 1-5; Rios, 1970: 74; Kilias, 1973: 204, fig. 146.

Distorsio (Rhysema) constricta mcgintyi. Coelho *et al.*, 1981: 132, fig. 14.

Distorsio (Distorsio) constricta mcgintyi. Beu, 1985: 62; Piech, 1995: 20.

Distorsio mcgintyi (sic). Parth, 1989b: 8-9, bottom left fig.; Lipe & Abbott, 1991: 14, illus.; Henning & Hemmen, 1993: 143, pl. 28, fig. 4.

Distorsio constricta. Beu, 2001: 712, fig. 1.9 (not *Triton constrictus* Broderip, 1833).

Remarks.—The species name often has been spelled “*mcgintyi*,” but this follows a misinterpretation of the former Code of Zoological Nomenclature, Appendix D III, Recommendation 21(a). This recommendation referred only to the formation of new names, and did not affect names proposed previously. Also, it is not included in the current edition of the Code. Therefore the original spelling “*mcgintyi*” (Emerson & Puffer, 1953: 101) should be used.

Distorsio mcgintyi is distinguished above, under *D. constricta*, from the three similar western American species *D. constricta*, *D. jenniernestae*, and *D. minoruohnishii*. It is very distinctive in the western Atlantic fauna because of its markedly greater distortion, its shorter and wider shape, and its markedly more uneven sculpture than those of *D. clathrata*. The sculpture is very evenly and regularly cancellate in *D. clathrata*, but four or more spiral cords are grouped together around the peripheral raised band in *D. mcgintyi*, and a zone anterior to the peripheral band and of approximately the same width as the band is slightly depressed and lacks spiral cords. *Distorsio mcgintyi* is a common fossil in the Caribbean region and northern South American, but early authors (notably Woodring, 1928) confused it with *D. clathrata* or *D. simillima*. Dominican Republic collections have particularly many specimens of *D. mcgintyi* from a large number of localities.

Specimens occurring commonly in the latest Pliocene-Early Pleistocene Moín Fm at Limón, Atlantic Costa Rica, are unusually strongly distorted, and were misidentified by me (Beu, 2001: 712) as *Distorsio constricta*. In particular, the protoconch of Limón specimens seemed a little more like that of Pacific than of Atlantic specimens. However, comparison of

a greater number of protoconchs and more careful comparison of teleoconchs demonstrated that (a) the protoconchs of *D. constricta*, *D. mcgintyi*, and *D. minoruohnishii* are virtually indistinguishable, and are similar to that of *D. simillima*, tall and relatively narrow, and parallel to the coiling axis of the teleoconch; and (b) although unusually strongly distorted in their coiling, Limón specimens are more nearly similar to *D. mcgintyi* than *D. constricta* in having a particularly coarsely nodulose, “knobbly”-looking apertural shield, the outer edge of the shield, along the outer lip, tending to curl outward in front of the lip, the third nodule from the top (posterior end) of the outer lip is greatly enlarged, the peripheral raised band bears four or more spiral cords rather than the two present in almost all specimens of *D. constricta*, and the spiral interspaces bear rather regular, even axial ridgelets as in *D. mcgintyi*. The wider sutural ramp, in the area to the left of the aperture in each intervariceal interval, and the correspondingly more distorted coiling of many of the Limón specimens than in specimens from other fossil localities studied here suggest that some sort of weakly restricted, distinctive population of *D. mcgintyi* is represented at Limón.

Dimensions.—USNM 714842, *Oregon* sta. 440, 28 m, off of Campeche, Mexico: H 52.6, D 33.6 mm; USNM 417689, *Eolis* sta. 312, 50 m, off of Government Cut, Miami, Florida: H 44.9, D 28.3 mm; USNM 421751, S of Tortugas, Florida: H 40.6, D 26.1 mm; figured specimen, NMB H 17921, from NMB 15863, Dominican Republic: H 51.5, D 31.1 mm; figured specimen, GNS WM10575, Recent, dredged in 60 m, W of Cedar Keys, Florida: H 55.2, D 34.5 mm; figured specimen, NMB H 17920, from NMB 19008, Late Pliocene-Early Pleistocene, Limón, Costa Rica: H 46.9, D 29.2 mm; other specimens from the same lot, GNS WM16953: H 40.7, D 25.6 mm; WM18903, strongly distorted specimen: H (incomplete) 37.7, D 24.7 mm.

Types.—*Distorsio constricta floridana* Olsson & McGinty, 1951 (preoccupied; renamed *D. mcgintyi* by Emerson & Puffer, 1953: 101), holotype ANSP 187684, dredged off of Palm Beach, Florida, in 57-76 m.

Other material examined.—**Recent:** 60 lots examined at GNS, LACM, SMF, and USNM (mainly), from North Carolina (northernmost: U.S. Fish Commission sta. 2596, 100 m, 30 km ESE of Cape Hatteras, USNM 92980, 1), South Carolina, Florida, Gulf of Mexico, Antillean islands (Barbados), E Costa Rica, and E Colombia.

Fossils: **Mexico: Pliocene:** TU 1046, Agueguexquite Fm, Mexico Hwy 180, Isthmus of Tehuantepec (GNS WM18901, 1 small, incomplete); San Eulalio, Veracruz (UCMP S-4054, 1; spire only, identity uncertain). **Atlantic Costa Rica: Latest Pliocene/Early Pleistocene,** Limón: NMB 18078 (2); 18079 (1); 18084 (2); 18113 (2); 18273 (2); 18275 (1); 18277 (1); 18278 (4); TU 953 (GNS WM18898, 1); 954

(GNS WM18899, 5); 956 (GNS WM18900, 1), 1239 (GNS WM18902, 1); 1240 = NMB 19008 (33; one illustrated, NMB H 17920, Pl. 13, Figs 2-3; GNS WM16953, 15; 2 illustrated, Pl. 13, Figs 7-8; WM18903, 17); USGS 21035 (1); 21036 (2); Moín Fm, Puerto Limón, collection of Bernard Landau (9); locality same as last (ZMA, 3); basal Moín Fm mudstone (Late Pliocene), Rte. 32, 3 km W of Puerto Limón, coll. J. A. Todd, February 1998 (BMNH Palaeontology Department, 1). Robinson (1991) recorded a further 11 specimens in the Tulane University collections from Limón that I have not examined (TU 953, 1 specimen; TU 1239, 1 specimen; TU 1240, 1 specimen; TU 1489, 8 specimens). **Atlantic Panama: Late Miocene:** Gatun Fm; NMB 18667 (1). **Pliocene:** Cayo Agua Fm; NMB 18734 (1); apparently Fish Hole Reef Member of Shark Hole Point Fm (see Appendix 3): USGS 8323, Minnitimbi Creek (1). **Pleistocene:** NMB 18743, Swan Cay (1). **Jamaica: Late Pliocene,** Bowden: NMB 10635 (1; figured, NMB H 18043; Pl. 18, Fig. 2); USGS 2580 (7); 23741 (9); USNM 369462 (1; specimen illustrated by Woodring, 1928: pl. 18, fig. 9, pl. 19, fig. 1, as *D. decussatus simillimus*); UCMP S-2 (1); BMNH Palaeontology Department, GG3895, ex C. T. Trechman collection (1). Robinson (1991) also recorded two specimens from the Bowden shellbed in TU 705. **Dominican Republic: Late Early Miocene:** Baitoa Fm; NMB 17282 (1); TU 1226 (GNS WM16918, 1); USGS 8668 (1); NMB 17265, Baitoa Fm, Río Yaque del Norte, collection of Bernard Landau (1). **Late Miocene:** Cercado Fm; NMB 16801 (1); NMB 16982, Cercado Fm, Río Cana, collection of Bernard Landau (1); USGS 26298 (1); Gurabo Fm; NMB 16910, bluff 3, Río Mao (8; 1 illustrated, Pl. 19, Figs 1, 4); TU 1293, Maury's bluff 1 (GNS WM16931, 6). **Late Miocene/Early Pliocene:** Gurabo Fm; TU 1231 (GNS WM16926, 15); 1246 (GNS WM18895, 2); 1250 (1); 1277 (GNS WM16903, 3; 1 illustrated, Pl. 18, Figs 1, 4); 1296 (GNS WM18896, 1); 1411 (GNS WM18897, 1); USGS 8519 (4); 26274 (1); 26275 (3); 26277 (1); PRI, Maury's loc. 200, zone D, Río Gurabo (2); PRI, Maury's loc. 206, bluff 1, Cercado de Mao (2); Bluff 1 of Maury, Río Mao, collected M. Taviani (Institute of Zoology, University of Bologna, 2). **Early Pliocene:** Gurabo Fm; NMB 15807 (3; 1 illustrated, NMB H 18057; Pl. 18, Figs 5, 8); 15809 (2); 15836 (1); 15841 (1); 15846 (4); 15855 (1); 15857 (1); 15859 (1; protoconch illustrated by SEM, H 18059); 15860 (2); 15861 (4); 15863 (4; one illustrated, NMB H 17921; Pl. 17, Figs 6, 8); 15864 (2); 15865 (1); 15866 (2); 15867 (2); 16808 (1); 16818 (3); 16824 (1); 16870 (1); 16880 (1); 17268 (1); TU 1210 (GNS WM16908, 3; WM18891, 2); 1211 (GNS WM16909, 2; WM18892, 3); 1212 (GNS WM18893, 2); 1215 (18); 1227 (GNS WM18894, 3); USGS 8538 (1); 8545 (2); 8547 (1); TU 1210, Gurabo Fm, Río Gurabo, collection of Bernard Landau (8); 1215, Gurabo Fm, Río Gurabo, collection of

Bernard Landau (4); 1354, Cañada de Zamba, collection of Bernard Landau (5). **Carriacou:** Grenadine Islands: **Middle Miocene:** NMB 10789 (1). **Trinidad: Middle Miocene:** USGS 21234 (1). **Venezuela: Late Early Miocene:** NMB 17516 (1); 17517, (1); 17518 (2); 17520 (1); 17527 (61). **Late Miocene:** NMB 13112 (2); 13667 (1); 17530 (16); Mataruca Member of Cujarao Fm, Carrizal, E of La Vela de Coro, Miocene (UCMP S-106, 5). **Pliocene:** NMB 12045 (1); 16668 (1; coarser nodules than any other material seen); Cerro Negro Member, Cubagua Fm, Cañon de las Calderas, Cubagua Island, collection of Bernard Landau (1).

Distribution:—*Distorsio mcgintyi* lives today in the western Atlantic, from Cape Hatteras, North Carolina (material listed above), USA, Florida, and Bermuda (Clench & Turner, 1957) to southernmost Brazil (“all Brazilian coast”; Rios, 1994: 91). Matthews (1968) recorded specimens found rarely in the gut of the toadfish or “pacomon,” *Amphychthus cryptocentrus*, caught off of Fortaleza, Ceará, Brazil. In addition to the above records from North Carolina, Menzies *et al.* (1966: 414) recorded two specimens collected alive on a submerged reef at the shelf edge, 70 km offshore from Cape Fear, North Carolina. Fossil specimens are reported here from most areas of the Caribbean region and the northern part of the eastern coast of South America wherever diverse faunas have been collected from Miocene to Pleistocene rocks. Despite my previous claim to the contrary (Beu, 2001: 712, fig. 1.9), *D. mcgintyi* is also the most common *Distorsio* species the latest Pliocene-Early Pleistocene Moín Fm at Limón, Atlantic coast of Costa Rica.

***Distorsio minoruohnishii* Parth, 1989**
Pl. 19, Figs 2-3, 10, 12

Distorsio minoruohnishii Parth, 1989b: 10, 2 figs; 1991: 11, 2 center left figs; Emerson & Piech, 1992: 109, figs 13-15b, 25; Henning & Hemmen, 1973: 144, pl. 28, fig. 5; Kronenberg, 1994: 86, text-fig. 18, pl. 2, fig. 5, pl. 4, fig. 4; Piech, 1995: 21.

Remarks.—*Distorsio minoruohnishii* was confused with *D. constricta* by all authors (including me) working on western American mollusks before it was segregated by Parth (1989b). It is distinguished above, under *D. constricta*, from the other western American living species *D. constricta*, *D. decussata*, and *D. jenniernestae*. Most specimens that I have examined are small (not commonly over 40 mm H) and strongly angled at the periphery, with two obvious peripheral spiral cords, and the very plain, smooth, cream to pale brown inner lip shield is quite distinctive. A single specimen from the Pleistocene rocks of the Pacific coast of Costa Rica is a typical specimen of *D. minoruohnishii*.

Dimensions.—Holotype: H 38.3, D 21.3 mm; reaching 51 mm H (Emerson & Piech, 1992: 111); figured specimen,

NMB H 17922, from NMB 18161, Cocalito Bay, Nicoya, Costa Rica: H 27.6, D 17.4 mm.

Types.—*Distorsio minoruohnishii*, holotype BMNH 1990025 (Pl. 19, Figs 10, 12), from “Oaxaca [State], Mexico”; type locality considered too broad and restricted by Emerson & Piech (1992) to Isla Macapule, Sinaloa, W Mexico.

Other material examined.—**Recent:** As with *Distorsio constricta* and *D. jenniernestae*, museum collections were not segregated when I examined them, and are not listed here. Emerson & Piech (1992: 109, 111) listed material from 29 localities, and had examined a further *ca.* 40 lots, ranging from off of Isla San José, Gulf of California (AMNH 76180) to off of Tumbes, Peru (LACM 72-83.6); 10 lots at GNS, from W Mexico and Panama.

Fossils: Pacific Costa Rica: Pleistocene: NMB 18161, Montezuma Fm, SE coast of Playa Cocalito, ENE of Montezuma village, Nicoya Peninsula (one, illustrated, NMB H 17922; Pl. 19, Figs 2-3).

Distribution.—*Distorsio minoruohnishii* lives at present from the Gulf of California, Mexico, south to off of Tumbes, Peru, in depths of 15-165 m (Emerson & Piech, 1992: 109). The single Costa Rican Pleistocene fossil reported here is from within the living range.

***Distorsio perdistorta* Fulton, 1938**
Pl. 19, Figs 5-9, 11

Distortrix reticulata. Dall, 1889: 221 (in part not *Murex reticularis* Linnaeus, 1758).

Distorsio perdistorta Fulton, 1938: 55, pl. 13, figs 3-3a; Emerson & Puffer, 1953: 102; Lewis, 1972: 34, figs 1, 3, 5-7, 11-34; Abbott, 1974: 166, fig. 1774; Nordsieck & Garcia-Talavera, 1979: 120, pl. 25, fig. 15 (as *D. decussatus* in fig. caption); Garcia-Talavera, 1983: 117; 1987: 253, pl. 2, fig. 8; Beu, 1985: 62, fig. 33; 1998b: 194, figs 59i-l; 2005: 57; Rios, 1985: 78, fig. 342; 1994: 91, pl. 30, fig. 360; Lai, 1989: 127, fig. 56; Parth, 1990: 108, fig. 7, 8; Henning & Hemmen, 1993: 145, pl. 30, fig. 4; Kronenberg, 1994: 88, text-fig. 20, pl. 3, fig. 2; 1999: 96, figs 1-4, pl. 1, figs 1-6; Piech, 1995: 21; Gofas & Beu, 2002: 104, fig. 9i; Zhang & Ma, 2004: 168, text-figs 103a-c, pl. 4, fig. 1; Kronenberg & Beu in Poppe, 2008: 628, pl. 259, fig. 4.

Distorsio perdistorta (sic). M. Smith, 1948: 22, fig. 11.

Distorsio horrida “Kuroda” Oyama & Takemura, 1959: *Distorsio* pl. 1, figs 11-12 (*nomen nudum*).

Distorsio (*Rhysema*) *horrida* Kuroda & Habe in Habe, 1961: 46, pl. 23, fig. 3, appendix: 17; Habe, 1964: 74, pl. 23, fig. 3.

Distorsio (*Distorsio*) *perdistorta*. Beu, 1985: 62, fig. 33; Springsteen & Leobrera, 1986: 118, pl. 32, figs 5a-b.

Distorsio (*Rhysema*) *perdistorta*. Okutani, 1986: 115, lower left fig.

Remarks.—*Distorsio perdistorta* is very easily recognized by its even, regular, cancellate sculpture of spiral cords and weak axial ridges, with several orders of finer spiral cords and threads

in the interspaces of the major cords (rather than widely and evenly cancellate cords and ridges, with little other sculpture, as in *D. clathrata*), by lacking a shoulder angle, and by its highly distorted growth pattern, with a strongly inflated, evenly rounded bulge immediately after each varix, followed by the standard *Distorsio* pattern of regularly decreasing inflation up until the succeeding varix. It therefore perhaps resembles *D. clathrata* most closely of the other species in the study area, but is differentiated easily by its much more marked distortion and inflation and its more complex spiral sculpture, so that it lacks the evenly clathrate appearance of *D. clathrata*. Some of the specimens from the eastern Atlantic (particularly from off of Angola) are a little more distorted and more coarsely sculptured than the others seen, but Kronenberg (1999) compared these with specimens dredged off of Florida, USA, and in the Indo-West Pacific, and concluded that they intergrade in all characters.

Dimensions.—*Distorsio perdistorta*, holotype: H 59.8, D 35.9 mm; USNM 762002, Gulf of Guinea, 100 m: H 65.3, D 40.0 mm; MNHN, Seamount 1 cruise, sta. CP79, Seine Bank, near Madeira: H 72.5, D 43.6 mm; Tenerife, Canary Islands, Zoological Museum, University of Bologna no. 2651: H 61.4, D 37.4 mm; TFM 997, near Shebo River, W Africa: H 72.3, D 46.3 mm.

Types.—*Distorsio perdistorta*, holotype BMNH 1938.7.13.13, from "Kii, Japan." *Distorsio (Rhysema) horrida*, holotype and one paratype NSMT Mo.39788, from Tosa Bay, Shikoku, Japan (Habe, 1964: 74).

Other material examined.—**Recent:** I listed (Beu, 1998b) material from nine localities in the New Caledonian region; it is not necessary to list here the large amount of Japanese and Philippines material in many museums and private collections. **W Atlantic:** U.S. Fish Commission sta. 2318, 90 m, off of Key West, Florida (USNM 83681, 1); dredged off of Key West, Florida, G. Nowell-Usticke collection, July 1970 (AMNH 190494, 2); SW of Dry Tortugas, Florida, USA, dredged 180 m, 1975 (1, specimen listed and illustrated by Kronenberg, 1999); SW of Dry Tortugas, Florida, USA, dredged 90 m, 1980 (1, same as last); W of Egmont Key, Florida, USA, dredged 220 m, 1966 (3, same as last); 200 m, fishermen's traps, Racket Bank, off of Barthelmy Island, West Indies (1, collection of D. Lamy). **E Atlantic:** Tenerife, Canary Islands, pres. F. Garcia-Talavera (Zoological Museum, University of Bologna, ZMUB 2651, 1); Los Hervideros, Lanzarote, Canary Islands (TFMC 998, 1); La Palma, Canary Islands (TFMC 990, 1); Los Abrigos, Tenerife (TFMC 991, 1); Puerto de la Cruz, Tenerife (TFMC 992, 1); Tenerife sur (TFMC 769, 1); 120-140 m, near Shebo River, W Africa (TFMC 997, 1 large); B. B. Collette's *La Rafale* Guinean trawling survey I, transect 12, sta. 6, Gulf of Guinea, 6°56'N, 12°05'30"W, 100 m (USNM 762002, 1); Seamount

1 cruise, sta. CP79, Seine Bank, near Madeira, 242-260 m, 32°49.0'N, 14°22.6'W, 10 October 1987 (MNHN, 1; Gofas & Beu, 2002: 104, fig. 9i); trawled by Belgian fishermen off of Ambriz, Angola, 110 m, 1964 (3; Kronenberg, 1999; material loaned by G. Kronenberg).

Distribution.—*Distorsio perdistorta* is much the most widespread species in the genus, and is the only one occurring in both the Atlantic and the Indo-West Pacific provinces. Lewis (1972) recognized it for the first time in the Caribbean fauna, and it has since been recorded from West Africa (Nordsieck & Garcia-Talavera, 1979; Beu, 1998b; Kronenberg, 1999) where records range from the Canary Islands to Angola. In many areas, it is a rather rare deep-water species, so it is not surprising that no fossil specimens have been recorded from the study area. The 15 Gulf of Mexico lots recorded by Lewis (1972: table 1) were collected in depths of 133-282 m, and of 11 specimens recorded from eight stations around New Caledonia by me (Beu, 1998b), all but one were collected in 339-540 m.

Distorsio perdistorta is recorded from Natal, South Africa, and Madagascar to southern Japan, the Philippine Islands, and New Caledonia (Beu, 1998b), and has also been observed (a) in MNHN material from the Solomon and Marquesas Islands in Polynesia, (b) in the western Atlantic, from the Gulf of Mexico and off of Florida (Lewis, 1972) south to southern Brazil (Rios, 1994: 91), and (c) in the eastern Atlantic from off of the Canary Islands (Nordsieck & Garcia-Talavera, 1979), Madeira to the Gulf of Guinea (Beu, 1998b), and off of Angola (Rolan & Ryall, 1999: 34; Kronenberg, 1999; material listed above). It probably occurs in deep water (ca. 200-500 m) throughout the Indo-West Pacific region and throughout the warm-water Atlantic. No fossils have been seen from the study area and, indeed, fossils of this species are almost unknown. The only fossils of which I am aware are the two specimens recorded from the Plio-Pleistocene of Timor by Robba *et al.* (1989) (seen, at Department of Geology & Paleontology, Università degli Studi di Milano-Bicocca).

Distorsio ringens (Philippi, 1887)

Pl. 20, Figs 1-5, 7; ?Pl. 53, Fig. 2

Tritonium ringens Philippi, 1887: 56, pl. 4, fig. 9.

Tritonium thersites Philippi, 1887: 56, pl. 4, fig. 3.

Distorsio decussatus (sic) ringens. Olsson, 1932: 189.

Tritonium (Distorsio) thersites. Tavera & Veyl, 1958: 161, 185.

"*Tritonium*" (*Distorsio*) *thersites*. Tavera, 1979: 92, pl. 19, figs 68-69.

Distorsio thersites. Nielsen, 2003: 95, pl. 17, figs 17-20.

Remarks.—Olsson (1932: 189) thought this species closely similar to *Distorsio decussata*, and ranked it as a subspecies of *D. decussata*. However, although undoubtedly closely related,

D. ringens differs from *D. decussata* in having (a) a wider and much more gently sloping sutural ramp, producing a markedly wider and more strongly angled inflated section of whorl after each varix and a more prominent, more nearly horizontal sutural ramp than in *D. decussata*, and (b) more prominent axial costae over the area below the shoulder angle, particularly on the early part of each intervariceal interval after each varix, than seen in any specimens of *D. decussata*, so that the area below the sutural ramp is moderately to extremely coarsely nodulose in *D. ringens*. The overall shape, quite tall and narrow with a relatively tall spire, moderate distortion and a straight anterior canal, and the two closely spaced spiral costae at the shoulder angle are closely similar to those of *D. decussata*. I have not seen a protoconch of *D. ringens*.

Distorsio ringens is highly variable in shape and in the coarseness of the sculpture, and there is no doubt that only one species of *Distorsio* occurs in the Miocene rocks of Chile. This opinion has been confirmed by Daniel Frassinetti (SGO.PI, pers. comm., January 1998). Therefore, there is also no doubt that Philippi (1887) merely named sculptural variants of a single species when he named both *Tritonium ringens* and *T. thersites*. Because of the possibility of secondary homonymy of *T. thersites* and the earlier *Triton thersites* Reeve, 1844 (a species of *Monoplex*; Beu, 1998b), it is preferable to retain the name *T. ringens* for the Chilean *Distorsio* species. As first reviser, I select *T. ringens* as the name to be used for the species named both *T. ringens* and *T. thersites* by Philippi (1887: 56). Besides the localities recorded here, Tavera & Veyl (1958) recorded specimens from two localities on Isla Mocha, southern Chile.

A single small, incomplete specimen (Pl. 53, Fig. 2) collected by Sven Nielsen (Institut für Geowissenschaften, Christian-Albrechts-Universität Kiel) from his locality PPN, Punta perro, coast 2-3 km N of Navidad, Navidad Fm (Oligocene-early Miocene fossils reworked into Late Miocene rocks; SGO.PI 6446) is unique for its extremely tall, narrow spire. The aperture and canal are missing from this specimen, so many critical characters are not visible. However, the rather weak sculpture, with unusually narrow spiral cords, is essentially the same as in *Distorsio decussata* and *D. ringens*, except for the sutural ramp being very narrow (perhaps because of the spire height). More material is required to determine whether this is a further, unnamed species or (as seems likely) a very aberrant specimen of *D. ringens*.

Dimensions.—Largest seen, SGO.PI, from Fiordo Newman, Golfo Tres Montes, southern Chile, coll. V. Covacevich & D. Frassinetti, *R/V Hero* cruise 2, September 1984, field no. 140984/5: H 81.8, D 51.5 mm.

Types.—*Tritonium ringens*, 6 syntypes examined at SGO.PI; Philippi's (1887: pl. 4, fig. 9) figured syntype, SGO.PI 744, is from the sea cliff at the village of Matanzas, 4 km SW

of Navidad, southwest of Santiago, central Chile, Oligocene-Early Miocene fossils displaced into Late Miocene-Early Pliocene rocks; 2 large syntypes, SGO.PI 739, labelled "Navidad & Matanzas," specimens closely resembling the lectotype (selected here) of *T. thersites*; 2 small incomplete syntypes, SGO.PI 742, from Navidad, coast SW of Santiago, Chile; 1 syntype, SGO.PI 4558, from Matanzas. *Tritonium thersites*, five syntypes examined at SGO.PI; Philippi's (1887: pl. 4, fig. 3) figured syntype, SGO.PI 840, from Ranquil, coast S of Concepción, south-central Chile (Ranquil Fm, Oligocene-Early Miocene fossils displaced into Late Miocene-Early Pliocene rocks; Finger *et al.*, 2007) is here designated the lectotype of *Tritonium thersites*; 2 paralectotypes SGO.PI 740, from Chiloé Island (again, Oligocene-Early Miocene fossils displaced into Late Miocene-Early Pliocene rocks; Finger *et al.*, 2007), both conspecific with lectotype; 2 paralectotypes SGO.PI 4557, also from Ranquil — one is an adult specimen of *D. ringens*, but the other is a broken, immature specimen of a *Sassia* species, possibly *S. kampyla* (Watson, 1885) (see below), necessitating the lectotype designation.

The well-known localities near Matanzas, SW of Santiago, Chile, first collected by Charles Darwin, have usually been thought to be Middle or Late Miocene in age. However, although recent evidence indicated a Late Miocene-Early Pliocene age for the Navidad Fm (Nielsen *et al.*, 2003), Finger *et al.* (2007) demonstrated that these localities consist of Late Oligocene-early Miocene fossils displaced into Late Miocene-Early Pliocene rocks. Strontium isotope stratigraphy also indicates a late Oligocene-Early Miocene age for these faunas (Nielsen & Glodny, 2006).

Other material examined.—**Fossils: Chile:** Late Oligocene-Early Miocene fossils reworked into Late Miocene-Pliocene rocks: material in collection of Museo Nacional de Historia Natural, Santiago: (a) Matanzas, beachfront cliff and wave-cut platform, coast SE of Santiago (12); (b) Punta Perro, coast 2-3 km N of Matanzas (1); (c) coastal cliff between Punta Perro and puebla La Boca (1); (d) SGO.PI 5549, coast N of Boca Rapel, mouth of Río Rapel, N of Navidad, October 1977 (5); (e) Isla Crosslet, Golfo Tres Montes, southern Chile, field no. 081083/5, coll. on *R/V Hero*, October 1983, Miocene (2); (f) Isla Smith, Golfo Tres Montes, field no. 060984/4, coll. J. Chambers, Miocene (1); (g) Isla Hereford, N of Isla Crosslet, Golfo Tres Montes, field no. 031183/10, Miocene (1); (h) Fiordo Newman, Golfo Tres Montes, field no. 140984/5, coll. on *R/V Hero*, September 1984 (1 large); (i) Isla Lemo, small island just inside bottom-east tip of Isla Ipun, between Stokes and Ipun Islands, Los Chonos Archipelago, coll. on *R/V Hero*, October 1983 (1); material in collections made by Sven Nielsen, now in SGO.PI and SMF: loc. RAP, Río Rapel, N of Navidad (15); loc. MAT 013, Matanzas, coast SW of Santiago (1); loc. LBZ 011, Las Brizas, coast between Matanzas and

mouth of Río Rapel (1); loc. RQK 003, Ranquil, coast S of Arauco, S of Concepción, Ranquil Fm (again Oligocene-early Miocene fossils displaced into Early Pliocene rocks; Finger *et al.*, 2007) (4 large, incomplete); coast at Tubul, Peninsula Arauco (1, extremely tall-spined, incomplete; possibly a distinct species); material formerly at Department of Paleontology, Purdue University, now at PRI, collected by W. J. Zinsmeister: loc. 255, Punta Perro, N of Matanzas (2); locs. 285 and 286 (1 illustrated, Pl. 20, Figs 5, 7), N of Río Rapel mouth, N of Matanzas (17); other specimens present also in Zinsmeister's locality collections 145 (2 illustrated, Pl. 20, Figs 1-3), 254 (1 illustrated, Pl. 20, Fig. 4), 262, 264, 272, 273, 274, 332, 333, 334, 335, and 339, all from the Matanzas-Río Rapel area.

Distribution.—*Distorsio ringens* was recorded by Olsson (1932: 189) from lower Zorritos beds (Miocene) at Zapotal, northern Peru. I have not seen the specimen, and cannot confirm the identification, but this extension to the north of other records would not be surprising in view of the wide range of *D. decussata* at present. Material that I have examined all comes from the Miocene (Oligocene-Early Miocene, mostly displaced into Late Miocene-Early Pliocene rocks) of Chile, where localities range from the Navidad area, southwest of Santiago, south to the islands of the Los Chonos Archipelago in the far south. Nielsen (2003) recorded it also from Isla Crosslet in the Los Chonos Archipelago. As Olsson (1932) pointed out, this occurrence in central to southern Chile clearly indicates warm-water conditions at the time of deposition. The extinction of the warm-water faunal element in Chile at the end of the Miocene resulted from the development of the cold, north-flowing Humboldt Current at that time (or at least, cooling of a formerly warm current) (Zinsmeister, 1977, 1978), and ultimately from the development of glaciation on western Antarctica at this time.

***Distorsio simillima* (G. B. Sowerby I, 1850)**

Pl. 20, Figs 6, 8-10; Pl. 21, Figs 1-8; Pl. 22, Figs 1-2, 6, 8-9

Triton simillimus G. B. Sowerby I, 1850: 48.

Persona simillima. Guppy, 1866: 288, pl. 17, fig. 13; 1874: 439; 1876: 522 (in part not *Triton simillimus* G. B. Sowerby I, 1850).

Distortia (sic) simillimus. Gabb, 1873: 212.

Distorsio simillimus. Gabb, 1881: 353.

Distortrix simillima. Dall, 1903a: 1584 (in part); Maury, 1917a: 272, pl. 43, figs 4-5; 1925: 216 (in part); Anderson, 1929: 138; Aguayo, 1948: 68.

Distorsio constrictus simillimus. Pilsbry, 1922: 356.

Distorsio (Distorsio) decussatus simillimus. Woodring, 1928: 300, pl. 18, figa 7-8 only (in part not *Triton simillimus* G. B. Sowerby I, 1850).

Distorsio cf. simillimus. Weisbord, 1929: 272, pl. 8, fig. 4.

Distorsio (Rhysema) decussata simillima. Pflug, 1961: 39, pl. 9, figs 4,

6, 9 (lectotype).

Remarks.—Large (to *ca.* 80 mm H in material examined), elongate *Distorsio* specimens occurring commonly in the Miocene to Pliocene rocks of the Caribbean region (Dominican Republic, Jamaica, and Panama; latest Pliocene-Early Pleistocene, Limón, Costa Rica) resemble *D. decussata* closely in (a) their tall, narrow shape, (b) their relatively weak distortion, (c) their sculpture of narrow, widely spaced spiral cords and axial ridges, with two of the spiral cords much more closely spaced around the periphery than elsewhere, (d) their long, fairly straight anterior canal, (e) in having two parietal ridges, rather than one, and (f) in having the third tooth inside the outer lip greatly enlarged. They differ from Pliocene to Recent specimens from the eastern Pacific in having several prominent, coarse secondary spiral cords and many fine tertiary spiral threads between the major spiral cords, whereas the sculptural interspaces are virtually smooth or have only a few fine tertiary threads on eastern Pacific specimens. The name *D. simillima*, based on specimens from the Late Miocene-Early Pliocene of the Dominican Republic, is available for this Atlantic form. Protoconchs have been observed on very few specimens, but where present, the protoconch of *D. simillima* is small, narrowly conical, and with its coiling axis parallel to that of the teleoconch, in contrast to that of *D. decussata*, which is larger, wider and lower, with its coiling axis tilted a little to that of the teleoconch. Some specimens from the Pliocene of Atlantic Panama are typical *D. simillima* (NMB 17836, Escudo de Veraguas, Bocas del Toro Basin, one specimen; NMB 18681, same data, two specimens) among many other localities where only specimens of normal *D. decussata* (smaller specimens lacking the prominent secondary cords of *D. simillima*) occur. Examination of large collections of Recent eastern Pacific specimens of *D. decussata* has shown that secondary spiral cords do not occur at all in the living population, and this has been confirmed by G. Kronenberg (pers. comm., 1995). Therefore, it is clear that there is a subtle but biogeographically significant distinction between Atlantic fossils and eastern Pacific Recent specimens that deserves taxonomic recognition. *Distorsio simillima* is considered here to be a species distinct from both *D. decussata* and *D. jungi* n. sp.

Dimensions.—Figured specimen, NMB H 17911, from NMB 16910, Dominican Republic: H 66.1, D 42.7 mm; figured specimen, NMB H 17915, from NMB 16869, Dominican Republic: H 61.1, D 35.6 mm; figured specimen, NMB H 17913, from NMB 18681, Panama: H 60.2, D 34.9 mm; NMB H17910, El Porvenir beds, largest specimen: H 62.1, D 39.0 mm; NMB H17909, El Porvenir beds: H 52.7, D 32.9 mm.

Types.—*Triton simillimus*, lectotype, designated by Pflug (1961: 40, pl. 9, figs 4, 6, 9), BMNH Palaeontology

Department, G83947, with 7 paralectotypes, from Río Yaque del Norte, Dominican Republic, Miocene, collected by Col. T. S. Heneken.

Other material examined.—**Fossils: Atlantic Costa Rica: Latest Pliocene/Early Pleistocene**, Limón: NMB 18273 (1); TU 956, hill slope behind Baptist church, between Pueblo Nuevo and Puerto Limón (GNS WM18908, 1; illustrated by SEM, Pl. 22, Figs 6, 8-9); listed also by Robinson (1991), wrongly identified as *D. decussata* through correspondence with me; USGS 4269 (1); 18693 (3); 20468 (1); TU 1240, Moin Fm (latest Pliocene-Early Pleistocene), Los Corales, Puerto Limón, collection of Bernard Landau (3). **Atlantic Panama: Pliocene**: Escudo de Veraguas Fm: NMB 17836 (1, illustrated, NMB H 17912; Pl. 21, Figs 2, 4); 18681, E end of Escudo de Veraguas Island, Bocas del Toro Basin (2; 1 illustrated, NMB H 17913; Pl. 20, Figs 6, 8). **Jamaica: Late Pliocene**, Bowden: NMB 10635 (1); 10651 (1); USGS 2580 (2); 23741 (3); USNM 115512 (1; specimen illustrated by Woodring, 1928: pl. 18, figs 7-8). **Haiti: Late Miocene**: USGS 18398 (1). **Dominican Republic: Late Early Miocene**: Baitoa Fm: Arroyo Hondo, Río Yaque del Norte, collection of Bernard Landau (3). **Late Miocene**: Cercado Fm: NMB 15899 (1); 15904 (1); 15905 (1); 16801 (1); 16836 (1); USGS 8522 (1); NMB, unnumbered, A. A. Olsson collection, Cercado de Mao (2); NMB 15906, Cercado Fm, Río Gurabo, collected M. Taviani (Institute of Zoology, University of Bologna, 1); Gurabo Fm: NMB 16910 (2, 1 illustrated, NMB H 17911; Pl. 21, Figs 1, 6); USGS 8733 (1); Bluff 1 of Maury, Río Mao, collected M. Taviani (Institute of Zoology, University of Bologna, 3); Las Cahobas Fm, San Juan region: USGS 26534 (1). **Late Miocene/Early Pliocene**: Gurabo Fm: NMB 15871 (1); 15876 (1); 16809 (3); 17268 (1); TU 1206 (GNS WM18909, 1); 1225 (GNS WM16917, 2; WM18916, 4); 1231 (= NMB 19006) (GNS WM16927, 11, + 1 in NMB); 1277 (GNS WM18917, 4); 1292 (GNS WM18918, 1); 1293 (= NMB 118583) (GNS WM18919, 2, + 1 in NMB); 1296 (GNS WM18920, 4); 1411 (GNS WM18921, 3); USGS 8519 (5); 26275 (1); 26277 (4); PRI, Maury's loc. 203, Zone E, Río Gurabo (1); PRI, Maury's loc. 207, Zone F, Río Gurabo (1); PRI, Maury's loc. 210, Zone B, Río Gurabo (3). **Early Pliocene**: Gurabo Fm: NMB 15803 (1); 15809 (1); 15810 (2); 15811 (1); 15815 (1); 15817 (1); 15836 (1); 15842 (3); 15863 (1); 15865 (1); 15867 (2); 15869 (1); 16810 (1); 16865 (9); 16866 (1); 16868 (4); 16869 (1, illustrated, NMB H 17915; Pl. 20, Figs 9-10); 17270 (1); TU 1210 (GNS WM16907, 2; WM18910, 10); 1211 (GNS WM16913, 5; 1 illustrated, Pl. 21, Figs 3, 8; WM18911, 12); 1212 (GNS WM18912, 6); 1213 (GNS WM16904, 1); 1215 (GNS WM18913, 3); 1219 (GNS WM16916, 7; WM18914, 4); 1227 (GNS WM18915, 1); USGS 8516 (6); 8528 (4); 8544 (2); 8545 (2); 8546 (3); 8547 (1); 8548 (1);

8549 (2); 8550 (2); 8551 (1); 8714 (1); TU 1210, Gurabo Fm, Río Gurabo, collection of Bernard Landau (7); 1215, Gurabo Fm, Río Gurabo, collection of Bernard Landau (9; 1 has many, close, prominent spiral cords on the base); 1219, Río Amina, collection of Bernard Landau (3); Dominican Republic, Sammlung Weyl, pres. Plug (SMF, 1). **Trinidad: Early-Middle Miocene**: NMB 11301 (3 small); 11306 (2 small). **Colombia: Pliocene**: USGS 7852 (1); 10101 (1); 11593 (3); 11594 (1); 11595 (1); PRI 22968, near Usiacuri, Departamento de Atlantico (1; specimen illustrated by Weisbord, 1929: pl. 8, fig. 4); UCMP S-8068, 500 m W of Puerto Colombia, Departamento de Atlantico (4); UCMP S-53, edge of Cano at Balsomo Landing, Departamento de Magdalena (2). **Venezuela: Miocene**: NMB H 11476, Buena Vista, Paraguaná Peninsula (1, partly enclosed in matrix, identity uncertain; specimen illustrated by Rutsch, 1930: pl. 17, fig. 7); NMB 16464 (1); 17526, El Porvenir beds (13; 2 illustrated, Pl. 21, Figs 5, 7, Pl. 22, Figs 1-2; NMB H 17909, H 17910). **Pliocene**: USNM, A. A. Olsson's loc. 206, Cumaná, Cubagua Island (2).

Distribution.—All of the previous fossil records of the *Distorsio decussata* species group from the western Atlantic area refer to *D. simillima*, except for the Cantaure Fm and La Candelaria beds specimens, referred above to *D. jungi* n. sp. and the Atlantic Panama material referred to *D. decussata*. *Distorsio simillima* is abundant in the Late Miocene-Early Pliocene of the Dominican Republic, and is recorded also from Miocene and Pliocene rocks of Jamaica, Haiti, Trinidad, Colombia, Venezuela, and the Atlantic coast of Panama (where, however, it is much less common than *D. decussata*). A few specimens (nine seen by me) from the late Pliocene-Early Pleistocene Limón Fm, Atlantic coast of Costa Rica, also have the distinctive secondary cords on the sutural ramp and the small, narrowly conical protoconch with its coiling parallel to that of the teleoconch axis that characterize *D. simillima*, and this is the youngest record of which I am aware. The species evidently had become rare by this time. The two specimens seen from the Chipola Fm of Florida are very incomplete, but seem likely to represent the new species *D. jungi*, from the coeval Cantaure Fm of Venezuela, rather than *D. simillima*.

***Distorsio smithi* (von Maltzan, 1884)**

Pl. 22, Figs 3, 5

Murex reticularis Linnaeus, 1758: 749 (in part, not including lectotype of Beu, 1987: 316).

Persona smithi von Maltzan, 1884: 65.

Distortrix ridens. Nicklés, 1950: 86, fig. 133 (not *Triton ridens* Reeve, 1844).

Distorsio smithi. Emerson & Puffer, 1953: 104; Bernard, 1984: 64, pl. 23, fig. 101; Garcia-Talavera, 1987: 253; Parth, 1989a: 52, upper left fig.; Henning & Hemmen, 1993: 147, pl. 29, fig. 6;

Kronenberg, 1994: 92, text-fig. 22, pl. 1, figs 10, 13a-b, pl. 3, fig. 12, pl. 4, fig. 5; Piech, 1995: 21; Ardovini & Cossignani, 2004: 131, 3 figs.

Distorsio (Rhysema) clathrata. Kiliyas, 1973: 200; 1981: 710 (in part not *Triton clathratus* Lamarck, 1816).

Distorsio (Distorsio) smithii (sic). Beu, 1985: 62.

Distorsio ridens. Guerreiro & Reiner, 2000: 117 (not *Triton ridens* Reeve, 1844).

Remarks.—Because *Distorsio smithi* often has been confused in the past with one or another of the western Atlantic species of *Distorsio*, thereby also confusing the picture of Atlantic *Distorsio* biogeography, a specimen is illustrated here for comparison with the American taxa discussed above. *Distorsio smithi* is the largest of *Distorsio* species – a specimen in UZMC is 87 mm H, another in MNHN is 88.7 mm H, Maltzan (1884) recorded specimens up to 92 mm H, and both Bernard (1984: 64) and Henning & Hemmen (1993: 147) reported a maximum size of 112 mm. It is also immediately recognizable because of (a) its exceedingly strongly constricted, narrow aperture, with a particularly narrow but deep columellar embayment, (b) its extremely strongly elevated columellar toothed ridge, (c) its strong distortion for such an elongate, tall-spined species, (d) its long, almost straight anterior canal, and (e) its unusual shape, with a bi-angled whorl profile, a flat, moderately wide, gently sloping sutural ramp bearing much more prominent spiral sculpture than in all the other species of the genus, and the weakly developed group of 2-3 spiral cords around the upper peripheral angulation. In other words, this is a highly distinctive species, widely sundered from all other species in many characters, evidently reflecting long separation in the eastern Atlantic. The European Miocene and Pliocene fossil species *D. cancellina* (Lamarck, 1803) [see Beu, 1998b: 199; Landau *et al.*, 2004: 71, pl. 6, figs 1-3; Chirli, 2007: 102, pl. 37, figs 4-10; as the synonym *D. tortuosa* (Borson, 1821)] resembles the *D. constricta* species group in general size and shape, but also resembles *D. smithi* in having a wide flattened area around the periphery, with a weakly constricted central zone. Widening and flattening the peripheral area further and strengthening its central constriction would produce the shell form of *D. smithi*, so it is conceivable (as well as biogeographically reasonable) that *D. cancellina* descended from the *D. constricta* species group, and was the immediate ancestor *D. smithi*.

Dimensions.—Largest specimens seen: UZMC, from GTS Thierry sta. 135/7, 200 m, 6°05'N, 2°15'E, off of West Africa: H 87.0, D 47.8 mm; MNHN, taken by fishermen off of Río de Oro, W Sahara: H 88.7, D 47.2 mm.

Types.—Kronenberg (1994: 92) reported that three of an originally greater number of syntypes of *Persona smithi* remain in the Humboldt University Zoological Museum, Berlin (not seen); he designated the largest of them (50.2 mm H) the

lectotype; from Gorée, Sénégal, West Africa, dredged in 20-25 m (Kronenberg, 1994: pl. 4, fig. 5). Von Maltzan (1884) mentioned other specimens up to 92 mm H.

Distribution.—Material examined is not listed for this eastern Atlantic species. *Distorsio smithi* occurs only along the coast of West Africa, from Mauretania to Angola (Kronenberg, 1994), in depths of ca. 10-70 m. Guerreiro & Reiner (2000: 117) also recorded it from São Vicente, Cape Verde Islands. I am not aware of a fossil record.

Genus *PERSONOPSIS* Beu, 1988

Personopsis Beu, 1988b: 90. Type species (by original designation): *Triton grasi* D'Ancona, 1872, Pliocene, Italy, and living, eastern and central Atlantic seamounts.

Remarks.—*Personopsis* is characterized by its much smaller size than in *Distorsio*, its less distorted coiling, its lower and weaker varices, and the location of the basal columellar nodules directly on the columella, rather than on the strongly elevated, hollow, spiral ridge that is so characteristic of *Distorsio*. *Personopsis* species resemble those of *Distorsio* in having the enlarged third nodule ("tooth") from the top of the aperture, inside the outer lip, larger than all of the other nodules or ridges inside the lip, but the degree of enlargement above its neighbors is much less marked than in many species of *Distorsio*.

Personopsis grasi (D'Ancona, 1872)

Pl. 18, Figs 3, 6

Triton grasi D'Ancona *ex* Bellardi *in litt.*, 1872: 262, pl. 14, fig. 18; De Stefani & Pantanelli, 1880: 209; reprint, Manganelli & Spadini, 2001: 255.

Persona grasi. Bellardi, 1873: 232, pl. 14, figs 18a-b; Foresti, 1876: 15; Fontannes, 1879: 36, pl. 4, figs 2a-b.

Distorsio (Personella) grasi. Inzani, 1988: 29 (Italian text), 30 (English text), pl. 6.

Personopsis grasi. Beu, 1988b: 91, pl. 3, fig. 11; 1998b: 208, figs 67i-k; Piech, 1995: 21; Ceregato *et al.*, 2002: 3, figs 2-4; Gofas & Beu, 2002: 104, figs 9A-H; Landau *et al.*, 2004: 74, pl. 6, figs 5-6.

Distorsio grasi. Spadini, 1994: 285, fig. 8.

Remarks.—*Personopsis grasi* is one of the largest and widest species yet recorded of *Personopsis*; Pliocene fossil specimens illustrated by me (Beu, 1998b: figs 67i-k) reach 25 mm H, and Foresti (1876: 15) recorded a "magnifico" specimen from Castrocara, near Siena, 35 mm H. Its relatively wide shape, low varices, wide, prominent spiral cords for the genus, and only moderately long anterior canal are distinctive. The third small nodule inside the outer lip is only slightly larger than the others, and the low, transverse ridges on the base of the colu-

mella commence abruptly at a strongly protruding "tooth" and decrease regularly in size toward the anterior. *Personopsis grasi* is similar to the Recent New Caledonian to Philippines species *P. purpurata* Beu, 1998, but differs in its slightly larger maximum size, its much less prominent uppermost columellar tooth, and its slightly more obviously triangular aperture, wider at the posterior (adapical) end than in *P. purpurata*. The second Recent New Caledonian-Vanuatu species, *P. trigonaperta* Beu, 1998, has a similar apertural shape to that of *P. grasi*, but has a still weaker uppermost columellar tooth, and is taller and narrower than *P. grasi*. Also, all of the Recent specimens of *P. grasi* seen to date resemble *P. trigonaperta* in being plain white, whereas *P. purpurata* has a purple tip to the anterior canal.

The specimens from the Middle Miocene (Badenian) of Lapugy (now in Romania), illustrated by Hoernes & Auinger (1879: 184, pl. 22, figs 14-16) under the name *Triton grasi*, have been examined at the Naturhistorisches Museum Wien. The specimens are now labeled *T. personatum* de Serres, 1829, but de Serres' (1829: 118, pl. 3, figs 11-12) illustrations show that this name is a synonym of *D. cancellina* (see also Landau *et al.*, 2004: 71-73). The specimens from Lapugy (NHMV 1874/XXV/20; 7 specimens) and those recorded by Hoernes & Auinger (1979) from Forchtenau, Vienna Basin (NHMV 1869/I/475, 2 specimens) represent an unnamed *Personopsis* species considerably narrower in shape and more finely sculptured than *P. grasi*, more nearly resembling *P. minae* (Gregorio, 1880) and *P. beui* (Maxwell, 1968) (see Beu (1998b: 208 for the taxa referred to *Personopsis*).

Dimensions.—Recent, Seamount 2 cruise, sta. CP191, Hyères Bank, 295 m: H 20.0, D 11.6 mm; sta. DW215, Irving Bank, 275 m: H 23.8, D 13.7 mm; Pliocene, Castrocaro, Italy: H 35, D 18 mm (Foresti, 1876: 15).

Types.—Ferrero Mortara *et al.* (1981: 56, pl. 7, fig. 3) recorded some of Bellardi's (in D'Ancona, 1872) syntypes of *Triton grasi* remaining in the collection of the Museo Regionale di Scienze Naturali di Torino; from the Piacenzian (Pliocene) of Castelnuovo, Asti, northern Italy (not seen).

Other material examined.—**Recent: W Atlantic:** 300 m, fishermen's traps, off of Vieux-Habitants, Basse Terre, Guadeloupe, French West Indies, coll. and pres. D. Lamy, January 2001 (GNS WM17190, 2; 1 illustrated, Pl. 18, Figs 3, 6; 3 specimens in collection of D. Lamy, Guadeloupe). **Central Atlantic:** S of Azores Islands, reported and illustrated by Gofas & Beu (2002): all material in MNHN, taken in *N/O Le Suroit* cruise Seamount 2, January-February 1993, collected by S. Gofas, B. Métivier, and A. Warén: **Hyères Bank:** sta. DW188, 31°30.0'N, 28°59.50'W, 310 m (1); sta. CP191, 31°30.20'N, 28°58.90'W, 295 m (1); **Irving Bank:** sta. DW205, 32°01.10'N, 27°57.20'W, 348 m (1 frag); sta. DW209, 32°59.20'N, 27°55.90'W, 460 m (1); sta.

DW218, 31°52.30'N, 28°03.60'W, 480 m (1); sta. DW215, 31°53.60'N, 28°02.90'W, 275 m (1 large); **Atlantis Bank:** sta. DW254, 34°05.30'N, 30°13.40'W, 280 m (1).

Fossils: Italy: Pliocene: "Plaisancien de Ligure, Zinola" (MNHN, 1; Gofas & Beu, 2002: figs 9A-B); "Astian, Bacedasco bei Piacenza" (H 5928, 1), and "Astian, Savona" (H 5879, 1; both in Mayer-Eymar collection, NMB). The last two localities are Piacenzian in age, whereas the first is Zanclean, Early Pliocene.

Other specimens have been recorded recently by Spadini (1995: 285, fig. 8) from Armaiolo, near Rapolano, Siena, and by Inzani (1988: 29, pl. 6) from between Villanova and Garlenda, inland from Albenga, Province of Savona. Inzani (1988: pl. 4, fig. 3) also repeated the figure of the syntype from Ferrero Mortara *et al.* (1981: pl. 7, fig. 3). Fontannes (1879: 36, pl. 4, figs 2a-b) recorded a specimen from "sands with *Ostrea* [i.e., *Pycnodonte*] cochlear [(Poli, 1795)] of Saint-Restitut (Drôme), very rare," in southeastern France (Pliocene). Foresti (1876: 15) recorded a further specimen from the Pliocene of Castrocaro, near Siena. De Stefani & Pantanelli (1880: 209) (reprinted by Manganelli & Spadini, 2001: 255) recorded a further specimen collected from Coroncina, also near Siena, in 1877. Ceregato *et al.* (2002) recently confirmed the occurrence of this species in the Pliocene of Castrocaro. Specimens were also recorded from the Pliocene of Estepona, southern Spain, by Landau *et al.* (2004: 74).

Distribution.—Until recently, *Personopsis grasi* was recorded only as a Late Miocene and Pliocene fossil from southeastern France and northern Italy. Besides the well-known Pliocene localities, Bellardi (1873: 232) recorded it from "Colli Torinesi, Termo-fourà, mioc. med., Coll. Rovasenda," a Late Miocene (Tortonian) locality. Gofas and I (2002: 104) reported all of the Recent material listed here, from (a) Guadeloupe, French West Indies, and (b) the central Atlantic seamounts, off of Madeira and south of the Azores Islands. It will probably be found to occur more widely in the Atlantic Ocean on deep hard substrata, in more than 250 m of water. I am not aware of fossils from the study area.

FAMILY RANELLIDAE Gray, 1854 (1825)
SUBFAMILY RANELLINAE Gray, 1854 (1825)
Genus *ARGOBUCCINUM* Herrmannsen, 1846

Argobuccinum Herrmannsen, 1846: 77. Type species (by original designation): *Murex argus* Gmelin, 1791 (= *Buccinum pustulosum* Solander in Lightfoot, 1786), Middle Miocene to Recent, circum-Southern Ocean.

Gondwanula Finlay, 1926: 399. Type species (by original designation): *Bursa tumida* Dunker, 1862 (= *Buccinum pustulosum* Solander in Lightfoot, 1786).

Mediargo Terry, 1968: 42. Type species (by original designation): *Gyrineum mediocre* Dall, 1909, Middle Miocene-Pliocene, west-

ern United States of America.

Remarks.—The genus *Argobuccinum* contains only a few species, most occurring as Oligocene to Pliocene fossils in western North America and northeastern Asia. Only one species, *Argobuccinum pustulosum* (Solander in Lightfoot, 1786), is recognized here in the living fauna. The genus is characterized by (a) its relatively short, wide shape, with a moderately short spire and a short, straight anterior canal, (b) its large last whorl, (c) its evenly and quite strongly inflated whorls, (d) its particularly low, wide varices situated at 180° around the spiral, but slightly prosocline and offset from whorl to whorl rather than strictly aligned, (e) its sculpture of many similar, narrow to moderately wide, very low, weakly to quite prominently nodulose spiral cords (5 on spire whorls and 10 on the last whorl, in the type species) and many interstitial threads, (f) its large, oval to almost circular aperture with lightly flared, strongly ridged lips and a particularly prominent parietal ridge, and (g) its very small, turbiniform protoconch, much smaller than those of *Ranella* and *Fusitriton*. Following a long evolutionary history in the northern Pacific Ocean during Oligocene and Miocene time (and probably earlier), it increased its range to the western coast of Chile and then to the Southern Ocean during Miocene and Pliocene time, and then became extinct in the northern Pacific (J. T. Smith, 1970; Beu, 1976b).

Terry (1968) designated as type species of *Mediargo* the western North American Miocene-Pliocene species *Gyrineum mediocre* Dall, 1909. In my opinion *G. mediocre* is the most likely candidate to have been the immediate ancestor of *Argobuccinum pustulosum*, the Pliocene to Recent type species of *Argobuccinum*. Therefore, it seems unlikely that *Mediargo* is a clade separate from *Argobuccinum*, and I regard *Mediargo* as a synonym of *Argobuccinum*.

***Argobuccinum pustulosum* (Solander in Lightfoot, 1786)**

Pl. 23, Figs 1, 3, 5, 7-9; Pl. 24, Figs 1-3

Buccinum pustulosum Solander in Lightfoot, 1786: 88; Dall, 1921: 125.

Murex argus Gmelin, 1791: 3547; Dillwyn, 1817: 694.

Tritonium argo-buccinum Röding, 1798: 127.

Cassidea tuberculata Fischer von Waldheim, 1807: 185; Ivanov & Kantor, 1991: 82; Ivanov *et al.*, 1993: 77, pl. 7, fig. 4.

Ranella polyzonalis Lamarck, 1816: pl. 414, figs 3a-b, "Liste des objets": 4.

Ranella argus. Lamarck, 1822: 151; Kiener, 1841: 11, pl. 8, fig. 1; Reeve, 1844b: pl. 3, fig. 12; Küster & Kobelt, 1856: pl. 37, figs 5-6; 1870: 125; 1878: 329.

Triton ranelliformis King, 1832: 347.

Ranella vexillum G. B. Sowerby II, 1835: pl. 84, fig. 3; 1841b: 51; Menke, 1844: 24; Reeve, 1844b: pl. 3, fig. 13; Hupé, 1854: 186; Rochebrune & Mabille, 1889: H41.

Ranella kingii d'Orbigny, 1841b: 451 (unjustified new name for

Triton ranelliforme King, 1832).

Argobuccinum argus. Herrmannsen, 1846: 77; von Martens, 1904: 41; Suter, 1913: 309, pl. 43, fig. 4; Bartsch, 1915: 93, 224; Barnard, 1963: 18, figs 2a, 3a; Dell, 1963: 218, pl. 2, figs 1, 5; J. T. Smith, 1970: 458, pl. 39, figs 7, 10-12; Arnaud & Beurois, 1972: 869-870.

Ranella ampullacea Valenciennes, 1858: 759, 762; von Schrenck, 1867: 603; Kantor & Sysoev, 2002: 121, figs 1A-B.

Ranella vexilla. Chenu, 1859: 155, fig. 713.

Bursa tumida Dunker, 1862: 239; 1863: 56, pl. 18, figs 8-9.

Bursa zelebori Dunker, 1863: 57 (*nomen nudum*).

Bursa (Apollon) proditor Frauenfeld, 1865: 894.

Bursa (Apollon) prodiata. Frauenfeld, 1867: 4, pl. 1, figs 1a-b.

Ranella (Apollon) proditor. Vélain, 1878: 100, pl. 2, fig. 5.

Ranella (Argobuccinum) argus. Tryon, 1880: 44, pl. 24, fig. 61; Watson, 1886: 400.

Ranella tristanensis Gray in Paetel, 1888: 106 (*nomen nudum*).

Argobuccinum vexillum. Dall, 1909: 226; Macpherson & Gabriel, 1962: 152, fig. 182.

Argobuccinum tumidum. Hedley, 1914: 297; May, 1923: 62, pl. 39, fig. 22; Powell, 1933: 185; 1937: 74, pl. 14, fig. 6, 1939: 215; 1979: 166, pl. 12, fig. 5; Fleming, 1951: 28; 1952: 79, 84; J. T. Smith, 1970: 469, pl. 39, figs 1, 3, pl. 41, figs 1-4, 8, 9.

Gondwanula tumida. Finlay, 1926: 399.

Ranella (Apollon) argus. Coulon, 1933: 139.

Ranella (Apollon) vexillum. Coulon, 1933: 139.

Argobuccinum (Argobuccinum) argus. Carcelles & Williamson, 1951: 285; Carcelles, 1954: 244, figs 5-6.

Argobuccinum (Argobuccinum) ranelliformis ranelliformis (sic). Dell, 1963: 219, pl. 2, fig. 2.

Argobuccinum (Argobuccinum) ranelliformis (sic) tumidum. Dell, 1963: 220, text-fig. 1.2, pl. 1, figs 1-4.

Argobuccinum (Argobuccinum) proditor proditor. Dell, 1963: 221, pl. 2, fig. 4; Kilias, 1973: 36, fig. 31; Beu, 1985: 56; Piech, 1995: 6.

Argobuccinum (Argobuccinum) proditor tristanense Dell, 1963: 222, pl. 2, figs 3, 6; Kilias, 1973: 37, fig. 32; Beu, 1985: 56; Piech, 1995: 6.

Argobuccinum pustulosum. Rehder, 1967: 16; Kilburn & Rippey, 1982: 75, pl. 17, figs 1a-b; Kilburn, 1984: 8, pl. A, figs f-h; Wilson, 1993: 241, pl. 41, fig. 8.

Argobuccinum ranelliforme. J. T. Smith, 1970: 462, pl. 39, figs 2, 4, 6, 9, pl. 40, figs 2, 6-7, 10-12; Ramírez, 1987: 153, fig. 182.

Argobuccinum tristanense. J. T. Smith, 1970: 466, pl. 39, figs 5, 8, pl. 40, fig. 1.

Argobuccinum proditor. J. T. Smith, 1970: 468, pl. 41, figs 5-7, 10.

Argobuccinum ranelliforme ranelliforme. Arnaud & Beurois, 1972: 869-870.

Argobuccinum ranelliforme tumidum. Arnaud & Beurois, 1972: 869-870.

Argobuccinum ranelliforme proditor. Arnaud & Beurois, 1972: 866, figs 1, 4, pl. 1, figs 1-2, 4 (not pl. 1, fig. 3, = *Ranella gemmifera* Euthyme).

Argobuccinum (Argobuccinum) argus argus. Kilias, 1973: 30, fig. 27; 1981: 699.

Argobuccinum (Argobuccinum) argus ranelliforme. Kilias, 1973: 33, fig. 29.

- Argobuccinum (Argobuccinum) argus tumidum*. Kilius, 1973: 34, fig. 30.
- Argobuccinum (Argobuccinum) pustulosum pustulosum*. Beu, 1985: 56, fig. 4; Piech, 1995: 6.
- Argobuccinum (Argobuccinum) pustulosum ranelliforme*. Beu, 1985: 56; Piech, 1995: 6.
- Argobuccinum (Argobuccinum) pustulosum tumidum*. Beu, 1985: 56; Piech, 1995: 6.
- Argobuccinum (Argobuccinum) pustulosum*. Henning & Hemmen, 1993: 13, pl. 1, fig. 1.
- Argobuccinum (Argobuccinum) ranelliforme*. Henning & Hemmen, 1993: 14, pl. 1, fig. 2.
- Argobuccinum (Argobuccinum) tumidum*. Henning & Hemmen, 1993: 15, pl. 1, fig. 3.
- Argobuccinum (Argobuccinum) proditor*. Henning & Hemmen, 1993: 15, pl. 1, fig. 4.
- Argobuccinum (Argobuccinum) tristanense*. Henning & Hemmen, 1993: 16, pl. 1, fig. 5.

Remarks.—*Argobuccinum pustulosum* is mentioned only in passing here, being a species recorded as a (Miocene?) Pliocene-Pleistocene fossil in Chile (J. T. Smith, 1970; Herm, 1969). A debate has been carried out in the scientific literature about the status of the variously named geographical forms, and after a period when there were wide differences of opinion, the result is now agreed, to some extent at least: all the forms living around the Southern Ocean at present are very closely related, and are descended from a western North American species (although from which species has not necessarily been agreed upon). Whether the various geographical forms are to be recognized as subspecies is a matter of personal choice, but the huge range of variation seen in each region seems to rule this out. Specimens from the southwestern African coast, north of Cape Town, are more like specimens from Amsterdam and Tristan da Cunha Islands (*A. proditor*, *A. tristanense*) than the short, wide, strongly nodulose shells from the southern coast of South Africa generally regarded as “typical” *A. pustulosum*, and R. Kilburn (formerly of Natal Museum; pers. comm., 1998) has suggested that this indicates that more than one taxon is involved. However, specimens from Australia and New Zealand (*A. tumidum*) include tall, narrow shells resembling the *proditor* form; some specimens from Chile have wide spiral cords, and are “typical” of the form *ranelliformis*, whereas others seem identical to Australian and New Zealand shells in sculpture. It seems just as likely that the southwestern and southeastern African forms are ecophenotypes rather than distinct taxa. The range of variation in each area seems similar, even if some forms are more dominant than others in some localities. In my opinion this is likely to be a single species around the entire Southern Ocean, but this is one of the many taxonomic problems in Mollusca that cannot be resolved conclusively without recourse to molecular techniques, and it is possible that up to five separate species are involved.

The holotype of *Ranella ampullacea* (in MNHN), supposedly collected by Barthe from “the Straits of Tartary” (Tartar Strait, between Sakhalin and Russia), is a broadly banded South American specimen of *Argobuccinum pustulosum*, and presumably simply bears a wrong locality. The other mention of this name of which I am aware is in the list by von Schrenck (1867: 603) of Mollusca recorded from northern Japan, where von Schrenck quite rightly queried the locality of the specimen. Kantor & Sysoev (2002: 121, figs 1A-B) illustrated the holotype and commented on the incorrect assignment of a northern Pacific locality.

Dimensions.—Large South American specimens: GNS WM15955, beach in front of airport runway, SE side of Isla Mocha, S of Concepción, southern Chile (38.5°S), coll. D. Frassinetti, June 1993: H 99.9, D 61.2 mm; GNS WM17745, Puerto Montt, Chile: H 109.0, D 68.8 mm; *Ranella vexillum*, syntypes: H 94.9, D 58.3 mm, H 85.0, D 50.0 mm, H 67.3, D 38.4 mm; *Bursa tumida*, syntypes: H 92.6, D 56.5 mm, H 91.2, D 55.6 mm, H 81.2, D 53.2 mm; *Argobuccinum tristanensis*, holotype: H 53.4, D 29.8 mm; *Triton ranelliformis*, largest syntype: H 72.2, D 42.0 mm; *Ranella (Apollon) proditor*, largest syntype: H 100.9, D 56.6 mm; *Cassidea tuberculata*, lectotype: H 61.6, D 38.4 mm (Ivanov & Kantor, 1991: 83); largest New Zealand specimen seen, GNS RM5691, from 120 m, off of Taiaroa Head, E Otago, South Island: H 135.1, D 81.2 mm.

Types.—No specimens remain today from the collection of the Duchess of Portland, for which the sale catalog by Lightfoot (1786) was prepared. Presumably the specimens were dispersed in the subsequent sale. The same is true for the material of Gmelin (1791) and of Röding (1798). *Cassidea tuberculata*, lectotype designated by Ivanov & Kantor (1991: 82-83), Zoological Museum, Moscow University no. ZMUM N L-518, without locality; illustrated by Ivanov *et al.* (1993: pl. 7, fig. 4) (not seen), a typical if rather tall and narrow specimen of *Argobuccinum pustulosum*. *Ranella polyzonalis*, holotype MHNG 1098/79 (Pl. 23, Figs 5, 8), labelled “*Ranella argus* Lamarck,” without locality. The specimen matches the illustration by Lamarck (1816: pl. 414, figs 3a-b). The holotype of *R. polyzonalis* is here designated the neotype of *Buccinum pustulosum* Lightfoot, 1786, the neotype of *Murex argus* Gmelin, 1791, and the neotype of *Tritonium argo-buccinum* Röding, 1798. The type locality is here designated as Jeffreys Bay, South Africa. *Triton ranelliforme*, 5 unregistered presumed syntypes in BMNH, 2 probable syntypes pres. Captain P. P. King, and 3 “possible” syntypes from the Broderip collection (labelled B2115 or B2252 inside the aperture), all unlocalized, stated by King (1832: 347) to be from “Sinum Peñas et oram occidentalum America meridionalis.” Although there is no hard evidence that the three from the Broderip collection actually were seen by King, Broderip is

not likely to have acquired specimens so early from any source other than King, so it is likely that they are syntypes. As noted above, the holotype of *Ranella ampullacea* (fide Kantor & Sysoev, 2002: figs 1A-B) is in MNHN; type locality here designated as Chiloé Island, Chile. *Ranella vexillum*, 3 syntypes BMNH 1950.11.28.17-19, from "Chiloé Id., Concepción, rocky places," 6-10 m; the medium-sized syntype (H 85.0, D 50.0 mm) is the specimen illustrated by both G. B. Sowerby II (1835: pl. 84, fig. 3) and Reeve (1844b: pl. 3, fig. 13). *Ranella kingii*, 3 syntypes BMNH 1854.12.4.533, from Isla Mocha, southern Chile. *Bursa tumida*, 3 syntypes BMNH 1973.11.3, from "New Zealand"; the largest specimen is the one illustrated by Dunker (1863 in 1863-1864: pl. 18, figs 8-9). *Ranella (Apollon) proditor*, 5 syntypes NHMV 689-693, from St. Paul Island; the largest syntype, NHMV 689, is the specimen illustrated by Frauenfeld (1867: pl. 1, figs 1a-b). *Argobuccinum proditor tristanense*, holotype BMNH 1887.2.9.1221, collected on the shore at Tristan de Cunha Island by the *Challenger* Expedition, with 4 lots of paratypes, BMNH 1887.2.9.1222-3, 2 paratypes, Nightingale Island, *Challenger*; BMNH 1973.11.2, 1 paratype, Tristan de Cunha Island; BMNH 1859.10.12.71, 1 paratype, Tristan da Cunha Island, *HMS Herald*; and BMNH 1925.11.17.1-6, 6 paratypes, Tristan da Cunha Island.

Other material examined.—**Recent:** Most of the many lots of Recent specimens in world museums are not listed here. **South America:** 24 lots examined at LACM and 7 at GNS; northernmost: intertidal, Caleta Leandro, Tumbes, Concepción Province, Chile, 36°38'S, 73°07'W, leg. University of Concepción, 23 November 1972 (LACM 72-208, 1 small); southernmost: intertidal, rocks and sand, SW side Bahía Buen Suceso, SE Tierra del Fuego, Argentina, 54°47.8'S, 65°15.5'W, USARP/SOSC *R/V Hero* cruise 712, sta. 71-2-15, 26 April 1971 (LACM 71-272, 3 large). As noted under *Priene scabrum* (Broderip, 1833) below, Aldea & Valdovinos (2005) recorded *Argobuccinum pustulosum* as extending northward only to Isla Santa Maria, Chile (37°00'12"S). **South Africa:** 43 lots examined at NMP, 12 from Namibia to SW Cape Province, and 31 from False Bay to Jeffreys Bay; 27 in GNS.

Fossils: Recorded by Herm (1969: 71) from Pliocene rocks at La Cueva, central Chile, and by J. T. Smith (1970) from Late Miocene(?) (probably Late Oligocene-Early Miocene fossils reworked into Late Miocene-Early Pliocene) rocks at Río Rapel, N of Navidad, SW of Santiago, Chile. However, Nielsen (2003: 93) doubted the occurrence of *Argobuccinum* in Miocene rocks of Chile, and I have seen no authentic Oligocene-Miocene material from near Navidad. Late Middle Pleistocene [oxygen isotope stage 5e and, at one locality (Denby Shellbed, Waihi Beach, Hawera, South Taranaki), stage 7] and younger fossils also occur commonly

in New Zealand uplifted terrace faunas.

Distribution.—*Argobuccinum pustulosum* (as interpreted here) lives now around the entire Southern Ocean, and is recorded from southern Africa (southern Namibia to East London), St. Paul and Amsterdam Islands, Australia, New Zealand, southern South America, and Tristan da Cunha and Nightingale Islands (Dell, 1963; J. T. Smith, 1970; Arnaud & Beurois, 1972). Fossils were recorded by J. T. Smith (1970: 465) from the Piso de Navidad (Late Miocene) at the mouth of Río Rapel, 2-3 km N of Navidad, SW of Santiago (specimen observed by Smith in collection of the Museo de Historia Natural, Quinta Normal, Santiago), but it is evidently rare, or perhaps mislocalized, because no specimens from Miocene rocks were observed by AGB and M. Griffin in Museo Nacional de Historia Natural, Santiago, in January 1998, and none have been collected subsequently by S. N. Nielsen (now in Institut für Geowissenschaften, Christian-Albrechts-Universität Kiel; pers. comm., 2007) during an extensive study of Chilean Tertiary mollusks, and from Pliocene and Pleistocene deposits of central and southern Chile (Herm, 1969; J. T. Smith, 1970).

Dall & Ochsner (1928: 97) recorded "*Argobuccinum argus*" from "upper zones [Pleistocene], Indefatigable Island," Galápagos Islands, but such a dramatic range extension to the north of the present range is highly unlikely, and the record requires confirmation. I am not aware of the present location of this material.

In southern Africa, *Argobuccinum pustulosum* is recorded from the western coast as far north as Namibia and along the southern coast as far eastward as East London (Kilburn & Rippey, 1982: 75). In Australia, the species is recorded from the entire southern coast, and as far north as southern New South Wales on the eastern coast. In New Zealand, it occurs throughout the country and at the Chatham, Snares, Campbell, and Auckland Islands and at Stewart Island, but is much less common in the north, and particularly in the northern North Island, than it is in the southern South Island, where a few specimens can be found in the intertidal zone. In South America, it occurs throughout most of Chile, south of *ca.* Caldera (J. T. Smith, 1970: fig. 5) and throughout the southern islands and the Falkland Islands, and up the coast of Argentina as far north as Miramar, 50 km south of Mar del Plata (MACN 8497-2, one very abraded specimen). Most specimens are trawled or dredged on the shelf in *ca.* 20-100 m throughout its range, but in the southern, cool areas, it can be found occasionally throughout its range in the intertidal zone of exposed rocky shores, feeding on ascidians. A specimen from southern England (in sand on bank of channel, Mangle Estuary, St. Ives, Cornwall, J. M. Light, August 1981; *ex* A. R. Arthur collection) is now in GNS (WM17742); presumably it was dropped from a ship.

Genus *FUSITRITON* Cossmann, 1903

Fusitriton Cossmann, 1903: 109. Type species (by original designation): *Triton cancellatus* Lamarck, 1816 (= *Neptunea magellanica* Röding, 1798), Pleistocene(?) and Recent, circum-Southern Ocean.

Cryotritonium von Martens, 1904: 38. Type species (by subsequent designation; Powell, 1951: 130): *Lampusia murrayi* E. A. Smith, 1891 (= *Neptunea magellanica* Röding, 1798).

Remarks.—The genus *Fusitriton* is highly distinctive because of (a) its tall spire and moderately long anterior canal, (b) its evenly and strongly inflated whorl profile, and deeply impressed suture and, consequently, its wide, circular aperture, (c) its very low, irregularly placed varices, (d) its subdued cancellate sculpture of low to moderately prominent axial costae and weak spiral cords, and (e) its large, simple, turbiniform protoconch. J. T. Smith (1970) reviewed the extensive western North American and Japanese fossil record, as well as the several forms living in the northern Pacific and the Southern Oceans. Since then, I reviewed (Beu, 1978a) the living species again, Habe (1979) added the species *F. takedai* Habe, 1979, from the Emperor Seamounts in the northern Pacific, and Amano (1997) added the further distinctive Japanese Pliocene-Early Pleistocene species *F. izumozakiensis* Amano, 1997. Luis Simone (Museu de Zoologia de Universidade de São Paulo, pers. comm., 2002) informed me that specimens of *Fusitriton* in shallow water and in deep water off of southern Brazil-Argentina fall into at least two species on anatomical grounds, even though their shells are difficult to distinguish, and Cossignani & Cossignani (2003) provided the name *F. brasiliensis* for the new deep-water species. This genus probably requires extensive re-evaluation. The most distinctive of the Recent “forms” (species?) is *F. murrayi* (E. A. Smith, 1891), because of its small size, narrow shape, weak sculpture, and pale, whitish coloration. Daniel Frassinetti (SGO.PI) showed me specimens of this “form” trawled off of northern Chile, again suggesting that the Southern Ocean “forms” might actually all be distinct species, some with wider distributions than have been suspected previously. However, pending re-evaluation, a conservative treatment is maintained here.

Kantor & Harasewych (2000) recently added the distinctive, bathyal, Antarctic genus and species *Obscuranella papyrodes* Kantor & Harasewych, 2000, to the Ranellidae. There is little doubt that this is related to *Fusitriton*, despite its highly distinctive, triangular operculum.

Fusitriton brasiliensis T. Cossignani & V. Cossignani, 2003

Fusitriton brasiliensis T. Cossignani & V. Cossignani, 2003: 3, unnumbered figs pp. 4-5.

Remarks.—The recently named species *Fusitriton brasiliensis* differs quite significantly from the shallow-water Magellanic species, *F. magellanicus* (Röding, 1798), in its wider shape with a more inflated anterior (abapical) part of the last whorl, its narrower, more widely spaced and more sharply defined axial ribs, its brighter coloration, and its much more consistently placed, moderately prominent varices, which on the holotype are situated at approximately each 200° around the spiral, or almost aligned up the opposing sides of the spire, except for becoming more numerous and less regular on the last whorl – although they are less regular over the entire teleoconch of the illustrated paratype and other specimens that I have examined. The varices on the holotype are as consistently present and placed as in *F. takedai*, but are much lower, more rounded in section, and less prominent than in *F. takedai*. Specimens are illustrated excellently in color on a webpage (<http://www.femorale.com.br/shellphotos>, last accessed 28 April 2006).

Dimensions.—GNS WM18983: H 91.1, D 47.5 mm; H 95.3, D 48.9 mm.

Types.—*Fusitriton brasiliensis*, holotype in Museo Malacologico Piceno, Cupra Marattima, Italy; 1 paratype in Mostra Mondiale Malacologia, Cupra Marittima; 3 paratypes in the collection of the authors, Cupra Marittima (T. Cossignani & V. Cossignani, 2003: 3); not seen; all from 1,200 m, taken in lobster traps off of Chui, Río Grande do Sul State, southern Brazil.

Other material examined.—**Recent: Brazil:** fishermen's crab traps, 1,200 m, off of Punta del Este, Uruguay, April 2007 (GNS WM18983; 2).

Distribution.—So far, material of *Fusitriton brasiliensis* has been reported only from deep water (1,200 m), taken in lobster or crab traps in the two localities listed here. It is probably widespread in deep water in the southwestern Atlantic.

Fusitriton magellanicus (Röding, 1798)

Pl. 23, Figs 2, 4, 6

Murex magellanicus var. β Gmelin, 1791: 3548.

Neptunea magellanica Röding, 1798: 116.

Triton cancellatus Lamarck, 1816: pl. 415, fig. 1, “Liste des objets”: 4; 1822: 187; Deshayes, 1843: 638; Küster & Kobelt, 1878: 246, pl. 66, fig. 1.

Triton leucostomoides G. B. Sowerby I, 1846: 618 (in part; see *Sassia leucostomoides*, below).

Fusus cancellatus. Reeve, 1848a: pl. 16, fig. 62.

Triton cancellatum. Hupé, 1854: 182.

Triton (Lagena) cancellatum. Chenu, 1859: 154, fig. 703.

Triton (Priene) cancellatus. Tryon, 1880: 34, pl. 16, figs 164-167, pl. 17, figs 170-172.

Triton (Lagena) magellanicus. Watson, 1886: 395.

Priene magellanica. Rochebrune & Mabille, 1889: H42.

Lampusia (Priene) murrayi E. A. Smith, 1891: 436, pl. 34, fig. 1.

Priene (Fusitriton) cancellatus. Cossmann, 1903: 109, text-fig. 8.

- Tritonium* (*Cryotritonium*) *murrayi*. von Martens, 1904: 38, pl. 3, fig. 16.
- Argobuccinum retiolum* Hedley, 1914: 73, pl. 11, fig. 5.
- Fusitriton retiolus*. Hedley, 1918: M66; Garrard, 1961: 14; Iredale & McMichael, 1962: 55; Macpherson & Gabriel, 1962: 155, fig. 185; J. T. Smith, 1970: 481, pl. 44, figs 1-11; Wilson & Gillett, 1971: 78, pl. 53, fig. 2; Powell, 1979: 167, pl. 33, fig. 8.
- Priene retiolum*. Finlay, 1924: 462.
- Fusitriton laudandum*. Finlay, 1926: 399, pl. 20, fig. 65; 1930: 250; Powell, 1933: 164; 1937: 74; 1950: 73, pl. 7; Iredale, 1937: 106.
- Fusitriton futuristi* Mestayer, 1927: 189, fig. 6.
- Austrofusus cancellatus*. Parodiz, 1942: 210, illus.
- Fusitriton magellanicus*. Carcelles, 1944: 247, pl. 2, fig. 23; Coelho *et al.*, 1981: 129, fig. 12; Cantera & Arnaud, 1984: 62; Calvo, 1987: fig. 81 (radula); Wilson, 1993: 241, pl. 41, fig. 10; Ramírez, 1987: 154, fig. 183.
- Fusitriton algoensis* Tomlin, 1947: 245, illus.; White, 1948: 3, figs 1-5.
- Fusitriton murrayi*. Barnard, 1949: 90.
- Argobuccinum* (*Fusitriton*) *magellanicum*. Carcelles, 1950: 59; 1954: 249, figs 1-4; Carcelles & Williamson, 1951: 286.
- Fusitriton cancellatum*. Powell, 1951: 130; 1960: 147.
- Fusitriton laudandum*. Powell, 1955: 97; 1962: 94; Dell, 1956: 85, fig. radula A3.
- Argobuccinum* (*Fusitriton*) *murrayi*. Barnard, 1963: 22, fig. 2b.
- Fusitriton cancellatus*. J. T. Smith, 1970: 475, pl. 42, figs 4-10; Rios, 1975: 80, pl. 22, fig. 326.
- Fusitriton cancellatus murrayi*. J. T. Smith, 1970: 480, pl. 43, figs 12-15.
- Fusitriton laudandum* (*sic*). Glasby, 1972: 383, fig. 2.
- Argobuccinum* (*Fusitriton*) *cancellatum cancellatum*. Kilius, 1973: 38, fig. 33.
- Argobuccinum* (*Fusitriton*) *cancellatum retiolum*. Kilius, 1973: 42, fig. 36.
- Argobuccinum* (*Fusitriton*) *laudandum*. Kilius, 1973: 43, fig. 37.
- Fusitriton magellanicus laudandum*. Beu, 1978a: 23, figs 6c, 10a-d, 11a-b, 12a-c (footnote: 22); 1985: 56, fig. 6; Henning & Hemmen, 1993: 20, pl. 2, fig. 5; Piech, 1995: 6.
- Fusitriton magellanicus retiolus*. Beu, 1978a: 22, figs 7d-f, 10f, 11c, h; 1985: 56; Henning & Hemmen, 1993: 21, pl. 2, fig. 6; Piech, 1995: 6.
- Fusitriton magellanicus magellanicus*. Beu, 1985: 56; Henning & Hemmen, 1993: 19, pl. 2, fig. 3; Rios, 1994: 87, pl. 29, fig. 338; Piech, 1995: 6.
- Fusitriton magellanicus murrayi*. Kilburn & Rippey, 1982: 76, pl. 17, fig. 10; Kilburn, 1984: 8, pl. A, figs b-c; Beu, 1985: 56; Henning & Hemmen, 1993: 20, pl. 2, fig. 4; Piech, 1995: 6.
- Not *Fusitriton magellanicus*. Nielsen & Valdovinos, 2008: 209, fig. 16 (= *Penion* sp.?, Buccinoidea).

Remarks.—Differences from *Fusitriton oregonensis* (Redfield, 1846) are described below. *Fusitriton magellanicus* is commonly dredged from offshore in sandy or muddy substrata around southern South America. The form that has been regarded as “typical” *F. magellanicus* by J. T. Smith (1970) and

me (Beu, 1978a) is the relatively short and wide, highly inflated, weakly sculptured form that seems to be the usual one collected off of the coasts of Uruguay and Argentina, as well as from southern Chile and the Falkland Islands. It now appears likely that, rather than a single circum-Southern Ocean species, the southern hemisphere forms of *Fusitriton* constitute several species. Apparently distinct species of *Fusitriton* in the southern hemisphere are:

- *brasiliensis* T. & V. Cossignani, 2003, deep water in the southwestern Atlantic.
- *laudandum* (Finlay, 1926), S New Zealand to N Kermadec Islands, abundant on volcanic seamounts N of New Zealand (possibly synonymous with *F. retiolus*; although both also possibly occur in New Zealand).
- *magellanicus* (Röding, 1798), southern South America: central Chile to southern Brazil.
- *murrayi* (E. A. Smith, 1891), South Africa and N Chile.
- *retiolus* (Hedley, 1914), southern and eastern Australia.

Dimensions. — Holotype of *Lampusia murrayi*: H 82.2, D 39.2 mm; *Fusitriton magellanicus*, 100 m, off of La Paloma, Rocha, Uruguay, GNS WM18492: H 124.2, D 70.0 mm; H 96.0, D 52.4 mm; off of Montevideo, Uruguay, GNS WM9302: H 113.5, D 60.7 mm.

Types.—No original type material is known from the collection described by Röding (1798). *Triton cancellatus*, 3 syntypes in MHNG, without locality. Specimen MHNG 1100/13 is a typical, well-inflated specimen of the common form from southern and eastern South America, matches the illustration by Lamarck (1816: pl. 415, fig. 1), and is here designated the lectotype of *Triton cancellatus* (Pl. 23, Figs 2, 6). This same specimen is also here designated the neotype of *Neptunea magellenica*. Paralectotype MHNG 1100/14/1 is a similar specimen to the lectotype, but its spire apex has been repaired by gluing on a narrower apex from a fasciolarid such as *Fusinus*. The lectotype designation is necessitated by the second paralectotype, MHNG 1100/14/2, which is a specimen of *Priene scabrum* (King, 1832). The type locality of *T. cancellatus* is here designated as off Maldonado, Uruguay. *Lampusia* (*Priene*) *murrayi*, holotype BMNH 1890.4.14.95, from *HMS Challenger* sta. 142, off of the Cape of Good Hope, South Africa, in 270 m. *Argobuccinum retiolum*, holotype AMS C.70730, from FIS *Endeavour*, 180-450 m, south of Gabo Island, NE Victoria, with 1 paratype C.70729, among “a few specimens from 50-100 fathoms [90-180 m], between Green Cape and Gabo Island” (Hedley, 1914: 74), New South Wales-Victoria border. *Fusitriton laudandum*, holotype AIM, AK 70333, trawled on the shelf in ca. 80 m, off Otago Heads, southern South Island, New Zealand. *Fusitriton futuristi*, holotype NMNZ M1399, from off of Cape Campbell, northern South Island, New Zealand. *Fusitriton algoensis*, no type material present in BMNH or NMW, presumably in South

African Museum (not seen).

Other material examined.—Most of the huge lots in many of the world's museum collections need not be listed here.

Recent: South America: 38 lots examined at LACM; northernmost on Pacific coast: 240-250 m, off Los Vilos, Chile, 31°56'S, 71°54'W, leg. H. Andrade, shrimp boat *Goden Wind* (LACM 72490, 3 large, collected alive); northernmost on Atlantic coast: 90 m, off of Isla de Lobos, Uruguay, March 1967 (LACM 27154, 2 large, collected alive); southernmost: 438-548 m, 13 km SW of Cape San Bartolome, Isla de los Estados [Staten Island], SE tip of Tierra del Fuego, Argentina, 55°00'S, 64°48.7'W, USARP/SOSC *R/V Hero* cruise 715, sta. 895 (LACM 71-342, 2, 1 collected alive).

Fossils: Known only from probable Holocene occurrences in New Zealand (GS12254, Owenga Beach "shell bank," SE Chatham Island, 1 frag) and in southern Tierra del Fuego (Holocene beach deposit, Golondrina Bay, Beagle Channel, coll. & pres. Sandra Gordillo, GNS WM15856, 1). The only other fossil specimen of which I am aware is the small juvenile collected by Charles Darwin from Pliocene rocks at Isla Guafo, southern Chile, during the voyage of the *Beagle*, and remaining among the type specimens of *Sassia leucostomoides* (G. B. Sowerby I, 1846) in BMNH (see below; Griffin & Nielsen, 2008: 299, pl. 21, figs 13-14).

Distribution.—*Fusitriton magellanicus*, as interpreted broadly here, occurs all around the southern ends of all the landmasses in the Southern Ocean, at most of the islands in between them, and on some isolated seamounts in the same area. I recorded (Beu, 1978a) it from all around New Zealand, although only a few, sparse records are known from the northern half of the North Island. However, it has recently proved to be common on hard substrata on submarine volcanoes of the Tonga-Kermadec Ridge. It also lives all over the Campbell Plateau to the south of South Island, as far south as Macquarie Island, and around the Chatham, Bounty, and Antipodes islands. Around Australia, *F. magellanicus* occurs only off of New South Wales and eastern Victoria, with one possible record from the far northwestern shelf of Western Australia (Wilson, 1993: 241). A large sample was taken at *R/V Eltanin* sta. 1346, on a seamount at 54°49'-50'E, 128°48'-129°46'S, in ca. 600 m, almost halfway between New Zealand and South America (J. T. Smith, 1970: 478; observed in NMNZ). Around southern South America, *F. magellanicus* occurs at least as far north on the Pacific coast as central Chile (material in Museo Nacional de Historia Natural, Santiago), around the southern islands, Cape Horn, and the Falkland Islands, and as far north on the Atlantic coast as Río Grande do Sul, southern Brazil (Coelho *et al.*, 1981; Rios, 1994: 87). Around southern Africa, it occurs from off of Namibia to southern Mozambique, in 155-550 m (Kilburn & Rippey, 1982: 76). Specimens have also been reported from the Crozet Islands

(Cantera & Arnaud, 1984: 620), and a specimen in MNHN (Pl. 23, Fig. 4) was taken in a lobster trap at 600 m off of Baie de la Possession, Réunion Island, Indian Ocean. Nielsen & Valdovinos (2008: 209, fig. 16) recorded many Pleistocene specimens as *F. magellanicus* from the Tubul Fm in south-central Chile, but their illustrated specimen lacks varices and is clearly a specimen of a buccinoidean such as a *Penion* species.

Fusitriton oregonensis (Redfield, 1846)

Triton oregonense Redfield, 1846: 163, pl. 11, figs 2a-b.

Fusus oregonensis. Reeve, 1848: pl. 16, figs 61a-b.

Triton (Buccinum) cancellatum. Middendorf, 1849: 164, pl. 3, figs 1-4; Arnold, 1903: 286, pl. 6, fig. 1 (not *Triton cancellatus* Lamarck, 1816).

Tritonium (Priene) cancellatus. Tryon, 1880: 34, pl. 16, figs 165-167 (in part not *Triton cancellatus* Lamarck, 1816).

Priene (Fusitriton) oregonensis. Cossmann, 1903: 109, text-fig. 8, pl. 5, fig. 2.

Priene oregonensis var. *angelensis* Arnold, 1907: 536, pl. 50, fig. 11.

Argobuccinum (Fusitriton) oregonensis. Dall, 1909a: 56; Oldroyd, 1927: 242, pl. 37, figs 1-2.

Gyrineum mediocre var. *corbiculatum* Dall, 1909a: 55, pl. 7, fig. 9.

Argobuccinum (Fusitriton) coosense Dall, 1909a: 55, pl. 7, fig. 4; Faustman, 1964: 134, pl. 3, fig. 21.

Argobuccinum (Priene) pacifica (sic) Dall, 1909a: 56, pl. 5, fig. 9, pl. 6, fig. 2.

Gyrineum sylviaensis Weaver, 1912: 73, pl. 12, fig. 126.

Ranella (Priene) pacifica. Grant & Gale, 1931: 735.

Ranella (Priene) corbiculata. Grant & Gale, 1931: 735.

Ranella (Priene) oregonensis. Grant & Gale, 1931: 737, pl. 27, fig. 12.

Ranella (Priene) oregonensis var. *angelensis*. Grant & Gale, 1931: 738.

Ranella (Priene) tugaruensis Nomura & Hatai, 1935: 126, pl. 12, fig. 4.

Fusitriton aff. *F. oregonensis*. Woodring, 1938: 23, pl. 5, figs 21-23.

Argobuccinum sylviaense. Weaver, 1943: 422, pl. 83, fig. 7.

Gyrineum corbiculatum. Weaver, 1943: 424, pl. 84, figs 1, 3.

Ranella oregonensis. Hatai, 1950: 133.

Fusitriton oregonensis. Kira, 1955: 43, pl. 21, fig. 9; 1962: 55, pl. 22, fig. 9; J. T. Smith, 1970: 485, pl. 45, figs 1-11, pl. 46, figs 1-2, 5-6, 8-9, 13-14, pl. 47, figs 2-3; Kuroda *et al.*, 1971: 124, pl. 28, fig. 4 only (in part); Kern, 1973: 89; Beu, 1978a: 22; 1985: 56; Henning & Hemmen, 1993: 22, pl. 2, fig. 1; Piech, 1995: 7; Okutani, 2000: 285, pl. 141, fig. 1.

Argobuccinum (Fusitriton) cancellatum oregonense. Kiliyas, 1973: 40, fig. 34.

Remarks.—I pointed out (Beu, 1978a) that *Fusitriton oregonensis* and the superficially similar circum-Southern Ocean species *F. magellanicus* increase the size of their shells in fundamentally different ways. *Fusitriton oregonensis* and the closely related northern Pacific taxa *F. galea* Kuroda & Habe in Habe, 1961, and *F. izumozakiensis* Amano, 1997, increase shell size

by maintaining a more-or-less constant number of axial costae in each intervariceal interval, but increasing the amplitude and spacing of the costae. However, the remaining northern Pacific species *F. takedai* and the Southern Ocean species *F. magellanicus* have adopted the opposite approach, increasing the number of axial costae in each intervariceal interval as the shell grows while maintaining the amplitude and spacing of the costae more-or-less constant. The taxa inhabiting the northern Pacific Ocean (apart from *F. takedai*) and the Southern Ocean therefore seem not to be very closely related, in a phylogenetic sense. J. T. Smith (1970) suggested that *F. magellanicus* was related to the Californian Pliocene species *F. scotiaensis* (Martin, 1914), so this is likely to have been the ancestor of the southern hemisphere population of *F. magellanicus*, and possibly also of *F. takedai*.

Fusitriton oregonensis is included in this report because of a rather surprising fossil record from Pleistocene terraces on the Baja California peninsula. This species lives today in shallow water (in some places in the intertidal zone; San Juan Islands, Puget Sound: J. T. Smith, 1970: 493-494) in the northern Pacific, from Niigata on the Japan Sea coast and Cape Inubo on the Pacific coast of Japan, around the Aleutian arc to the Gulf of Alaska, and south to off of San Nicolas Island, off of San Diego, California. Although some Californian records are from quite shallow water (150-230 m, but containing hermit crabs), most are from deep water (alive in 2,000-2,500 m; J. T. Smith, 1970: 491), reflecting the cold-water preference of this species, following the isotherms down to deeper water in the south of its range. The occurrences of a few incomplete specimens in the faunas of uplifted Pleistocene terraces near San Diego and in Baja California therefore seem to imply strong coastal upwelling that allowed cold-water taxa to live in shallow water near these sites during interglacial periods. Kern (1973) noted also that *F. oregonensis* "is abundant in deepwater Pliocene rocks of the Los Angeles basin."

Dimensions.—GNS WM17783, 50 m, off of Cape Erimo, Hokkaido, Japan: H 115.1, D 58.2 mm; GNS WM16094, Victoria breakwater, British Colombia, Canada: H 98.6, D 52.5 mm.

Types.—J. T. Smith (1970) reviewed known type material for *Fusitriton oregonensis* and its synonyms. Redfield's collection was left to ANSP (Johnson, 2006: 12), but type material of *Triton oregonensis* is not present in this collection, and is assumed to be lost. The type locality is "Straits of St. Juan de Fuca," Washington State, northwestern USA. It is not appropriate to designate a neotype here; this should be done by an author with access to better North American material from the type locality, and it is still possible that type material remains in an American museum, e.g., the late Harald Rehder (formerly of USNM) suggested to me that Redfield's collection might be in the State Museum of New York, Albany. However, it is

likely that Redfield's type specimen was from another private collection, and is lost. *Priene oregonensis* var. *angelensis*, holotype USNM 164975, from Third Street tunnel, Los Angeles, California, Pliocene (Grant & Gale, 1931: 738). *Gyrineum mediocre* var. *corbiculatum* Dall, holotype USNM 153900 (J. T. Smith, 1970: pl. 46, figs 5, 8), from Coos Bay, Oregon, Pliocene. *Argobuccinum (Fusitriton) coosense*, holotype USNM 153903, from Coos Bay, Oregon, Pliocene. *Argobuccinum (Priene) pacifica*, holotype USNM 153902, from Coos Bay, Oregon, Pliocene. *Gyrineum sylviaensis*, holotype CAS 7601 (J. T. Smith, 1970: pl. 46, fig. 12) from Monsanto Fm (Miocene-Pliocene) near Monsanto, Washington State, USA. *Ranella (Priene) tugaruensis*, holotype in Institute of Geology and Palontology, Tohoku University, Sendai, IGPS 6158 (J. T. Smith, 1970: pl. 46, figs 9, 13), from Pliocene rocks of Aomori Prefecture, northern Honshu, Japan.

Other material examined.—It is superfluous to list the huge collections of Recent material of *Fusitriton oregonensis*; a summary was provided by J. T. Smith (1970). Fossils from almost all localities north of Mexico also are irrelevant to this report. **Fossils: California: Pliocene:** LACMIP loc. 305, San Diego Fm, K Ranch, hills S of Tijuana River, San Diego Co [1 frag; occurs with *Argobuccinum mediocre* (Dall, 1909), *Reticutriton elsmereensis* (English, 1914), *Monoplex amictus* (Reeve, 1844) and *Crossata ventricosa*]. **W Mexico: Pleistocene:** CAS, Stanford University loc. 805, terrace cover (oxygen isotope stage 5e), Bahia de Santa Inés, Baja California Sur (one large last whorl). J. T. Smith (1970) also recorded "fragments from San Nicolas and San Clemente Islands and from San Jose del Cabo, Baja California," all in Pleistocene terrace cover beds.

Distribution.—Living, northern Pacific Ocean, from central Honshu, Japan, to San Diego, California, USA (see in more detail above). *Fusitriton oregonensis* occurs sympatrically with *F. galea* in Sagami Bay, central eastern Honshu (Kuroda *et al.*, 1971: pl. 28, figs 4-5; both species illustrated under the name *F. oregonensis*). Fossil, Miocene to Pleistocene in Japan; probably in Miocene rocks of Alaska; Plio-Pleistocene of Alaska to southern California; rare in Pleistocene terrace cover beds of Baja California Sur, Mexico.

Genus *HALGYRINEUM* Beu, 1998

Halgyrineum Beu, 1998b: 63. Type species (by original designation): *Gyrineum louisae* Lewis, 1974, Late Pliocene-Early Pleistocene, Limón, Costa Rica; Recent, Indo-West Pacific and Atlantic.

Remarks.—I proposed (Beu, 1998b) *Halgyrineum* for the single species *Gyrineum louisae*, because of its completely different sculptural plan and overall appearance from all of the other species referred to *Gyrineum*. The whorl surface is evenly convex, rather than angled at the periphery as in most *Gyrineum*

species, and is covered with regularly spaced gemmae. The gemmae are produced at the intersections of numerous spiral cords (6 on spire whorls and 11 on the last whorl) with up to 17 axial costae in each intervariceal interval. This therefore contrasts strongly with all undoubted *Gyrineum* species, which have three or four spiral cords on spire whorls and seven on the last whorl, crossing only 6-10 axial costae, reduced still further on the last whorl of some species. Correspondingly, *H. louisae* has 10 transverse ridges inside the outer lip, whereas *Gyrineum* species all have seven. Also, the fine, close, crisply cancellate interstitial microsculpture of *H. louisae* contrasts with the few, low, wide interstitial spiral cords and smooth interspaces seen on *Gyrineum* species. The shell is also more strongly dorsoventrally compressed than any *Gyrineum* species and, rather than being strictly aligned down the opposing sides of the spire as in all *Gyrineum* species, the varices of *H. louisae* are slightly offset, so that each varix is slightly in front of the corresponding one on the preceding whorl. The almost smooth, flared inner lip is also quite different from the narrow, coarsely ridged inner lip of *Gyrineum* species. *Halgyrineum louisae* is also the only known member of the subfamily Ranellinae with a multiwhorled, cancellate protoconch indicating a planktotrophic larva; all species of *Gyrineum* have a smaller, smooth, turbiniform protoconch. Species of *Argobuccinum*, *Fusitriton*, and *Ranella* also have planktotrophic larvae, but their protoconchs lack cancellate sculpture. *Halgyrineum louisae* is the only species of ranelline found widely in both the central Indo-West Pacific and Atlantic provinces, and this wide range presumably results from its long-lived planktotrophic larvae. I noted (Beu, 1998b) that a formerly continuous range throughout the tropical ocean was presumably disrupted by the uplift of the CAI in late Pliocene or early Pleistocene time, but has not been followed by the evolution of morphological differences between the Atlantic and Indo-West Pacific populations. This history is supported by the occurrence of latest Pliocene-Early Pleistocene fossils of *H. louisae* in the Moín Fm at Limón, Costa Rica.

Halgyrineum louisae (Lewis, 1974)

Pl. 24, Figs 4, 7-10

Gyrineum louisae Lewis, 1974: 11, figs 1-3; Fechter, 1975: figs 4-6, 9; Cernohorsky, 1978c: 62, pl. 17, fig. 5; Kay, 1979: 225, fig. 79L; Beu, 1985: 56; Robinson, 1990: 133, fig. 1a-c; Henning & Hemmen, 1993: 27, pl. 3, fig. 9; Piech, 1995: 7.

Gyrineum atlanticum Fechter, 1975: 64, figs 1-3, 7-8.

Halgyrineum louisae. Beu, 1998b: 64, figs 6p, 19a-i; Gofas & Beu, 2002: 99, figs 6D-H.

Gyrineum louisae (sic). Ardovini & Cossignani, 2004: 129, bottom right fig.

Remarks.—The characters of the species are those of the genus.

Halgyrineum louisae is widely distributed but rare. Records are from depths of 80-750 m, so its apparent rarity possibly is at least partly accounted for by its offshore rocky habitat, which has been sampled little in most of the range of the species. It is somewhat surprising, then, that *H. louisae* occurs in the relatively shallow-water fauna of the Moín Fm at Limón, although the abundance of some other shallow offshore taxa such as *Monoplex krebssii* and *Distorsio mcgintyi* in the same unit suggests that part of the Moín Fm was deposited in a depth of at least 50 m, and perhaps more.

Dimensions.—Holotype of *Gyrineum louisae*: H 19, D 12 mm (Lewis, 1974: 11); holotype of *G. atlanticum*: H 26.1, D 15.9 mm (Fechter, 1975: 64); Seamount 2 cruise, sta. 209, Irving Bank, 460 m: H 26.3, D 15.0 mm; GNS WM 14604, MD32 Réunion sta. DR47, off Réunion Island, Indian Ocean: H 21.0, D 12.1 mm; TU 1239, latest Pliocene-Pleistocene, Limón, Costa Rica: H 31.5 mm, D 16.5 mm (Robinson, 1991: 313); TU 1240, latest Pliocene-Pleistocene, Limón, Costa Rica: H 22.5, D 13.5 mm.

Types.—*Gyrineum louisae*, holotype in B. P. Bishop Museum, Honolulu, Hawaii; from 330 m, off Pokai Bay, Oahu, Hawaii. *Gyrineum atlanticum*, holotype in Zoologischen Staatssammlung München, no. M9c/33 (not seen); from Great Meteor Bank, central Atlantic, in 314-323 m.

Other material examined.—**Recent: Indo-West Pacific:** I recorded (Beu, 1998b) the following Indo-West Pacific material, listed here with new records in MNHN: **Norfolk Ridge, New Caledonia:** Smib 8 cruise sta. DW159 (MNHN, 1); sta. DW163 (MNHN, 1); Beryx 2 cruise sta. DW40 (MNHN, 1, illustrated; Pl. 24, Figs 9-10); Banc Kaimon Maru, Lithist cruise sta. DW12, 235-280 m, 24°45.7'S, 168°08.1'E (MNHN, 1); **Marquesas Islands, French Polynesia:** *M/V Pele* sta. FH-1, 80-81 m, off Baie Hanavave, western coast of Fatu Hiva (USNM 7986290, 1); Musorstom 9 cruise sta. DW1146, 200 m, 9°19'S, 140°06'W (MNHN, 1), sta. DR1182, 90-120 m, 8°45.6'S, 140°03.9'W (MNHN, 2), sta. DW1208, 117 m, 9°48.9'S, 139°09.5'W (MNHN, 1), sta. DR1223, 90-150 m, 9°44.5'S, 138°51.3'W (MNHN, 1); **Réunion Island, Indian Ocean:** MD32, Réunion sta. DR47, 205-215 m (MNHN, 2; GNS WM14604, 1). **Atlantic Ocean: Central and E Atlantic seamounts:** material taken during *N/O Le Suroit* cruise Seamount 2, all at MNHN (listed by Gofas & Beu, 2002): **Meteor Bank:** sta. CP138, 38°01.90'N, 28°29.0'W, 300 m (1); **Hyères Bank:** sta. DW188, 31°30.0'N, 28°59.5'W, 310 m (2); sta. DW190, 31°29.0'N, 29°00.0'W, 750 m (1); **Irving Bank:** sta. 205, 32°01.10'N, 27°57.20'W, 348 m (1); sta. 209, 31°59.20'N, 27°55.90'W, 460 m (1); **Atlantis Bank:** sta. DW274, 34°05.10'N, 30°13.60'W, 280 m (1).

Fossils: Atlantic Costa Rica: Latest Pliocene-Early Pleistocene: Moín: TU 1239 (1, USNM 416234, specimen

illustrated by Robinson, 1990: figs 1a-c; and 2 incomplete terminal varices); 1240 = NMB 19008 (NMB H 17923, 1, illustrated; Pl. 24, Figs 4, 7-8).

Distribution.—Recent specimens were reported by me (Beu, 1998b) from Réunion Island, Indian Ocean, from the Marquesas Islands (where it seems to occur in much shallower water than elsewhere) and from off of southern New Caledonia in the Pacific, and from several seamounts in the central and eastern Atlantic. With the type material, from Hawaii and from Meteor Bank in the Atlantic, and with the Seamount 2 cruise material reported here and by Gofas and me (2002), this indicates that *Halgyrineum louisae* probably occurs uncommonly, mostly below 200 m, on hard substrata throughout the warm-water Indo-West Pacific and Atlantic provinces. Fossils are reported so far only from the latest Pliocene-Early Pleistocene Moín Fm at Limón, Costa Rica.

Genus *PRIENE* H. & A. Adams, 1858

Argobuccinum H. & A. Adams, 1853: 104 (junior homonym of *Argobuccinum* Hermannsen, 1846).

Priene H. & A. Adams, 1858: 654. Type species (by subsequent designation, Cossmann, 1903: 109): *Triton scaber* King, 1832, Pliocene to Recent, Chile.

Liobindsia Coen, 1947: 85. Type species (by monotypy): *Liobindsia dimidiata* Coen, 1947 (= *Triton scaber* King, 1832).

Remarks.—J. T. Smith (1970: 513) pointed out the divergence of opinion over the years about the relationships of *Priene*. Some authors have considered that its shell shape, with a very short anterior canal, strongly convex whorls, and very low, wide, obscure varices, indicate that it is closely related to *Argobuccinum*, whereas others have felt that its long-bristled periostracum and its external sculpture, with cancellate spiral cords and axial ridges, indicate that it is more closely related to *Fusitriton*. I agree with Smith in regarding it as a genus distinct from both of these similar genera. *Priene* is one of few ranelline genera that do *not* have a long fossil record in western North America (*i.e.*, the paleo-northern Pacific Ocean) and its origins are unclear. However, it bears considerable similarity to some early Cenozoic fossils in western North America, particularly “*Ranella*” *californica* Gabb, 1869 (J. T. Smith, 1970: pl. 49, figs 1-2). This suggests that, like most or all other Ranellinae, *Priene* probably had its origins in the paleo-northern Pacific Ocean.

Bouchet & Warén (1986: 492, fig. 110) illustrated the holotype of *Liobindsia dimidiata* Coen, 1947, and pointed out that it is a synonym of *Priene scabrum*.

Priene scabrum (King, 1832).

Pl. 24, Figs 5-6; Pl. 25, Figs 2-3, 5-6; Pl. 51, Figs 6, 8

Triton scaber King, 1832: 348; d'Orbigny, 1841b: 450, pl. 62, fig. 13; Reeve, 1844a: pl. 11, fig. 14.

Triton rudis Broderip, 1833: 6; Reeve, 1844a: pl. 14, fig. 53.

Polia scabra. Gray, 1839: 111, pl. 36, fig. 16.

Ranella scabra. Kiener, 1841: 30, pl. 15, figs 1-1a, 2; Hupé, 1854: 185.

Tritonium (Argobuccinum) scaber. H. & A. Adams, 1853: 104; Chenu, 1859: 154, fig. 705.

Tritonium (Argobuccinum) rude. H. & A. Adams, 1853: 104; Chenu, 1859: 154, fig. 704.

Tritonium (Priene) scaber. H. & A. Adams, 1858: 654.

Tritonium (Priene) rude. H. & A. Adams, 1858: 654.

Argobuccinum scabrum. Tapparone-Canefri, 1876a: 118; Dall, 1909b: 226.

Triton (Priene) rudis. Tryon, 1880: 34, pl. 16, fig. 169.

Priene scaber. Cossmann, 1903: 109.

Argobuccinum rude. Dall, 1909b: 226.

Liobindsia dimidiata Coen, 1947: 85; Bouchet & Warén, 1986: 492, fig. 110.

Argobuccinum (Priene) scaber. Carcelles & Williamson, 1951: 285.

Argobuccinum (Priene) rude. Carcelles, 1954: 246, fig. 9.

Argobuccinum (Argobuccinum) scabrum. Carcelles, 1954: 247, figs 7-8.

Argobuccinum (Priene) scabrum. Dell, 1963: 225, pl. 1, fig. 7; Beu, 1985: 56; Kilias, 1973: 51, fig. 43; Henning & Hemmen, 1993: 17, pl. 1, fig. 6; Piech, 1995: 6.

Argobuccinum (Priene) rude. Dell, 1963: 226, pl. 1, fig. 6; Kilias, 1973: 50, fig. 42; Henning & Hemmen, 1993: 18, pl. 1, fig. 7.

Priene scabra. J. T. Smith, 1970: 512, pl. 43, figs 2-4, 7-11; Ramírez, 1987: 156, figs 184-185.

Priene rude. J. T. Smith, 1970: 517, pl. 43, figs 1, 5-6; Guzmán *et al.*, 1998: 45, illus.

Priene scabrum. Guzmán *et al.*, 1998: 45, illus.; Romero *et al.*, 2003: 57, figs 4A-E (eggs and veligers).

Remarks.—*Priene scabrum* is easily recognized by (a) its short shell with strongly inflated whorls, (b) its very short, wide siphonal canal, (c) its low, wide varices, (d) the varices each being situated slightly in front of that on the whorl above rather than strictly aligned down the opposing sides of the spire, (e) its relatively large, almost circular aperture with a row of large, rounded nodules inside the outer lip, and (f) its sculpture of either cancellate spiral cords and narrow, closely spaced axial costae, or more prominent, wide axial costae crossed by relatively weak spiral threads.

Most authors during this and the 20th century have accepted that two species of *Priene* live in Chile at present: the relatively weakly sculptured, cancellate *Priene scabrum* and the more coarsely sculptured, dominantly axially costate *P. rude*. However, J. T. Smith (1970: pl. 43, figs 3-4) illustrated Pliocene fossils from Coquimbo, Chile, in which the sculpture changes down the shell from that of the *scabrum* form

to that of the *rude* form, and a Pleistocene specimen from Herradura, Caldera, Chile, collected by Prof. D. Herm (GNS WM9624; see below) changes from the *rude* to the *scabrum* form down the shell. Henning & Hemmen (1993: 18) referred to Smith's illustrations, and noted that "if living intergrades still exist, *rude* has to be treated as a variety of *scabrum*." Such intergrades are not common in the living fauna, but two specimens in the LACM collection are illustrated here to show that intergrades do occur. The illustrated specimens demonstrate both possibilities, a specimen that commences with the *scabrum* sculpture and later develops into the *rude* form (Pl. 25, Figs 2-3) and a specimen that commences with the *rude* sculpture and later develops into the *scabrum* form (Pl. 25, Figs 5-6). This combination of sculptural possibilities seems to rule out the specimens being hybrids between two distinct species, particularly because genuine hybrids between marine molluscan species are exceedingly rare (but see several putative *Cypraea* and strombid hybrids illustrated by Poppe and by Kronenberg in Poppe, 2008: pls 149, 209-213, 217). This is therefore accepted as one species, apparently consisting of a strongly dimorphic population in which at least 98% of specimens falls into one or the other of the two sculptural morphs. Anecdotally, most Chilean malacologists and ecologists in recent years have accepted that this is one variable species. The genetics of this unusual species would be interesting to investigate.

J. T. Smith (1970: 513) stated that "*Priene* is named for an ancient Greek city whose Latin derivative is feminine," and so used the feminine "*scabra*" ending for the specific epithet rather than the expected neuter "*scabrum*." However, she then used the neuter "*rude*" form for the other species she recognized in the genus. I follow Latin grammar and almost all other authors during the 20th century and decline the species name to agree with the neuter generic name.

Dimensions.—LACM 72-208, intertidal, Caleta Leandro, Tumbes, Concepción Province, Chile, leg. University of Concepción, 23 November 1972: H 71.5, D 44.8 mm (largest seen); BMNH syntypes of *Triton scaber*: H 62.1, D 40.0 mm, smallest H 20.0, D 12.6 mm; BMNH syntypes of *T. rudis*: H 50.6, D 31.9 mm, H 47.8, D 30.1 mm, H 42.7, D 27.7 mm.

Types.—*Triton scaber*, 7 possible syntypes BMNH unreg., 4 from Broderip's collection, 3 possibly syntypes from P. P. King, said by King (1832: 348) to be from Valparaíso, Chile, "brought up on an anchor," ex Cuming collection. *Triton rudis*, 3 syntypes, BMNH 1968525, from "Iquique, Peru," the smallest apparently that illustrated by Reeve (1844a: pl. 14, fig. 53), from Iquique, northern Chile, ex Cuming collection (Iquique was formerly in southern Peru); 2 lots at SMF represent further syntypes of this species, because they are both from the collection of Hugh Cuming. Two specimens of the *T.*

rudis form from "Peru" were exchanged with Hugh Cuming for Red Sea material by Eduard Rüppell in 1841 or 1845 (R. Janssen, SMF, pers. comm., 18 March 2007), and are labelled "syntypes" of *T. rudis* (SMF 306410/1-2). Three other specimens from "Valparaíso" also were received by Rüppell under the name *T. scaber* in exchange from Cuming in 1841 or 1845 (SMF 306411/1-3). Although there is no definite proof that these specimens were seen by King or Broderip, they all seem likely to be syntypes, because Cuming collected in Chile and Peru, and lived for several years in Valparaíso (where *Priene scabrum* is common on the beach; pers. obs.). *Liohindsia dimidiata* Coen, 1947, holotype in Hebrew University of Jerusalem, a specimen of *Priene scabrum* without locality (Bouchet & Warén, 1986: 492, fig. 110); not seen.

Other material examined.—**Recent: Peru and Chile:** 47 lots examined at LACM; northernmost: off Lorenzo Island, near Callao, Peru, 12°05'52"S, 77°12'45"W (LACM-AHF 364-35, 2, collected alive); southernmost: intertidal, Lirquen, Bahia Concepción, Chile, 36°41'S, 72°58'W (LACM 72-207, 1). **Easter Island:** Isla de Pascua, coll. P. L. Strube, March 1922 (MACN 13090, 1); this locality seems unlikely and needs confirmation, because the species has not been reported from Easter Island previously.

Fossils: Peru: Pleistocene: raised beach, Isla Veja, Bahia Independencia, 14°16'S, 72°12'W (BMNH Palaeontology Department, G 36249-36252, 4 specimens). **Chile: Pliocene:** SGO.PI, from Coquimbo, Carretera Panamericana, 4 m above beach (4); horizon Serena 1, S Playa Chorrillo, Caldera, coll. D. Herm (GNS WM9263, 1, *rude* form). **Pleistocene:** Herradura, Caldera, coll. D. Herm (GNS WM9624, 1; changes from *rude* form to *scabrum* form on last intervartical interval); Herradura Bay, Coquimbo, Dr. Coppinger, *HMS Alert* (BMNH Palaeontology Department, G 89, 4).

J. T. Smith (1970) also reported specimens from Coquimbo, north of Valparaíso (Pliocene), as Pleistocene fossils in uplifted terrace cover beds (Tongoy Fm) at Coquimbo and La Serena, and in uplifted terrace cover beds at heights between ca. 12 and 800 m, inland from Bahia San Nicolas, ca. 400 km southeast of Lima, Peru. DeVries (1988: 129) also reported specimens from basal shell ledges of the Golf Course Member of Taime Fm (Late Pliocene) at Bahia Taime, northwestern Peru.

Distribution.—Recent specimens of *Priene scabrum* were recorded by J. T. Smith (1970) as ranging from Chimbote, central Peru, south to Puerto Montt, just north of Isla Chiloe in the northern part of southern Chile, and south to Isla Mocha (38°24'51"S; Aldea & Valdovinos, 2005). Earlier records from as far south as the Straits of Magellan are not substantiated by modern collections. *Priene scabrum* has only a relatively narrow zone of overlap with *Argobuccinum pus-tulosum*, which Aldea & Valdovinos (2005) recorded as far

north as Isla Santa Maria (37°00'12"S). The record (here) of *P. scabrum* from Easter Island needs confirmation before it can be accepted. Fossils are recorded from Pliocene rocks at Coquimbo and Caldera, Chile, and at Bahia Taime, Peru, and are widespread in Pleistocene terrace deposits from central Chile north to northern Peru.

Genus **RANELLA** Lamarck. 1816

Ranella Lamarck, 1816: explanation to pls 412-414. Type species (by subsequent designation, Children, 1823): *Ranella gigantea* Lamarck, 1816 (= *Murex olearium* Linnaeus, 1758), Eocene to Recent, Europe-Mediterranean; Recent, eastern and western Atlantic, South Africa, Indian Ocean islands, Tonga-New Caledonia, and New Zealand.

Gyrina Schumacher, 1817: 77, 253. Type species (by monotypy): *Gyrina maculata* Schumacher, 1817 (= *Murex olearium* Linnaeus, 1758).

Eugyrina Dall, 1904: 132. Type species (by original designation): *Ranella gigantea* Lamarck, 1816 (= *Murex olearium* Linnaeus, 1758).

Mayena Iredale, 1917: 324. Type species (by original designation): *Biplex australasia* Perry, 1811, Late Miocene-Recent, New Zealand and southern Australia.

Gyrinopsis Dall, 1925: 18. Type species (by monotypy): *Gyrinopsis cowlitzii* Dall (1925: 18, pl. 18, figs 4, 6; "Eocene of Washington, near the Cowlitz River ..., USNM catalogue no. 333539") (= *Ranella washingtoniana* Weaver, 1912), Eocene, western USA (junior homonym of *Gyrinopsis* Handlirsch, 1906, Coleoptera).

Remarks.—*Ranella* is a distinctive, world-wide genus of Ranellinae, of rather low diversity, but nevertheless a little more diverse than any other ranelline genus. It is recognizable by (a) its elongate shape and tall spire and, in most species, its long, narrow, and rather straight anterior siphonal canal, (b) its prominent varices each slightly offset from those of the preceding whorl down the opposing sides of the spire, (c) its rather subdued sculpture other than a peripheral row of nodules at the shoulder angle (some species have two or three lower rows of nodules), (d) its distinctive, flat-faced varices with, in most species, the outer lip (*i.e.*, the apertural face of the terminal varix) turned sharply outward at right angles to the interior surface of the shell, forming a varix of almost square cross-section, (e) its weakly armoured aperture other than a row of small to large nodules along the inner edge of the outer lip, and (f) its large, tall, smooth, multiwhorled protoconch.

Species of which I am aware that are referable to *Ranella* are:

- *australasia* (Perry, 1811), Late Miocene-Recent, New Zealand and southern Australia.
- *chilena* n. sp., Oligocene-Early Miocene fossil reworked into Late Miocene rocks, Navidad, Chile.

- *eogassinense* (Sacco, 1904), Bartonian (Late Eocene), Gassina, Italy (probably = *R. olearium*).
- *gemmifera* (Euthyme, 1889), Recent, western Atlantic, South Africa, and St. Paul and Amsterdam islands, southern Indian Ocean.
- *intercostalis* (Tate, 1888), Middle Miocene, Victoria, Australia.
- *kaiparaensis* (Finlay, 1924), Early Miocene, New Zealand.
- *katherineae* Squires, 1983, early Middle Eocene, California.
- *louellae* Beu, 1988, Paleocene, California.
- *olearium* (Linnaeus, 1758), Eocene-Recent, Europe-Mediterranean; Recent, eastern and western Atlantic, South Africa, Indian Ocean islands, New Caledonia-Tonga, and New Zealand.
- *tuomeyi* (Aldrich, 1886), Early Eocene, Alabama, USA (Beu 1988b: 77, pl. 2, figs 4-6).
- *washingtoniana* Weaver, 1912, Late Eocene, western USA.
- *yasumurai* Amano, 1997, Pliocene, Japan.
- n. sp. A, Late Miocene-Late Pliocene, New Zealand and southern Australia.
- n. sp. B, Early Miocene, New Zealand.
- n. sp. C, Early Miocene, New Zealand.
- n. sp. D, Middle Eocene, New Zealand.
- n. sp. E, Eocene, Gan, near Pau, southern France (collection of Cyrille Dolin, Bouillancy, France).
- n. sp. F, Miocene(?), Isla Mocha, Chile, in collection of Sven Nielsen (pers. comm., March 2009).

***Ranella chilena* n. sp.**

Pl. 26, Figs 1-4, 6-8

Ranella sp. nov. Nielsen, 2003: 93, pl. 17, figs 1-2.

Description.—Shell of moderate size for genus (to 88 mm H), short and wide for genus, with moderately tall, stepped spire, moderately short siphonal canal twisted strongly to left and toward dorsum, and wide, moderately sloping, flat to slightly concave sutural ramp. Varices prominent, wide, of almost square section with flat apertural face at right angles to whorl surface and strongly convex abapertural face, strictly aligned down opposing sides of spire on earliest 2-3 whorls, then offset from whorl to whorl, offset increasing gradually down spire to reach *ca.* 10° on last whorl. Spiral sculpture of 4 and a weak fifth primary cords on last whorl, forming elevated ridges on varices but scarcely raised above their neighbors on whorl surface, with 4 to 7 narrow, widely spaced secondary cords only slightly narrower than main cords in each spiral interspace and many more on sutural ramp and canal; all secondary interspaces filled with many fine spiral threads. Initial 1-2 teleoconch whorls with prominent cancellate sculpture of three raised spiral cords crossing narrow, closely spaced axial

costae, 10 costae per intervariceal interval; spiral cord on sutural ramp weakening rapidly down shell, axial costae becoming fewer and larger. On later spire whorls, low axial costae commence at shoulder and descend to lower suture, forming prominent, narrowly rounded nodules of triangular section on shoulder angle and next lower main spiral cord; five costae in each intervariceal interval of all material examined; on last whorl, nodules mainly restricted to shoulder angle, with only small nodules on lower cord; weak nodules on third and fourth spiral cords over later half of each intervariceal interval of some specimens. Weak growth lines forming the only other axial sculpture. Aperture nearly circular; outer lip reflected over adapertural face of terminal varix, with 16-17 low, rounded nodules along sharp angle at inner edge of varix, positioned in 7 slightly elevated groups each of 2-3 nodules, with weak radial furrows extending across outer variceal face from spaces between nodule groups; inner lip with very large, prominent parietal ridge, remainder strongly thickened over neck, smooth over upper third of height, lower two thirds bearing many transverse ridges, low and faint across central columellar area, strengthening downward (anteriorly) to form three prominent ridges on base of columella and 3-4 smaller ones decreasing in prominence down upper part of canal. Protoconch large (ca. 4 mm H), tall and narrowly turbiniform, of ca. 4 whorls; apex missing in all material examined, remainder smooth and polished.

Dimensions.—Holotype: H 87.7, D 60.0 mm. None of the other specimens is complete; largest paratype, at Purdue University: H 36.2, D 25.9 mm.

Types.—Holotype SGO.PI 3706, from Navidad Fm (Oligocene-Early Miocene mollusks in a Late Miocene-Pliocene matrix; Finger *et al.*, 2007), coastal cliff and wave-cut platform in front of Matanzas village, 4 km SW of Navidad, SW of Santiago, central Chile, collected by V. Covacevich and D. Frassinetti; with 3 paratypes from the same locality, 2 fairly large but incomplete (SGO.PI 37097, SGO.PI 5837) and 1 small with well preserved (if slightly incomplete) protoconch and sculpture (SGO.PI 5838; Pl. 26, Figs 4, 7-8); 1 paratype (Pl. 26, Fig. 6) from the same locality formerly at Department of Earth and Atmospheric Sciences, Purdue University, Indiana, USA, collected by W. J. Zinsmeister (his loc. 254, now at PRI); 1 paratype from the type locality (SMF 333437) collected by S. N. Nielsen.

Remarks.—*Ranella chilena* n. sp. has been seen only from the type locality, where it is far from common. It is a very typical species of *Ranella* (*sensu stricto*) in having its varices slightly offset from whorl to whorl rather than strictly aligned, in having varices of almost square section, in having sculpture dominated by the row of pointed nodules around the shoulder angle, with one to three weaker rows of nodules below, and in having a row of low nodules on the sharp angle form-

ing the inner edge of the outer lip. The smallest paratype in the same lot as the holotype is a very well-preserved juvenile specimen with a nearly complete protoconch (Pl. 26, Figs 4, 7-8), showing that it is the typical large, moderately tall, smooth protoconch present on all *Ranella* species.

Ranella chilena n. sp. is similar in overall appearance to *R. olearium*, type species of *Ranella*, but differs in its much shorter and wider shape than that of *R. olearium*. It is most similar to *R. kaiparaensis* (Finlay, 1924) from the Early Miocene rocks of Pakaurangi Point, Kaipara Harbour, northern New Zealand. The shape and appearance of *R. chilena* n. sp. are similar to those of *R. kaiparaensis*, but the two known specimens of *R. kaiparaensis* are a little taller and narrower and have more prominent nodules, both at the shoulder angle and below it, than in *R. chilena* n. sp. An unnamed species represented by a single specimen from Hokianga Harbour south head, northern New Zealand, is similar to both *R. kaiparaensis* and *R. chilena* n. sp. in shape, but has much more prominent nodules than on either similar species, with three prominent rows of nodules on the last whorl. Most other species of *Ranella* are more nearly similar to *R. australasia* than to *R. chilena* n. sp., and have varices of more rounded section, a more steeply sloping sutural ramp with less prominent nodules around the periphery, and larger nodules inside the outer lip than in *R. chilena*.

Encinas *et al.* (2006) and Finger *et al.* (2007) have demonstrated that the well-known central Chilean "Miocene" localities from Navidad to Chiloé Island, collected by Darwin as well as many more recent students, consist of Oligocene-Early Miocene mollusks, similar to those of Peru [and, it might be added, a few such as *Sassia armata* (Hupé, 1854) in common with Oligocene-Early Miocene rocks in Argentinean Patagonia] displaced into Late Miocene-Early Pliocene rocks. Encinas *et al.* (2006) proposed a new scheme of formational subdivisions of these rocks, but Sven Nielsen (Institut für Geowissenschaften, Christian-Albrechts-Universität Kiel; pers. comm., 2007) informs me that all the tonnoideans recorded in the present work are from Navidad Fm. The mollusks, including *Ranella chilena* n. sp., *Crassicymatium crassicornatum* n. gen., n. sp., *Ameranella verrulosa* (G. B. Sowerby I, 1846), *Sassia armata*, and *Distorsio ringens*, are all here assumed to be Oligocene-Early Miocene in age, displaced into Navidad Fm, of probable Late Miocene age.

Distribution.—*Ranella chilena* n. sp. is recorded only from Navidad Fm (Oligocene-Early Miocene fossils displaced into Late Miocene rocks) at the type locality, Matanzas, near Navidad, southeast of Santiago in central Chile. This is the only record of *Ranella* from the eastern Pacific.

Etymology.—The specific name reflects the species' occurrence in Chile, the first record of the genus there.

Ranella gemmifera (Euthyme, 1889)

Pl. 25, Figs 7-9, 11

- Ranella leucostoma*, var.(?). G. B. Sowerby III, 1886: 8; 1892: 9.
 ?*Triton leucostoma* var. *nigromaculata* "Löbbecke" Paetel, 1888: 105 (nomen nudum).
Tritonium gemmiferum with var. *minor* Euthyme, 1889: 277, 280, pl. 7, fig. 1 (as "*gemmiferum*" in fig. caption).
Ranella leucostoma var. *poecilostoma* von Martens, 1904: 53.
Septa leucostoma. E. A. Smith, 1906: 41.
Charonia poecilostoma. E. A. Smith, 1915: 285.
Eugyrina gemmifera lepta Bartsch, 1915: 93, pl. 8, figs 1, 4.
Argobuccinum (Eugyrina) gemmifera. Barnard, 1963: 23, figs 2c, 3b.
Argobuccinum ranelliforme proditor. Arnaud & Beurois, 1972: pl. 1, figs 3a-b only (in part not *Buccinum pustulosum* Lightfoot, 1786).
Argobuccinum (Mayena) australasium gemmiferum. Kiliyas, 1973: 46, fig. 40; 1981: 700.
Argobuccinum gemmiferum. Finlay & Vink, 1982: 132, figs 1-6.
Ranella australasia gemmifera. Kilburn & Rippey, 1982: 75, pl. 17, fig. 11; Kilburn, 1984: 8, pl. A, figs d-e; Beu, 1985: 57; Henning & Hemmen, 1993: 35, pl. 5, fig. 2; Rios, 1985: 80, pl. 29, fig. 352; 1994: 87, fig. 337; Piech, 1995: 5.

Remarks.—Until Finlay & Vink (1982) recorded *Ranella gemmifera* from the western Atlantic (Cuba to Brazil) it had not appeared in the faunal syntheses of the region (Clench & Turner, 1957; Abbott, 1974) and so it was surprising to see it recorded for the first time. Now it is clear than any ranellid or bursid (as well as some members of most of the other tonnoidean families) that occurs in South Africa or, in many cases, in West Africa, can be expected to occur in small numbers in the fauna of the tropical western Atlantic, and of Brazil in particular. Recent years have seen a number of previously unrecorded species recognized in the western Atlantic: *Monoplex trigonus* (Gmelin, 1791) (J., W. & F. Gibson-Smith, 1970), *Charonia lampas* (Linnaeus, 1758) (Rios & Tostes, 1981), *Reticutriton pfeifferianus* (Reeve, 1844) (Oliveira & Trinchão, 1993), and *Monoplex mundus* (Gould, 1850), *M. vespaceus* (Lamarck, 1822), and *Ranularia gallinago* (Reeve, 1844) (Piech, 1993). Marcus Coltro (São Paulo, Brazil) has also informed me of reliable records of living specimens of *Charonia tritonis* and *Lotoria lotoria* (Linnaeus, 1758) in Brazil.

Ranella gemmifera is a relatively small, thick-shelled, rather coarsely sculptured species of *Ranella*, with a short, straight anterior canal, a strongly contracted base, and a flared, strongly ridged outer lip. It is very similar to the common shallow-water *Ranella* species of New Zealand and southern Australia, *Ranella australasia*. The similarity is so close that I previously have ranked these two forms as geographical subspecies of one species (Beu, 1985). However, specimens from Australia and New Zealand all have a plain white aperture, whereas specimens from the western Atlantic and South Africa all have

prominent, wide black bars between the white ridges inside the outer lip, blending in some specimens to produce an almost completely black outer lip. Other, less obvious, consistent differences also can be found, such as the generally more nodulose sculpture, the much greater preponderance of axially ribbed specimens, and the more flared outer lip, especially toward the anterior (abapical) part of the lip, of the Atlantic-South African form. The apertural color difference is dramatic and obvious, and suggests that they should be ranked as separate species, as was also concluded by E. A. Smith (1915), who separated them under the names *Charonia australasiana* (sic) (Perry, 1811) and *C. poecilostoma* (von Martens, 1904). As with many other such slight differences, these forms require molecular investigation before it is clear whether they are really species or geographical subspecies. Numerous Brazilian specimens are illustrated excellently in color on a webpage (<http://www.femorale.com.br/shellphotos>, last accessed 28 April 2006).

Several authors in recent years have used the spelling "*gemmifera*." The original spelling of the species name in the text by Euthyme (1889) was *gemmiferum*, although he spelled the name "*gemmiferum*" on the bottom of the plate and in the plate caption. There seems little doubt that the intended spelling was *gemmiferum* ("bearing gemmae"), the alternative being a typographical error by the lithographer, copied in the caption. The spelling "*gemmifera*" is adopted here formally as the name for this species by my first reviser's action, and should be used in future.

Dimensions.—Figured syntype of *Tritonium gemmiferum*, H 94.0, D 58.2 mm; unfigured syntype, H 42.9, D 26.9 mm; holotype of *Eugyrina gemmifera* var. *lepta*, H 83.5, D 46.0 mm; Durban, South Africa, NMP 195: H 108.9, D 57.2 mm; Jeffreys Bay, South Africa, NMP 5288: H 100.1, D 62.0 mm; False Bay, Capetown, NMP 4666: H 100.5, D 57.0 mm; GNS WM17269, 35-40 m, off Cabo Frio Island, Arrial do Cabo, Rio de Janeiro State, Brazil: H 106.4, D 59.6 mm; H 96.1, D 54.0 mm.

Types.—*Tritonium gemmiferum*, 2 syntypes in MNHN, from "Port Elizabeth"; donated by Université Catholique de Lyon. The illustrated syntype is much the larger of the two (H 94.0 mm) and is here designated the lectotype of *T. gemmiferum*. *Ranella leucostoma* var. *poecilostoma*, type material presumably in Humboldt University Zoological Museum, Berlin (not seen). *Eugyrina gemmifera* var. *lepta*, holotype USNM 227777, from Port Alfred, South Africa, collected by Turton.

Other material examined.—**Recent: South Africa:** 98 lots examined at NMP and 17 lots at GNS, ranging from False Bay, Capetown (dived in 15 m, NMP 4666, 1 large live-collected) to 110-150 m, off of Quissico, southern Mozambique (NMP L.4761, 1). **Brazil:** local fishermen's nets, 200 m, off of

Cabo Frio, Rio de Janeiro State (GNS WM17261, 1); scuba, 35-40 m, off Cabo Frio Island, Arrial do Cabo, Rio de Janeiro State (GNS WM17269, 2). **St. Paul and Amsterdam Islands**, southern Indian Ocean: Although *Ranella gemmifera* has not been recorded from St. Paul and Amsterdam Islands previously, one of the specimens from St. Paul and Amsterdam illustrated as "*Argobuccinum ranelliforme proditor*" by Arnaud & Beurois (1972: pl. 1, figs 3a-b) clearly is a specimen of *R. gemmifera*, and one specimen of *R. gemmifera* is present in a sample of four specimens of *Argobuccinum pustulosum* from St. Paul and Amsterdam Islands pres. P. M. Arnaud (lobster traps, 40 m, Île Amsterdam; GNS WM13712, 1).

Distribution.—In the western Atlantic, *Ranella gemmifera* has been reported only from Varadero Beach, near Matanzas, Cuba, and from Cabo Frio, Ilha dos Papagaios, Rio de Janeiro State, southern Brazil (Finlay & Vink, 1982; Rios, 1985, 1994). Further specimens are reported here from off of Cabo Frio, from where they are regularly offered for sale. In South Africa, it lives commonly from False Bay, Cape of Good Hope, to Durban, Natal (Kilburn & Rippey, 1982: 76) and to southern Mozambique (material examined at NMP). Specimens are also recorded here from St. Paul and Amsterdam islands, southern Indian Ocean. Presumably specimens occur sparsely as pseudopopulations throughout the western Atlantic from Cuba to southern Brazil, as a result of larval transport from South Africa. I am not aware of any fossil record.

***Ranella olearium* (Linnaeus, 1758)**

Pl. 26, Fig. 5; Pl. 27, Figs 1, 3, 5; Pl. 28, Figs 1, 3, 7

Murex olearium Linnaeus, 1758: 748; 1767: 1218; Gmelin, 1791: 3535.

Murex reticularis Born, 1780: 300, pl. 11, fig. 5; von Salis Marschlins, 1793: 371; Brocchi, 1814: 402 (not *Murex reticularis* Linnaeus, 1758).

Ranella gigantea Lamarck, 1816: pl. 413, fig. 1, "Liste des objets": 4; 1822: 150; Potiez & Michaud, 1838: 426; Grateloup, 1840: pl. 29, fig. 8; Kiener, 1841: 25, pl. 1, fig. 1; Deshayes, 1843: 540; Reeve, 1844b: pl. 1, fig. 3; Weinkauff, 1868: 70; Küster & Kobelt, 1870: 128, pl. 40, fig. 1; D'Ancona, 1872: 59, pl. 8, figs 1-2; Bellardi, 1873: 241; Aradas & Benoit, 1876: 273; Fontannes, 1879-1882: 37, pl. 4, fig. 3; Bucquoy *et al.*, 1883: 28, pl. 3, fig. 1; Hoernes & Auinger, 1884: 188, pl. 23, figs 1-5; Cossmann, 1903: 111, pl. 4, fig. 21.

Gyrina maculata Schumacher, 1817: 253.

Ranella reticularis. Borson, 1821: 60; Philippi, 1844: 183; Petit de la Saussaye, 1852c: 193; Hörnes, 1856: 211, pl. 21, figs 1-2 (not *Murex reticularis* Linnaeus, 1758).

Ranella incerta Michelotti, 1847: 256, pl. 10, fig. 4.

Ranella bronni Michelotti, 1847: 258.

Ranella gigantea var. *turritoreticularis* Mylius, 1891: 7; Sacco, 1904: 39, pl. 10, fig. 28; Noszky, 1940: 23.

Ranella (Argobuccinum) gigantea. Tryon, 1880: 42, pl. 24, fig. 69.

Apollon giganteus. Kobelt, 1883: 11, pl. 32, figs 1-3 (as *Apollon* in

caption).

Ranella reticularis with vars. *borniana*, *bicanalata*, *altavillensis*, *frigida*, *mediterranea*, *parvivaricosa* and *meneghinii* Gregorio, 1884: 109-111.

Ranella gigantea var. *atlantica* Monterosato, 1890: 164; Dautzenberg & Fischer, 1906: 34.

Eugyrina gigantea. Dall, 1904: 132; Cooke, 1916a: 3.

Triton (an Eutritonium) eogassinense Sacco, 1904: 36, pl. 10, fig. 12.

Ranella gigantea and var. *pertuberculifera* Sacco, 1904: 39, pl. 10, figs 26-27, 29.

Mayena multinodosa Bucknill, 1927: 312, pl. 35, fig. 2.

Fusitriton multinodosa. Finlay, 1930: 249.

Ranella (Apollon) gigantea. Coulon, 1933: 139.

Ranella ostenfeldi Iredale, 1937: 104, pl. 17, fig. 1.

Ranella (Apollon) gigantea with vars. *rarinodosa* and *budensis* Noszky, 1940: 23-24, pl. 1, fig. 30.

Argobuccinum giganteum with vars. *oceanica*, *curvicauda*, *magnifica*, *tenuis*, *intusdentata*, *nodosecarinata* and *dilatata* Coen, 1941: 174.

Gyrina gigantea. Dance, 1959: 351, pl. 9, figs 1-2; Dance & Dell, 1960: 418; Barnard, 1963: 155.

Ranella olearium. Dell & Dance, 1963: 159, pls 16-17; Arnaud & Beurois, 1972: 873, pl. 1, figs 5a-b; Beu, 1978b: 36; Figueiras & Sicardi, 1980: 205, pl. 4, fig. 26; Finlay & Vink, 1982: 133; Cosel, 1983: 7, pl. 2, figs 1-4; Rios, 1985: 80, pl. 28, fig. 351; Smith & Heppell, 1991: 24; Diaz & Puyana, 1994: 173, fig. 645; Henning & Hemmen, 1993: 33, pl. 5, fig. 3; Scarabino, 2003: 216; Landau *et al.*, 2004: 51, pl. 3, figs 5-6.

Argobuccinum giganteum with vars. *exilis*, *nodosum*, *rarituberculata*, *duplonodosum*, *inflatum* and several unavailable polynomial names. Settepassi, 1970: Cymatiidae: i, pls 1-4 bis (with long synonymy).

Bursa barcellosi Matthews, Rios, & Coelho, 1973: 51, figs 1-5.

Argobuccinum (Ranella) olearium. Kilius, 1973: 53, fig. 44.

Ranella olearium barcellosi. Rios, 1994: 86, fig. 336.

Ranella olearia. Kilburn, 1984: 8, pl. A, fig. a; Beu, 1985: 57; Bouchet & Warén, 1993: 793, figs 1948-1949; Vega-Luz & Vega-Luz, 1995: 7; Piech, 1995: 5; de Boer, 1996: 5; Cachia *et al.*, 1996: 112, pl. 11, fig. 1; Giannuzzi-Savelli *et al.*, 1997: 266, figs 876, 877a-c; Guerreiro & Reiner, 2000: 101; Gofas & Beu, 2002: 92, figs 2A-F; Ardovalini & Cossignani, 2004: 130, bottom right fig.; Chirli, 2007: 88, pl. 32, figs 3-10 (with long synonymy).

Remarks.—*Ranella olearium* is one of the best-known mollusks of the Mediterranean-eastern Atlantic area, and during the last century, proved to be common off of South Africa, at Île Amsterdam in the southern Indian Ocean, and around New Zealand, including the Chatham Islands. It was not reported from the western Atlantic by Clench & Turner (1957), so it has been surprising to see a number of records reported in recent years from widely separated areas of the western Atlantic. Malatesta (1960: 127; 1974: 272), Priolo (1964: 521), Landau *et al.* (2004: 51) and Chirli (2007: 88) provided extensive lists of further references in the European literature. Brazilian specimens are illustrated (as *R. "olearia barcellosi"*)

excellently in color on a webpage (<http://www.femorale.com.br/shellphotos>, last accessed 28 April 2006).

Ranella olearium is obvious wherever it occurs because of its large size (up to *ca.* 240 mm H). It is much the largest species of *Ranella* reported to date, and is distinguished also by (a) its tall, narrow shape and particularly tall spire, (b) its strongly convex whorls and almost circular aperture, (c) its long, narrow, straight anterior siphonal canal (long for a tonnoidean, at least), (d) its very prominent varices of square section, slightly offset from whorl to whorl down the opposing sides of the spire, and (e) its highly variable sculpture, ranging from an almost smooth shell surface bearing subdued spiral cords, to closely covered with rows of small nodules, to bearing one or two rows of large, angular nodules around the periphery. The sculptural variation and the very wide, disjunct stratigraphical and geographical ranges have led to the proposal of a large number of synonyms, and not all of those proposed for European fossils or all of those proposed for minor varieties are listed in the synonymy here. Now that the taxonomy and range have been clarified, thanks largely to Dell & Dance (1963), *R. olearium* is seen to be another of the ranellids that, like *Charonia lampas* and *Monoplex parthenopeus* (von Salis Marschlin, 1793), has had a long history in the Europe-North Atlantic area during at least Eocene to late Neogene time, migrated through the Atlantic to South Africa and, quite late in Neogene time, has been carried around at least part of the Southern Ocean to New Zealand in the circum-Antarctic current (Beu, 1978b; Cosel, 1983). This wide, disjunct dispersal presumably results from a long-lived planktotrophic larval stage, so it is not really surprising to find that some specimens turn up in the western as well as the eastern Atlantic. However, there is no fossil record of this species in the Americas. It is perhaps surprising, though, that there are still no authentic records from Australia, despite it being moderately common in *ca.* 100-500 m off New Zealand.

The specific name *olearium* (neuter), proposed in this form by Linnaeus (1758: 748) within the genus *Murex* (otherwise treated by him as masculine), evidently was intended to be a noun (Latin, an oil storage jar), and so is indeclinable.

Dimensions.—AMNH 169202, 120 m, fish trap off of Castare, Caribbean coast of Tobago: H 144, D 69 mm; GNS WM17259, 400 m, 780 km SE of Itajaí, Santa Catarina State, Brazil: H 215.1, D 107.6 mm; H 202.1, D 99.8 mm; Norfolk Ridge, southern New Caledonia, Norfolk 2 Expedition, MNHN, sta. CP 2095, 24°46'S, 168°10'E, 283-310 m, largest seen: H 236 mm (spire apex missing), D 120 mm.

Types.—Syntype of *Murex olearium*, the specimen illustrated by Dell & Dance (1963: 161-162, pl. 16, fig. 1) in Linnaeus' collection, housed by the Linnean Society of London. Linnaeus (1758: 748) cited as illustrations Rondelet (1555: 88), Colonna (1606: pl. 53), Rumphius (1705: pl. 49,

fig. I), and Gualtieri (1742: pl. 50, fig. A). Those by Rondelet and Colonna were not available to me. The cited illustration by Rumphius (1705) shows a rather inaccurate dorsal view of *Ranella olearium* of this paper, and whereas that by Gualtieri (1742) does indeed show *R. olearium* of the present report, no material of this species is present in Gualtieri's collection, examined by me during January 2000 in the Museo di Storia Naturale e del Territorio, Università di Pisa, in the Certosa di Calci, outside Pisa. Clench & Turner (1957: 228) selected the illustration by Gualtieri (1742: pl. 50, fig. A) as the "type figure" for *Murex olearium*, in effect selecting Gualtieri's illustrated specimen as the lectotype, although this has no formal status. Wallin (1993) did not record syntypes in the Zoological Museum of Uppsala University. The specimen in Linnaeus' collection in London is therefore the only original syntype still in existence, and is here designated the lectotype of *M. olearium*. Linnaeus provided the correct locality "*in Europa australi, M. Mediterraneo.*" The type locality is here designated as Palermo, Sicily. *Ranella gigantea*, 3 syntypes in MHNG, 1098/74-76, from "Méditerranée"; the largest syntype is coarsely nodulose and matches Lamarck's (1816: pl. 413, fig. 1) figure closely in all details, and is here designated the lectotype of *R. gigantea*. *Gyrina maculata*, no type material known; the lectotype of *R. olearium* is here designated the neotype of *G. maculata*. *Mayena multinodosa*, holotype AIM AK70457, with 3 paratypes, from the Cavalli Islands, off of Whangaroa, northern New Zealand, in lobster traps in *ca.* 50 m, occupied by pagurids. *Ranella ostfeldi*, holotype AMS C.70727, trawled off of Greymouth, western coast of South Island, New Zealand. *Bursa barcellosi*, holotype in Museu Oceanográfico de Rio Grande do Sul, Brazil, no. MORG 17755, with 6 paratypes [MORG 17747; Laboratório de Ciências do Mar, Universidade Federal do Ceará, Fortaleza, Brazil, LABOMAR 512; Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil, Moll. no. 3647; Museu Nacional de Historia Natural de Montevideo, Uruguay, MNHN 8779; USNM 709826 (illustrated, Pl. 27, Figs 3, 7); and collection of B. N. Barcellos, Rio Grande do Sul], all dredged in 100-280 m off of Rio Grande do Sul, southern Brazil (only the USNM paratype seen). Settepassi's material is in the Museo Civico di Zoologia, Roma. I do not know the location of type material of the remaining synonyms.

Other material examined.—**Recent: W Atlantic: Bermuda:** 440 m, 4.5 km off S shore of Bermuda, A. Guest & J. R. H. Lightbourn (DMNH 96988, 2 large). **Tobago:** 120 m, off of Castare, Caribbean coast of Tobago Island, from fish trap, 1971 (AMNH 169202, 1 large); 160 m, fish trap off of Castare, Caribbean coast of Tobago, *ex* Hal Lewis collection (ANSP 339436, 1 large). **Guadeloupe:** fishermen's traps off of Guadeloupe, lesser Antilles (1, collection of D. Lamy; illustrated, Pl. 27, Fig. 3). **Colombia:** Choco sta. 620, 290-

325 m, off of Cabo de la Vela, Goajira Peninsula, Colombia (SMF 228856, 1, original of Cosel, 1983: 7, pl. 2, fig. 1; SMF 228857, 1, original of Cosel, 1983: pl. 2, fig. 2). **Brazil:** 80 m, off of Albardão, Río Grande do Sul, Brazil, *Redentor III* (SMF, 1); 70 m, off of Albardão, Río Grande do Sul, Brazil, coll. L. Barcellos (SMF, 1 large); 100 m, off of Albardão, Río Grande do Sul, Brazil (USNM 709826, 1 paratype of *Bursa barcellosi*; Pl. 28, Figs 3, 7); off of Rio Grande do Sul, southern Brazil (GNS WM17502, 1); fishermen's nets in 400 m, 780 km SE of Itajaí, Santa Catarina State, Brazil (GNS WM17259, 2).

Other western Atlantic specimens recorded to date are: lobster traps in 220-260 m, *ca.* 2 km off of Castle Roads, SE Bermuda, "several" specimens, 1 in USNM (Finlay & Vink, 1982: 133); and the southernmost record, 2 specimens in Museo Nacional de Historia Natural, Montevideo, taken alive in a gill net off of northern Uruguay, 34°49.5'-43.3'S, 52°06.5'-01.5'W, in 270-276 m (Scarabino, 2003).

Distribution.—*Ranella olearium* has been known for several centuries as a Mediterranean species, collected in deep water by fishermen throughout at least the western Mediterranean. In the eastern Atlantic, the northernmost record is that of de Boer (1996) from the beach at Ameland, a Dutch island in the Wadden Sea; de Boer (1996) suggested that it might be a late Pleistocene fossil. Previous northern records have been from off of southern Ireland (Cooke, 1916a; O'Riordan, 1972) and in the Bay of Biscay (Kiliyas, 1973); it occurs sporadically throughout the area to at least as far south as Angola (Dance, 1959: 351). Gofas and I (2002: 92, fig. 3) demonstrated that material from the Azores Islands and offshore of the eastern Atlantic banks reaches only half the adult size of the rest of the population. The only western Atlantic records of which I am aware are listed above, and indicate a sporadic and uncommon occurrence from Bermuda, throughout the Caribbean, and south to southern Brazil and northern Uruguay (Rios, 1985: 80; 1994: 86; Scarabino, 2003). These all seem likely to be pseudopopulations recruited from the eastern Atlantic. Off the coast of South Africa, it occurs abundantly from off of the Tugela River, Zululand, to Port Alfred (Kilburn & Rippey, 1982: 76; 10 lots examined at NMP). A specimen from Tristan da Cunha, southern Atlantic, is present at NMP (lobster traps in 70-180 m, NMP K.5628). A specimen from off of Lourenço Marques, southern Mozambique, is present in the Tulane University collection. It was reported from Ile Amsterdam, in the southern Indian Ocean, by Arnaud & Beurois (1972) (one specimen presented to GNS by P. M. Arnaud), and a specimen at MNHN was taken in cruise MD32/Réunion, sta. CP181, in 300-410 m, off Réunion Island, Indian Ocean. The specimen recorded by von Martens (1904: 64) as *Argobuccinum proditor* from Deutsch Tiefsee-Expedition sta. 167, 496 m, NE of Amsterdam Island, also is a juvenile shell of *R. olearium* (SMF 306407). Most surpris-

ingly, two fine adult specimens were collected during a recent MNHN expedition to Tonga (Bordau 2 cruise, sta. CP1609, "seamount," 385-405 m, 1 large empty adult; sta. CP1641, NW of Tongatapu, 395 m, 1 large empty adult). Specimens were also taken recently around southern New Caledonia, on the Norfolk Ridge, by MNHN: Norfolk 1 cruise sta. CP1708, Banc Jumeau-est, 381-384 m, 1 small dead; Norfolk 2 Expedition sta. CH2115, 1 large live-collected; sta. CP2130, 1 large live-collected; and sta. CP2095, 24°46'S, 168°10'E, 283-310 m, 1 live-collected, largest specimen seen (see dimensions above). In New Zealand, it is moderately common all around both main islands in *ca.* 300-500 m, and in relatively shallow water (80-100 m) at the Chatham Islands; a specimen was recorded from the Kermadec Islands, in the southwestern Pacific, by me (Beu, 1978b). Despite its abundance around New Zealand and occurrence as far north as New Caledonia and Tonga, there are still no authentic records from Australia. Fossils are known from Oligocene to Pliocene rocks around the Mediterranean and in southern Europe, but none are known throughout the rest of its range, *i.e.*, its present wide range evidently has been achieved recently. The specimen illustrated by Sacco (1904: 36, pl. 10, fig. 12) as *Triton eogassinense*, from the Bartonian (Late Eocene) of Gassino, Italy, is another synonym based on a rather distorted Eocene specimen of *R. olearium*, which (like several of the other very wide-ranging tonnoideans, most notably *Charonia lampas*) then has an Eocene to Recent time range. I am not aware of fossils from the tropical American study area.

Genus *AMERANELLA* Beu, 1988

Ameranella Beu, 1988: 79. Type species (by original designation): *Nyctilochus kewi* Dickerson, 1915, Late Eocene, Washington-California, western USA.

Remarks.—I proposed (Beu, 1988) the genus *Ameranella* to contain three species, the Chilean Oligocene-Early Miocene species *A. verruculosa* (G. B. Sowerby I, 1846), the western North American, Late Eocene species *A. kewi* (Dickerson, 1915), and the western North American, Oligocene species *A. terrysmithae* (Hickman, 1980). This group of relatively small species (the largest, *A. verruculosa*, reaches *ca.* 100 mm H) differs from *Ranella* species in having its varices more nearly aligned, rather than slightly offset from whorl to whorl as in *Ranella*, in having nodulose spiral cords that form higher, more prominent nodules where they cross the varices than in *Ranella*, in having a slightly more flared outer lip, and in having a markedly smaller protoconch than in species of *Ranella*. The largest species, *A. verruculosa*, has particularly large and prominent, narrow nodules on the varices and does not seem to be closely related, in a phylogenetic sense, to any other

Ranellinae. However, the similar but smaller and more weakly sculptured western North American species share most of the significant characters of the genus with *A. verruculosa*, and seem to be early species of the genus.

Ameranella verruculosa (G. B. Sowerby I, 1846)

Pl. 25, Figs 1, 4, 10, 12; Pl. 27, Figs 2, 4, 6;

Pl. 28, Figs 2, 4, 6

Triton verruculosus G. B. Sowerby I, 1846: 260, pl. 4, fig. 63.

Triton verruculosum. d'Orbigny, 1852: 78.

Tritonium verruculosum. Philippi, 1887: 57 (in part; not pl. 4, fig. 10); Möricke, 1896: 561.

Tritonium exiguum Philippi, 1887: 57, pl. 3, fig. 23 (in part).

"*Tritonium*" (*Ranella*?) *verruculosum*. Tavera, 1979: pl. 19, figs 67a-b.

"*Tritonium*" (*Litorium*) *bicegoi*. Tavera, 1979: 90, pl. 19, fig. 66 (not *Sassia bicegoi* Ihering, 1899).

Ameranella verruculosa. Beu, 1988: 83, pl. 3, figs 1-4, 6-7; Nielsen, 2003: 94, pl. 17, figs 3-7; Griffin & Nielsen, 2008: 310, pl. 24, figs 14-15.

Cymatium cf. *verruculosus*. Covacevich & Frassinetti, 1990: 68, fig. 29.

Remarks.—Sowerby's (1846: pl. 4, fig. 63) drawing of the holotype of *Ameranella verruculosa* shows only the dorsum, and because the nodules on the intervariceal surface appear foreshortened, it gives a somewhat false impression of the appearance of this species. Most material examined has shorter nodules on the intervariceal intervals but longer nodules on the varices than in Sowerby's illustration, and the most striking character of this species is certainly its highly unusual, large nodules protruding from the varices where they are crossed by the spiral cords. Sowerby's original illustration in fact gives the impression that this is a species of Bursidae, but more complete material shows that the aperture is relatively simple, *i.e.*, it lacks a posterior siphonal canal, and the lips are relatively weakly armored, with only a row of low nodules inside the outer lip and low transverse ridges on the columella. There is no doubt that *A. verruculosa* belongs to Ranellinae rather than Bursidae.

At first I thought that the specimen from Lo Abarca [SGO.PI 4827; illustrated, Pl. 25, Figs 1, 4; from Capas de Lo Abarca (Late Miocene-Early Pliocene), near San Sebastian, *ca.* 90 km north of Navidad, central Chile; Covacevich & Frassinetti, 1990] represented an unnamed species of *Ranella*, because it is much larger (H 92.4 mm, incomplete) than any other specimens of *Ameranella verruculosa* that I have seen, and has fewer, lower, and wider peripheral nodules. Also, the variceal shape is unknown, because the varices are broken and corroded. However, the steeply sloping sutural ramp, the consequently tall, weakly stepped spire, and the weak teleoconch sculpture make it likely that this is a very large specimen of

A. verruculosa (or possibly an unnamed descendent species). More material is needed to be certain of the status of this specimen.

Dimensions.—Largest referred here, from Capas de Lo Abarca (Early Pliocene?), SGO.PI 4872: H 92.4, D (incomplete) 47.9 mm; holotype: H (incomplete) 34.3 mm (Griffin & Nielsen, 2008: 309, caption).

Types.—*Triton verruculosus*, holotype BMNH Palaeontology Department, G26396 (Griffin & Nielsen, 2008: 300, pl. 24, figs 14-15), from "Navidad," Chile, *i.e.*, Navidad Fm (Oligocene-early Miocene, displaced into Late Miocene-Pliocene rocks) at either Matanzas Beach or cliffs N of Río Rapel, near Navidad, coast SW of Santiago, Chile; collected by Charles Darwin.

Other material examined.—**Fossils: Chile: Late Oligocene/Early Miocene:** Philippi collection, material identified by Philippi (1887) as *Tritonium verruculosum*: SGO.PI 839, from Navidad; 6 specimens, of which the 4 smallest are *Ameranella verruculosa*, but the 2 largest, including the specimen illustrated by Philippi (1887: pl. 4, fig. 10), are *Sassia armata*; same collection, SGO.PI 741, from Matanzas (2 specimens, but both are *S. armata*); Punta Perro, *ca.* 400 m N of Puebla La Boca, S side of mouth of Río Rapel, SGO.PI (5); between Puebla La Boca and Punta Perro, SGO.PI (2); SGO.PI 5536, Rapel Norte, N of mouth of Río Rapel (2); SGO.PI.4827, Capas de Lo Abarca (Late Miocene-Early Pliocene) at Lo Abarca, 4 km inland from the coastal town of San Sebastian, *ca.* 90 km N of Navidad, SW of Santiago, central Chile (1 large; Covacevich & Frassinetti, 1990; Pl. 25, Figs 1, 4); formerly at Department of Earth and Atmospheric Sciences, Purdue University, now at PRI, collection no. 264, sandstone 10 m above beach, Punta Perro, S point of mouth of Río Rapel, coll. W. J. Zinsmeister (1); loc. 286, base of sea cliff, coast 1 km N of mouth of Río Rapel, coll. W. J. Zinsmeister (1); loc. 327, 100 m S of loc. 326, coll. W. J. Zinsmeister (2; 1 illustrated, Pl. 27, Figs 2, 6); loc. 331, 3 m above beach, sea cliff 150 m N of loc. 286, coll. W. J. Zinsmeister (2); loc. 332, sea cliff 3 m higher than loc. 331, coll. W. J. Zinsmeister (9; 2 illustrated, Pl. 27, Fig. 4; Pl. 28, Figs 2, 4, 6); loc. 335, N side of mouth of Río Rapel, coll. W. J. Zinsmeister (1); material collected by Sven Nielsen at SGO.IP and SMF: loc. RAP 026, Río Rapel, N of Navidad, Oligocene-Early Miocene (1, large, illustrated, Pl. 25, Fig. 10, now SGO.IP 16450); loc. RAP 027, Río Rapel (1, with 1 *S. armata*); loc. RAP 028, Río Rapel (1); loc. RAP 029, Río Rapel (1) (1, illustrated, Pl. 25, Fig. 12, now SGO.IP 16449); RAP 099 (1, now at Universidad de Concepción, Chile); PPP 010, Punta Perro, mouth of Río Rapel (1); LBZ 027, Las Brizas (8); LBZ 030, Las Brizas (1); RAN, Ranquil (1); RQK 008, Ranquil (1).

Distribution.—*Ameranella verruculosa* is recorded only from the Navidad area, SW of Santiago in central Chile, where it

occurs only in Navidad Fm (Oligocene-Early Miocene fossils displaced into Late Miocene-Early Pliocene rocks; Nielsen *et al.*, 2003; Encinas *et al.*, 2006; Finger *et al.*, 2007). One large specimen from the Capas de Lo Abarca (Early Pliocene?; near San Sebastian, ca. 90 km north of Navidad) is referred here with some hesitation, because its varices have been corroded and broken off.

SUBFAMILY CYMATIINAE Iredale, 1913 (1854)

(Conserved under ICZN Article 40.2; placed on the Official List of Family Group Names in Zoology by ICZN Opinion 1650, 1991)

Genus *CABESTANA* Röding, 1798

Cabestana Röding, 1798: 130. Type species (by subsequent designation, Dall, 1904: 134): *Murex cutaceus* Linnaeus, 1767, Recent, Mediterranean and West Africa.

Aquillus Montfort, 1810: 579. Type species (by monotypy): *Murex cutaceus* Linnaeus, 1767.

Dolarium Schlüter, 1838: 20. Type species (by monotypy): *Dolarium caduceus* Schlüter, 1838 (error for *cutaceus*, = *Murex cutaceus* Linnaeus, 1767).

Neptunella Gray, 1854: 38. Type species (by monotypy): *Murex cutaceus* Linnaeus, 1767.

Cymatilesta Iredale, 1936: 307. Type species (by original designation, Iredale, 1936: 336): *Septa spengleri* Perry, 1811, Pleistocene and Recent, New Zealand and southeastern Australia.

Remarks.—*Cabestana* is a distinctive genus of Ranellidae, with a shell somewhat resembling those of species of *Monoplex*, but with a narrow central radular tooth, not the conspicuously wide one of *Cymatium* and closely related genera, and with a short, smooth, turbiniform protoconch as in many species of *Sassia*, not the tall, multiwhorled, planktotrophic protoconch of *Cymatium*. *Cabestana* seems much more nearly related to *Sassia* than to *Cymatium*.

An important point to note in interpreting the evolutionary history of *Cabestana* is that, of all the species of Ranellidae that live in both the Mediterranean and West Africa at present, *C. cutacea* (Linnaeus, 1767) is the sole species that lacks an extensive fossil history in southern Europe and the Mediterranean region. The only records of which I am aware of *C. cutacea* as a fossil are from Pleistocene uplifted terrace deposits (West Africa: Lecointre, 1952; Glibert, 1963: 116; Brébion, 1979: pl. 2, fig. 10); Altavilla, Palermo, Sicily (Libassi, 1859: 42, fig. 18, a juvenile provided with the synonym *Murex subcutaceus* Libassi); Segre (1954: 64, pl. 3, figs 2a-b, 3a-b) illustrated specimens from the Tyrrhenian (late Pleistocene) terrace cover beds of the Gulf of Terranova Pausiana, Sardinia; Tyrrhenian (Pleistocene), Saracinello, Reggio Calabria, southern Italy, a juvenile that I have examined in the collection of Paolo

Crovato, Napoli; “numerous well preserved specimens” recorded from a Pleistocene deposit at Barma Grande, Monaco, by Leonardi (1935: 20, pl. 4, fig. 4); and other records listed by Landau *et al.* (2004): Greco & Lima (1974: 72-73), Calcara (1842: 15), Francaviglia (1940: 67), Malatesta (1957: 185), Mars (1956: 42), Power (1838: 127), Ruggieri (1967: 313), Ruggieri *et al.* (1968: 217), Ruggieri & Greco (1965: 53), and Scalia (1900: 22 and 1907: 35). The most unexpected is a record from the young (oxygen isotope stage 5e?) uplifted deposit at the back of the beach at Praia, Santa Maria Island, Azores (Garcia-Talavera, 1990a: 441), a locality now outside the range of *C. cutacea*. Franceschini (1906: 45) listed both “*Tritonium cutaceum* L.” and “*Tritonium subcutaceum* Libassi” (with var. *curta* Buquoy *et al.* listed as a variety of the latter) living in the Mediterranean, but these clearly all refer to *C. cutacea*. *Cabestana cutacea* is largely limited to the western Mediterranean, but Fischer (2005) reported a specimen from Koroni, Peloponnese, Greece, and Dimitris Poursanidis (Department of Marine Science, University of the Aegean, Mytilene, Greece, pers. comm., May 2007) reported a specimen that he collected in Crete. Some other tonnoidean species live off of West Africa only, such as *Monoplex tranquebaricus* (Lamarck, 1816), *Turritriton kobelti* (Maltzan, 1884), and *Distorsio smithi*, and these all have no fossil or Recent record in the Mediterranean, but *C. cutacea* is the only species living in the Mediterranean at present that has no pre-Pleistocene fossil record there. In contrast, *Cabestana* has a fossil history from at least the earliest Miocene in New Zealand [*C. tetleyi* (Powell & Bartrum, 1929), Otaian (Early Miocene), Waiheke Island, Auckland, and Waitakian (latest Oligocene-basal Miocene), Mataura River, Southland]. It seems feasible, then, that *Cabestana* evolved from *Sassia* in the southern hemisphere, possibly from a large, prominently sculptured *Sassia* species similar to *S. tortirostris* (Tate, 1886) (Late Eocene-Middle Miocene, New Zealand and southeastern Australia), and subsequently spread to the Atlantic and so to the North Atlantic-Mediterranean area. All species correctly referred to *Cabestana* have similar sculpture of low, wide spiral cords subdivided by a median groove, not greatly different from the sculpture of *Sassia tortirostris*.

Species that in my opinion are correctly referred to *Cabestana* are:

- *africana* (A. Adams, 1855), Recent, South Africa. The *dolarium* (Linnaeus, 1767) form was considered by Kilburn (in Kilburn & Rippey, 1982: 74) to occur in both the Mediterranean-West African and South African populations and, indeed, it is likely that Linnaeus’ syntype is from West Africa; it is tentatively regarded as a synonym of *Cabestana cutacea*. The relationship between *C. africana* and *C. cutacea* requires genetic study.
- *casus* (Kensley & Pether, 1986), Late Pliocene(?), Namibia-

southwestern Africa.

- *cutacea* (Linnaeus, 1767) (= *dolarium* Linnaeus, 1767, and *subcutacea* Libassi, 1859), Pleistocene-Recent, Mediterranean-West Africa. As first reviser, I select *Cabestana cutacea* as the valid name to be used for the species named both *Murex cutaceus* and *M. dolarium* by Linnaeus (1767).
- *felipponei* (Ihering, 1907), Pleistocene(?), Holocene-Recent, southwestern Atlantic.
- *spengleri* (Perry, 1811) (= *bolteniana* A. Adams, 1855, *barthelemyi* Bernardi, 1857, and *procerum* Iredale, 1929), Pleistocene-Recent, New Zealand and southeastern Australia.
- *tabulata* (Menke, 1843) (= *waterhousei* A. Adams & Angas, 1863, *frigidulum* Iredale, 1929, *debiliior* Finlay, 1930, *segregata* Powell, 1933, *tepida* Iredale, 1936, *manawatuna* Fleming, 1943, and *otagoensis* Powell, 1954), Middle Miocene-Recent, New Zealand and southern Australia (Menke's holotype, in SMF, confirms the application of this name).
- *tetleyi* (Powell & Bartrum, 1929), Early Miocene, New Zealand.

***Cabestana felipponei* (Ihering, 1907)**

Pl. 28, Figs 5, 8

- Tritonium felipponei* (sic) Ihering, 1907: 443, pl. 17 (not pl. 18, as in text), figs 122a-b; Ihering(?), 1908: 1.
- Cymatium felipponei*. Carcelles, 1944: 246, pl. 2, fig. 26; Rios, 1970: 71, pl. 17, upper right fig.; 1975: 78, pl. 21, fig. 316; Penchaszadeh & de Mahieu, 1975: 446, figs 1A-D, 2A-C.
- Cymatium* (*Cabestana*) *felipponei*. M. Smith, 1948: 8, pl. 4, fig. 1; Clench & Turner, 1957: 203, pl. 116, fig. 2; Figueiras & Sicardi, 1971: 123; Kiliyas, 1973: 97, fig. 72; Figueiras & Sicardi, 1980: 202; Coelho *et al.*, 1981: 118, fig. 4.
- Cabestana felipponei*. Beu, 1985: 57; Rios, 1985: 77, pl. 27, fig. 336; 1994: 90, pl. 30, fig. 353; Henning & Hemmen, 1993: 39, pl. 6, fig. 4; Piech, 1995: 15; Clavijo *et al.*, 2005: 385.

Remarks.—Although Ihering (1907) originally spelled the species name “*filipponei*,” he named it after the collector of the holotype, Florentino Felippone, and most subsequent authors have correctly emended the spelling to that of the collector's name.

This is the one species of *Cabestana*, living or fossil, occurring in the study area. Two species groups of *Cabestana* occur in the southern hemisphere. The first group includes *C. spengleri*, Pleistocene and living, New Zealand and southeastern Australia, *C. casus* (Kensley & Pether, 1986: 166, figs 14-15, as *Argobuccinum casus*; the species name is an indeclinable noun), from the Late Pliocene(?) “50-m complex” raised beaches in the Hondeklip area, western coast of southwestern

South Africa north of Cape Town, and *C. africana*, living in South Africa. These species have a relatively heavy shell with sculpture of relatively wide, closely spaced spiral cords, and the interior of the outer lip turns out over the terminal varix; most are also larger than species of the other group. The second species group includes only *C. felipponei* and *C. tabulata*, Middle Miocene to Recent, New Zealand and throughout southern Australia. These two species have a thinner and more finely sculptured shell than species in the first group, with narrower, more prominent, more widely spaced, more deeply subdivided spiral cords, but the varices are higher and thinner than in the other group, and have the outer lip stopping at the inner edge of the terminal varix, rather than extending smoothly out over the face of the varix. The type species, *C. cutacea*, living in the Mediterranean and West Africa, is in some ways intermediate between the two southern species groups, because its sculpture is more like that of *C. spengleri* whereas its varices are even more prominent than those of the *C. tabulata* species group, and its outer lip stops at the inner edge of the terminal varix as in *C. felipponei* and *C. tabulata*.

Cabestana felipponei appears, then, to be most closely related to *C. tabulata*. *Cabestana felipponei* differs from *C. tabulata* in being smaller (to ca. 70 mm rather than ca. 150 and, rarely, 200 mm H), in having a shorter shape with more strongly inflated whorls, and in having slightly wider spiral cords with narrower interspaces and with the intermediate, narrow spiral cord more weakly developed. Several specimens of *C. felipponei* are illustrated excellently in color on a webpage (<http://www.femorale.com.br/shellphotos>, last accessed 28 April 2006). Penchaszadeh & de Mahieu (1975) illustrated the typical pilose *Cabestana* periostracum and the hemispherical egg mass, resembling half an orange, of *C. felipponei*, closely similar to those of New Zealand specimens of *C. spengleri* and *C. tabulata*.

Dimensions.—Holotype(?), identified as “the figured specimen”: H 40, D 24 mm (Ihering, 1907: 444); syntype(?), NMW, “Mar del Plata”: H 40.1, D 23.6 mm; beach, La Paloma de Rocha, Uruguay, GNS WM15221: H 35.9, D 25.0 mm; Punta del Este, Maldonado, Uruguay, GNS WM15222: H 34.8, D 20.5 mm; Punta del Este, MNRJ 6162: H 40.1, D 24.0 mm.

Types.—The holotype (figured syntype?) of *Tritonium felipponei* is at MACN (not seen); from Maldonado, Uruguay (Ihering, 1907: 444) (presumably, like most other material of *Cabestana felipponei* from this locality, cast ashore on the beach). Ihering (1907: 444) also recorded that “Dr Felippone sent me another example of the same species [syntype?] 53 mm long, from Punta Carretas, Montevideo, where he found it in the post-Tertiary deposits.” A specimen identified as a “co-type” (syntype?) of *Lotorium felipponei* “Dall” from Mar del Plata, Argentina, is at NMW. It is a bleached and abraded,

white shell, apparently also a Holocene fossil, labelled "from the collection of Louis de Bois, who had contact with Tomlin and Felippone." However, Ihering did not mention this specimen, and it is unlikely to be original type material.

Other material examined.—**Recent: Brazil:** Playa de Guarariba, Vitoria, Espirito Santo State (MCZ 191191, 2). **Uruguay:** alive, Punta del Este, Maldonado (GNS WM15222, 1); beach, La Paloma de Rocha (GNS WM15221, 2); Punta del Este, Maldonado (MNRJ 6162, 1; MACN 28941, 1; MACN 17540, 5; MACN 15140, 3; MACN, 1; MCZ 201787, 2; MCZ 191194, 1); Maldonado (MACN 11342, 1; MACN, 1); Cabo Santa Maria, Rocha (MACN 15307, 4; MACN 23573, 2, with 2 *Monoplex parthenopeum*; MCZ 118713, 1); Montevideo (LACM. A-2777, 1); Rocha (LACM 31468, 1); Punta del Vile (LACM A-2778, 1); Uruguay, Staadt collection (MNHN, 2); Puerto Paloma, Rocha, Staadt collection (MNHN, 3). **Argentina:** Mar del Plata (MACN 12946, 1 live-collected; MACN 12236, 1; MACN 12904, 1; MACN 13084, 1; MACN 11807, 1); 60 m, off of Mar del Plata (BMNH 1927.6.8.1, 1); Puerto Quequen, ca. 100 km S of Mar del Plata (MACN 14171, 1); 37°20'S, 56°60'W, dredged alive (MACN 15103, 1); dredged off of Comodoro Rivadavia, 34°40'S, 58°18'W, 100 m (MACN 23487, 8 live-collected juveniles; MACN 23475, 1).

Fossils: Uruguay: Holocene: MLP Invertebrate Paleontology no. 1403, "Platense" (i.e., Holocene fossil), Punta Carretas, Montevideo, J. Frenguelli, 20 January 1929 (1). Ihering (1907: 444) also recorded a specimen from Punta Carretas, and Clavijo *et al.* (2005: 385) repeated Ihering's record in their catalog of Uruguayan Quaternary mollusks.

Distribution.—Coelho *et al.* (1981: 118) recorded specimens of *Cabestana felipponei* from the states of Espirito Santo and Rio de Janeiro, southern Brazil. This species is therefore recorded from southern Brazil (northernmost record: Guarariba, Vitoria, Espirito Santo; Clench & Turner, 1957) to 37°40'S, off the coast of central Argentina. Fossils are known only from Holocene (and possibly in part late Pleistocene?) deposits around Montevideo, Uruguay, and apparently from Mar del Plata, Argentina.

Genus *CHARONIA* Gistel, 1847

Tritonium Röding, 1798: 125. Type species (by tautonymy): *T. tritonis* (= *Murex tritonis* Linnaeus, 1758), Miocene to Recent, Indo-West Pacific and, rarely, eastern Pacific and western Atlantic (junior homonym of *Tritonium* Müller, 1776).

Triton Montfort, 1810: 587. Type species (by monotypy): *T. tritonis* Montfort, 1810 (in part, = *Murex tritonis* Linnaeus, 1758; in part, = *M. lampas* Linnaeus, 1758) (junior homonym of *Triton* Linnaeus, 1758, and of *Triton* Laurenti, 1768).

Charonia Gistel, 1847: 559; 1848: 170. Type species (by monotypy): *Murex tritonis* Linnaeus, 1758 [senior homonym of *Charonia*

Mabille (1886: 280), = *Concholepas* da Costa, 1776].

Tritonellium "Valenciennes" Mörch, 1877: 25 (not *Tritonellium* Valenciennes, 1858, a replacement name for *Tritonium* Müller, 1776).

Buccinatorium Mörch, 1877: 26. Type species (by subsequent designation, Clench & Turner, 1957: 193): *Triton nobile* Conrad, 1848 (= *T. variegatum* Lamarck, 1816), Miocene to Recent, Atlantic and Mediterranean.

Semiranella Gregorio, 1880: 99. Type species (by original designation): *Triton (Semiranella) gemmellari* Gregorio, 1880, Eocene, Italy (= *Charonia lampas* Linnaeus, 1758; Beu, 1998b: 66).

Septa "Perry" Dall & Simpson, 1901: 416 (not *Septa* Perry, 1810).

Eutritonium Cossmann, 1904: 123. Type species (by original designation): *Murex tritonis* Linnaeus, 1758.

Nyctilochus "Gistel" Dall, 1912: 58 (not *Nyctilochus* Gistel, 1848).

Remarks.—Lozouet (1998, 1999) has expanded the content of the genus *Charonia* significantly. He first thought that *C. crassa* (Grateloup, 1847) is a coarsely and evenly nodulose species distinct from *C. lampas* (Linnaeus, 1758) (Lozouet, 1998: fig. 17d, e), but examination of the type material (Lozouet, 1999: pl. 8, figs 16-17) demonstrated that *C. crassa* is a synonym of *C. lampas*, and the French Early Oligocene (Rupelian) form was named as the distinct species *C. veterior* Lozouet (1999: 16, pl. 8, figs 14-15). He also described the distinctive new species *C. guichemerri* (Lozouet, 1998: 94, figs 17a-b), which resembles a very coarsely nodulose specimen of *C. variegata* (Lamarck, 1816). *Charonia guichemerri* reaches a markedly larger size than the holotype suggested (P. Lozouet, MNHN, pers. comm., 2000) and appears likely to have been ancestral to the complex of *C. tritonis* (Linnaeus, 1758), and perhaps directly ancestral to *C. seguenzae* (Aradas & Benoit, 1870). However, the Eocene forms on which Gregorio (1880) based the subgenus *Semiranella* and the Early Miocene form *C. ventricosa* (Grateloup, 1833) (Lozouet, 1998: fig. 17c) are indistinguishable from juvenile specimens of the living, very widespread species *C. lampas* (fide Beu, 1998b). It is becoming clear that *Charonia* had a more complex evolutionary history than had been suspected previously, and that the genus is most diverse in Oligocene-Miocene rocks of the Aquitaine Basin, France (recorded species: *C. guichemerri*, *C. lampas* forms *crassa* and *ventricosa*, *C. seguenzae*, and *C. veterior*).

Charonia lampas (Linnaeus, 1758)

Pl. 29, Figs 1-6

Murex lampas Linnaeus, 1758: 748; 1767: 1216 (in part).

Tritonium opis Röding, 1798: 125; H. & A. Adams, 1853: 102.

Triton tritonis Montfort, 1810: 587, illus. (in part not *Murex tritonis* Linnaeus, 1758).

Septa rubicunda Perry, 1811: pl. 14, fig. 4.

Murex gyronoides Brocchi, 1814: 401, pl. 9, fig. 9; Pinna & Spezia, 1978: 149, pl. 36, figs 1-1a.

- Murex nereis* Dillwyn, 1817: 728 (in part).
- Triton nodiferum* Lamarck, 1822: 179; Petit de la Saussaye, 1852c: 194; Hoernes, 1856: 201, pl. 19, figs 1-2; Bellardi, 1873: 207; Dunker, 1882: 27; Coulon, 1933: 124.
- Triton australe* Lamarck, 1822: 179; Reeve, 1844a: pl. 4, fig. 12a, pl. 5, fig. 12b; Chenu, 1859: 151, fig. 686; Hutton, 1873: 13.
- Tritonium mediterraneum* Risso, 1826b: 203.
- Triton ventricosum* Grateloup, 1833: 162; Lozouet, 1998: fig. 17C; 1999: pl. 8, fig. 17.
- Triton crassum* Grateloup, 1840: pl. 29, fig. 20; Lozouet, 1999: pl. 8, fig. 16.
- Triton nodiferus*. Reeve, 1844a: pl. 3, fig. 9; Tryon, 1880: 10, pl. 1, figs 2-3, pl. 3, fig. 17, pl. 4, fig. 3; Hutton, 1885: 932.
- Triton sauliae* Reeve, 1844a: pl. 5, figs 17a-b; 1844c: 112; Krauss, 1848: 148; Lischke, 1871: 45.
- Triton ranelliforme* Sismonda in Michellotti, 1847: 252; Bellardi, 1873: 208, pl. 14, fig. 1 (junior primary homonym of *T. ranelliforme* King, 1832).
- Tritonium partschii* Hoernes, 1848: 18.
- Triton subcolubrinum* d'Orbigny, 1852: 78.
- Tritonium solitarium* Beyrich, 1856: 181, pl. 12, figs 1a-b.
- Tritonium nodiferum*. Drouët, 1858: 34.
- Triton pliniae* Mayer in Bellardi, 1873: 209, pl. 14, fig. 3.
- Tritonium australe*. Hutton, 1878: 18; 1880: 63.
- Triton (Semiranella) gemmellari* Gregorio, 1880: 99, pl. 4, figs 21-22 only (not pl. 7, fig. 62).
- Triton nodiferus*. Kobelt, 1883: 16 (with further synonymy); 1890: pl. 33, fig. 1, pl. 34, fig. 1.
- Triton gyrinoides* formae *inflectilabrum*, *labropolium*, *imperans*, *ficarazzense*, and *singillum* Gregorio, 1884: 99-100.
- Triton gyrinoides* forma *propificarezense* Gregorio, 1885: 129.
- Tritonium glabrum* Locard, 1886: 154, 558.
- Triton nodifer*. Watson, 1886: 389; G. B. Sowerby III, 1892: 8.
- Tritonium pustulata* with vars. *minor* and *varicosa* Euthyme, 1889: 273, 276, pl. 6, figs 3-4.
- Triton gyrinoides* formae *normalis*, *flabellatum*, *intermedium*, *transiens*, *scalaratum*, *conodontatum*, *cochleosocium*, *bicanaliculatum*, *verrucosum*, *minus-verrucosum*, *callosum*, *diramatum*, *carinatum*, *latespiratum*, *naniusculum*, *pellegrinense*, and *subnormalis* Gregorio, 1893: 11-18, pls 1-5.
- Triton (Semiranella) valrovinensis* Gregorio, 1894: 30, pl. 5, fig. 117.
- Simpulum nodiferum* vars. *major* and *minima* Pallary, 1900: 293.
- Septa englishi* Newton, 1905: 341, illus.
- Lotorium rubicundum*. Hutton, 1904: 75; Moss, 1908: 19, pl. 3, 2 figs.
- Septa rubicunda*. Iredale, 1910: 71; Suter, 1913: 303, pl. 1, fig. 3, pl. 43, fig. 1.
- Triton lampas* var. *euclia* Hedley, 1914: 65, pl. 18, fig. 1.
- Charonia lampas*. Iredale, 1915: 458; Oliver, 1915: 458; Crowley, 1961: 17, pl. 1; O'Riordan, 1972: 371; Brehaut, 1973: 41; Turk, 1976: 29; de Ligt, 1987: 385; Smith & Heppell, 1991: 24; Wilson, 1993: 243, pl. 41, figs 15a-b; Vega-Luz & Vega-Luz, 1995: 7; Cachia *et al.*, 1996: 115, pl. 11, fig. 5; Gainey & Turk, 1997: 78; Beu, 1998b: 69, figs 20b, d-g, 21 (with further synonymy); 1999: 8, figs 8-19; Gofas & Beu, 2002: 95, figs 4A-C; Zhang & Ma, 2004: 110, text-fig. 69; Ardovini & Cossignani, 2004: 126, 2 lower figs; Landau *et al.*, 2004: 53, pl. 4, fig. 1; Chirli, 2007: 97, pl. 35, figs 9-16 (with long synonymy).
- Nyctilochus alfredensis* Bartsch, 1915: 94, pl. 4, fig. 4; Turton, 1932: 11, pl. 24, fig. 804.
- Eutritonium salbriacense* Cossmann & Peyrot, 1924: 268, pl. 16, figs 3-4.
- Eutritonium (Sassia) aperturale* Cossmann & Peyrot, 1924: 286, pl. 17, figs 10-11, 16.
- Septa rubicunda*. Bucknill, 1924: 51, pl. 4, fig. 3.
- Charonia capax* Finlay, 1926: 397, pl. 20, fig. 67; 1928: 246; Iredale, 1937: 106; Powell, 1952: 175; 1962: pl. 14, fig. 9.
- Charonia capax euclioides* Finlay, 1926: 398, pl. 20, fig. 68; Powell, 1933: 161.
- Charonia euclia instructa* Iredale, 1929b: 172, pl. 41, fig. 5.
- Charonia gyrinoides*. Bayer, 1933: 55; Bellatante, 1954: 71.
- Charonia gyrinoides rubicunda*. Bayer, 1933: 55.
- Charonia gyrinoides* var. *sauliae*. Bayer, 1933: 56; Bellatante, 1954: 71.
- Charonia pustulata*. Bayer, 1933: 71; Barnard, 1963: 25, fig. 2e; Kennelly, 1964: 67, pl. 15, fig. 76; 1966: 163, pls 1-2.
- Charonia alfredensis*. Bayer, 1933: 72.
- Triton australis*. Coulon, 1933: 124.
- Charonia rubicunda*. Cotton, 1945: 257; Powell, 1952: 175; Macpherson & Gabriel, 1962: 164, fig. 196; Rios & Tostes, 1981: 277.
- Charonia euclia*. Cotton, 1945: 257.
- Charonia nodifera*. Nicklès, 1950: 87, fig. 134.
- Charonia gyrinoides* var. *rubicunda*. Bellatante, 1954: 71.
- Charonia powelli* Cotton, 1957: 120, pl. 6, lower fig.
- Charonia sauliae*. Kira, 1961: 63, pl. 21, fig. 11; 1962: 56, pl. 22, fig. 11.
- Charonia sauliae macilenta* Kuroda & Habe in Habe, 1961: 46, pl. 23, fig. 10, appendix: 17.
- Chelonias(sic) sauliae macilenta*. Habe, 1964: 75, pl. 23, fig. 10.
- Tritonium (Charonia) nodiferum* and var. *elongatus* Settepassi, 1970, *Charonia*: ii, pls 1-3, pl. 4, fig. 13, pl. 4a, figs 15-16, pl. 4b, fig. 17.
- Charonia mirabilis* Parenzan, 1970: 156, fig. 3, pl. 32, fig. 615.
- Charonia lampas lampas*. Beu, 1970b: 211, pl. 2, figs 6, 9; 1985: 57; Kilburn, 1984: 8; Gerber *et al.*, 1989: 24; Piech, 1995: 16; Ávila *et al.*, 1998: 499; Guerreiro & Reiner, 2000: 102.
- Charonia lampas pustulata*. Beu, 1970b: 213, pl. 2, figs 8, 10, pl. 8, figs 11-14; 1985: 57; Kilburn, 1984: 8, fig. front cover; Piech, 1995: 16.
- Charonia lampas sauliae*. Beu, 1970b: 214, pl. 3, figs 15-17; 1985: 50; Okutani, 2000: 291, pl. 144, fig. 39; Higo *et al.*, 2001: pl. 48, fig. G1604.
- Charonia lampas rubicunda*. Beu, 1970b: 215, pl. 3, fig. 13, pl. 4, figs 18-23; 1985: 57, fig. 11; Powell, 1979: 168, pl. 12, fig. 2; Coelho *et al.*, 1981: 114, fig. 2; Piech, 1995: 16.
- Charonia lampas capax*. Beu, 1970b: 217, pl. 5, figs 24-29; Powell, 1979: 158, pl. 12, fig. 1.
- Charonia (Charonia) rubicunda*. Kilias, 1973: 58, fig. 46; Kilias, 1981: 701.
- Charonia (Negyrina) alfredensis*. Kilias, 1973: 79, fig. 59.
- Charonia lampas weisbordii* Gibson-Smith, 1976: 3, pl. 1, figs 1-5.
- Tritonium (Charonia) nodiferum mirabilis*. Parenzan, 1976: 427.

Siphonalia fusoides. Hu & Tao, 1991: 340, pl. 60, figs 3-4 (not *Buccinum fusoides* Reeve, 1846).

Charonia lampas macilenta. Okutani, 2000: 291, pl. 144, fig. 40.

Remarks.—The enormous synonymy of *Charonia lampas* has been discussed, the type specimens identified and listed, and the variation and geographical range described by me (Beu, 1998b, 1999), and much of this need not be repeated here. The synonymy above merely lists the names proposed for this species. Useful, extremely extensive lists of further usages in the European literature on fossils are provided by Priolo (1964: 530), Malatesta (1974: 268), and Chirli (2007: 97).

Charonia lampas does not appear in Clench & Turner's classic monograph of the western Atlantic Ranellidae, but Gibson-Smith (1971, 1976) reported it from the Late Pliocene Mare Fm in northern Venezuela, so it was not surprising that a few records began to accumulate from the late 1970s onward of specimens living along the coast of Brazil (Rios & Tostes, 1981). Several Brazilian specimens are illustrated excellently in color on a webpage (<http://www.femorale.com.br/shellphotos>, last accessed 28 April 2006). Other fossils are reported here from the Dominican Republic (Miocene or Early Pliocene) and from Florida (Pliocene?; not localized), so *C. lampas* has a very sporadic but long-continued and widespread presence in the western Atlantic. A brightly colored adult specimen (in the collection of D. Lamy) almost completely lacking peripheral nodules also has recently been collected off of Martinique, West Indies, and closely resembles the very smooth Florida Pliocene(?) fossil. *Charonia lampas* is easily distinguished from the larger, partly sympatric *C. variegata* by (a) its paler color pattern, which consists of spots and dashes of red-brown rather than the rather regular, crescentic, brighter bars on the spiral cords of *C. variegata* and *C. tritonis*, (b) its finely rugose rather than smooth and polished surface, (c) most specimens having nodules around the shoulder angle that are absent from most *C. variegata*, (d) the lower and less obvious transverse ridges on the columellar and parietal area, all of which are white rather than having a prominent dark brown background as in *C. variegata*, and (e) the more flared and much smoother interior of the outer lip, which is more constricted, only lightly flared, but much more strongly sculptured with white transverse ridges on a dark brown background in *C. variegata*. The very much larger *C. tritonis* differs from both *C. lampas* and *C. variegata* in having a much taller and narrower spire and little sign of a shoulder angle; it differs further from *C. lampas* in having a dark brown inner lip as in *C. variegata*, and differs further from *C. variegata* in having much wider white ridges on the dark brown inner lip, and a smoother, more strongly flared outer lip resembling that of *C. lampas*. The early juvenile stages and protoconchs of all three species are closely similar.

Although I have previously (Beu, 1970b) advocated the

recognition of geographical subspecies for the various forms of *Charonia lampas* in different parts of the world, continuing experience with the taxonomy of Ranellidae has shown that there are practical difficulties with the application of most, if not all, of the geographical subspecies recognized in the past for tonnoideans. *Charonia lampas* provides perhaps the most graphic example. I recognized (Beu, 1970b) subspecies in the Mediterranean and Atlantic (*C. lampas lampas*), in South Africa (*C. lampas pustulata*), in Australia and New Zealand (originally as two subspecies, *C. lampas rubicunda* in Australia and *C. lampas capax* in New Zealand, but it was obvious long ago that a distinction between these could not be supported), and in Japan (*C. lampas sauliae*). The minor differences between these forms apply only to some of the specimens, and then only to those living in shallow water, particularly the intertidal zone, where the shells are brightly colored. Continuing experience has shown that specimens from the western Mediterranean, much of the eastern Atlantic as far south as Angola (Gofas *et al.*, 1984: pl. 26a), from New Zealand, and from Japan are virtually indistinguishable by *any* characters, whereas specimens from off of Sénégal tend to have a very bright color pattern of white and dark brown maculations, specimens from Brazil and South Africa tend to have a bluish tone and many have particularly large nodules on the shoulder angle, specimens from southern Western Australia are an unusually dark brown, and specimens from the central New South Wales coast tend to be short, red, and strongly spirally corded. Note, though, that one of the specimens from the Canary Islands illustrated by Ardovini & Cossignani (2004: 126, lower right fig.) closely resembles specimens from Sydney, New South Wales. It must be stressed that these "subspecific" distinctions apply only to *intertidal* specimens. All *C. lampas* specimens from depths greater than *ca.* 50 m are quite indistinguishable, from anywhere in the world. Only a few offshore, elongate, pale specimens are known from New Caledonia (Beu, 1998b); what subspecies name should be applied to them? In my opinion, the time has come to accept that these "subspecies" intergrade completely, do not have the geographical limits that were assigned to them in the first place, and are not practical for offshore specimens; they seem to serve little purpose. I now advocate the recognition only of broad-ranging species, unless a true geographical subspecies situation can be demonstrated from genetics. All specimens examined here are identified merely as *C. lampas*.

Dimensions.—Fish traps, off of Agaete, NW Gran Canaria, Canary Islands, GNS WM18925: H 359.3, D 201.5 mm; Cabo Frio, Rio de Janeiro State, Brazil, GNS WM13664: H 203.4, D 109.8 mm; GNS WM17270: H 190.8, D 99.2 mm; *Charonia lampas weisbordi*, holotype: H 131.3, D (incomplete) 71.8 mm; BMNH Palaeontology Department, GG20379, Río Yaque del Norte, Dominican Republic: H

174, D 98 mm; TU 1210, Río Gurabo, Landau collection: H 160, D 62 mm; USNM 398480, Florida Plio-Pleistocene, A. A. Olsson collection: H 68.1, D 34.9 mm.

Types.—See Beu (1998b: 70); lectotype of *Murex lampas* designated by me (Beu, 1998b) as the specimen illustrated by Rondelet (1555 in 1554-1555: 81; Beu, 1998b: fig. 21). This figure has been reproduced again clearly (although in the original mirror image) by Schierenberg (1999: 52) from a later work by Boussuet (1558). The paralectotype illustrated in the other figure cited by Linnaeus (1758: 454) and Gualtieri (1742: pl. 50, fig. D), is present in Gualtieri's collection in the Museo di Storia Naturale e del Territorio, Università di Pisa, in the Certosa di Calci, outside Pisa, Gualtieri collection no. 2235, but is a specimen of *Tutufa bubo* (Linnaeus, 1758). *Murex gyrinoides*, holotype illustrated by Pinna & Spezia (1978: pl. 36, figs 1-1a), from the Piacenzian (Pliocene) near Piacenza, Italy, in Museo di Storia Naturale di Milano, no. i5139. *Triton nereis*, no type material remaining [see quotation from Dean (1936) under *Marsupina bufo*, above]. *Triton nodiferum*, lectotype (designated by me; Beu, 1998b) MHNG 1495/54; same specimen designated by me (Beu, 1998b) as neotype of *Tritonium opis*; type locality of both designated by me (Beu, 1998b) as Palermo, Sicily. *Triton australe*, larger syntype (MHNG 1099/71) designated by me (Beu, 1998b) as lectotype, and neotype of *Septa rubicunda*; type locality designated by me (Beu, 1998b) as Port Jackson, New South Wales. *Tritonium mediterraneum*, type material lost (Arnaud, 1978: 125). *Triton sauliae*, figured syntype in Jane Saul collection, University Zoological Museum, Cambridge (Bishop & Way, 1976), from Japan. *Triton pliniae*, 2 syntypes in Mayer-Eymar collection, NMB, juvenile specimens of *C. lampas*, from Cassinelle, near Aquis, northern Italy, Late Oligocene. *Tritonium partschii* was soon synonymized by its author with *C. lampas* (under the name *Triton nodiferum*) (Hoernes 1852: 201); type material presumably in NHMV, from Miocene of the Vienna Basin, not seen. *Tritonium pustulata*, 2 syntypes at MNHN, from South Africa. *Septa englishi*, holotype BMNH Palaeontology Department, G17371, Late Miocene, from near Bustenari, Roumania. *Triton lampas* var. *euclia*, holotype AMS C70728, from 180 m in the Great Australian Bight. *Nyctilochus alfredensis*, holotype USNM 186785, an immature specimen of *C. lampas* forma *pustulata* from Port Alfred, South Africa. *Charonia capax* and *C. capax euclioides*, both dredged off of Otago Heads, eastern South Island, New Zealand, in ca. 40-80m, holotypes AIM AK70138-9. *Charonia euclia instructa*, holotype AMS C57726, from 90-110 m, off of Montague Island, southern New South Wales. *Charonia powelli*, holotype at South Australian Museum, Adelaide, D14517, from Ellensbrook Beach, southern Western Australia. *Charonia sauliae macilenta*, holotype NSMT Mo.49895, from off of Cape Ashizuri, Shikoku, Japan. *Charonia mirabilis*, figured syntype

(Parenzan, 1970: 156, fig. 3; not stated to be the holotype) in the private collection of "Sig. A. Caricati," from "Milazzo e l'Isole Vulcano." Italy (*i.e.*, Parenzan had more than one specimen); a form with elongate, forward-directed "teeth" more than 20 mm long around the outer lip, produced by extensions of the labral nodules (not seen). Parenzan (1970: 158) considered the possibility that it was merely a mutation or monstrosity of *C. lampas*, and soon afterward, Melone & Garavelli (1970) and Parenzan (1976: 427) himself reduced it to a form of *C. lampas*. Such aberrant specimens are not rare in the Mediterranean; a similar specimen is in GNS (WM 17754, dredged off Île Rousse, Corsica, *ex* A. Arthur collection). *Charonia lampas weisbordii*, holotype PRI 29700 (Pl. 29, Figs 4, 6), a Late Pliocene fossil from the Mare Fm at Cabo Blanco, Venezuela; with several fragmentary paratypes. I am not aware of the location of the type material of the remaining synonyms.

Other material examined.—Localities from most of the species' ranges are not listed. **Recent: Antillean islands:** fishermen's traps in 120-150 m off Rivière Pilote, Martinique, 2003 (unusually smooth, bright orange-brown specimen, 175 mm H, collection of D. Lamy). **Brazil:** scuba diver, 40 m, alive on sand bank among rocks, off of Cabo Frio, Ilha do Papagaio, Estado Rio de Janeiro, Brazil, coll. G. Guimaraes, *ex* collection of L. R. Tostes (GNS, WM 13664, 1; *ex* MNRJ 3897; specimen illustrated by Coelho *et al.*, 1981: fig. 2); scuba on rocks, 40-42 m, Cabo Frio Island, Arraial do Cabo, Rio de Janeiro State (GNS WM17270, 1). **South Africa:** 79 lots examined at NMP, 28 lots at GNS, ranging from Kleinmond, a short distance east of False Bay, western Cape Province (NMP B6895, 1) to off Rocktail Bay, N Zululand (*R/V Meiring Naudé* sta. ZD1, 100 m, 27°11.4'S, 32°51.0'E, NMP D.7605, 1). **Atlantic:** Vema Seamount, southern Atlantic (NMP F6383, 1); Great Fish Bay, Moçamedes, Angola (NMP J677, 1); Luanda, Angola (NMP F7279, 1); near Ugab River mouth, Skeleton coast, Namibia (NMP E1806, 1); Terrace Bay, Skeleton coast, Namibia (NMP E1831, 1); Skeleton coast, Namibia (NMP E1858, 1).

Fossils: Florida: Plio-Pleistocene: without locality (USNM 398480, 1 small, A. A. Olsson collection; Pl. 29, Fig. 2; closely resembling Recent Martinique specimen). **Dominican Republic: Miocene-Pliocene:** "Miocene, Yaque River, Santo Domingo," pres. Geological Society of London, 1911; from the original T. S. Heneken collection, 1848 (BMNH Palaeontology Department, GG20379, 1; Pl. 29, Figs 1, 3, 5); the preservation suggests that it is possibly from Baitoa Fm, late Early Miocene (E. H. Vokes, pers. comm., April 2008), but the presence of *Hirsutella margaritae* in its matrix (John Saunders, pers. comm., 1982) indicates that it is possibly from the following locality. **Early Pliocene:** TU 1210, Gurabo Fm, Río Gurabo, E bank, first bluff down-

stream from bridge on Los Quemados-Sabaneta road (see localities given by Saunders *et al.*, 1986: text-fig. 5; 1 specimen in collection of Bernard Landau). **Venezuela: Late Pliocene:** Mare Fm, Cabo Blanco, coll. J. & W. Gibson-Smith (holotype of *C. lampas weisbordi* Gibson-Smith, 1976, PRI 29700; Pl. 29, Figs 4, 6; NMB 17512, Gibson-Smith collection from the same locality, 21 specimens, mostly fragmentary, and mostly paratypes of *C. lampas weisbordi*); Weisbord's locality G261b, W bank Quebrada Mare Abajo, Mare Fm (Pliocene) (PRI 26194, 1; frag illustrated by Weisbord, 1962: pl. 25, fig. 9); all data same as last (PRI 26195, 1; frag illustrated by Weisbord, 1962: pl. 25, figs 10-11); NMB 17513 (2 frags).

Distribution.—I summarized (Beu, 1998b) the known range. *Charonia lampas* lives at present in the western Mediterranean (being replaced by *C. seguenzae* in the eastern Mediterranean), and in the eastern Atlantic is reported from southern Britain, where specimens have been taken in some numbers from 1972 onward, from Ireland and Cornwall to Dover and the Channel Islands (Crowley, 1961; O'Riordan, 1972; Brehaut, 1973; Turk, 1976; de Ligt, 1987; Gainey & Turk, 1997) south to Angola (Gofas *et al.*, 1984), including the Atlantic banks and islands (Gofas & Beu, 2002). Gainey & Turk (1997) summarized earlier British records, and records of mating and egg laying by specimens kept for some years in the Plymouth Marine Aquarium. Pallary (1938: 30) discussed a specimen in the Université Saint-Joseph, Beirut, supposedly from Beirut, but doubted the reliability of the locality. F. Garcia-Talavera (TFMC) reported that in the Canary Islands, where both *C. lampas* and *C. variegata* occur, they are segregated by depth; *C. variegata* is the shallow-water species, collectable by snorkeling, whereas *C. lampas* occurs only in more than 30 m of water, and is collected by trawling. Canary Islands specimens reach an enormous size, to *ca.* 400 mm H, the largest that I have seen. In the western Atlantic, Recent specimens are reported only from Martinique, West Indies (a single specimen seen) and Brazil (Santa Catarina to Bahia; Rios, 1885: 74; 1994: 90). As with *Ranella olearium*, these are probably all pseudopopulations recruited from the eastern Atlantic; the Martinique specimen resembles those from Sénégal, and Brazilian specimens resemble South African ones. I reported (Beu, 1998b) single specimens from St. Helena and from the Dahlak Islands in the Red Sea. In South Africa, it occurs rarely along the Skeleton Coast of Namibia and commonly from False Bay, Cape of Good Hope, to the northern coast of Natal. Arnaud & Beurois (1972) reported it from St. Paul and Amsterdam Islands in the southern Indian Ocean (1 specimen in GNS, pres. P. M. Arnaud), and M. J. C. Martin (Nice, formerly of Réunion; pers. comm., August 1999) sent me photographs of a specimen from Tuléar, Madagascar. In Australia, it occurs from Jurien Bay in southern Western Australia around the southern and eastern coasts to Swain Reefs, easternmost

Great Barrier Reef, Queensland (Wilson, 1993), and is more common in collections from New South Wales and southern Queensland than further south. Five specimens were reported from New Caledonia, in 230-410 m, and one from Capel Bank in the Coral Sea by me (Beu, 1998b); 19 further specimens have now been seen from the Norfolk Ridge near southern New Caledonia, in MNHN (Banc Jumeau-est, Lithist cruise sta. DW13, 400 m, 1 live; Banc Jumeau-ouest, Lithist cruise sta. CP16, 379-391 m, 1 dead; sta. CP17, 247-281 m, 2 dead; Norfolk 1 cruise, sta. CP1668, 234-261 m, 1 dead; sta. CP1669, 302-325 m, 5 dead; sta. CP1670, 382-386 m, 1 dead; sta. CP1676, 227-232 m, 1 dead; sta. CP1677, 233-259 m, 1 dead; sta. DW1707, 381-493 m, 2 dead; sta. CP1708, 381-384 m, 1 dead; Norfolk 2 Expedition sta. CP2319, 1 dead; sta. DW2124, 1 live; sta. CP2095, 24°46'S, 168°10'E, 283-310 m, 1 live, with the huge specimen of *Ranella olearium* reported above). Many specimens also were observed alive by me on a bare volcanic peak at *ca.* 280-300 m, above all hydrothermal vent influence, on Healy submarine volcano between New Zealand and the Kermadec Islands, accompanied only by equally common *Monoplex parthenopeus*, during the "Ring of Fire" submersible expedition in May 2005 (video footage in GNS and in New Zealand National Institute of Water and Atmospheric Science). In New Zealand, it occurs all around both main islands and at the Chatham Islands, and it is quite common at Raoul Island in the Kermadec Islands. These southern populations are separated by an enormous gap from the northwestern Pacific population, which occurs from Taiwan to central Honshu, Japan, and, rarely, as far south as the Philippine Islands. An exceedingly widely dispersed larval population presumably keeps these widely disjunct benthic populations in genetic continuity. Fossils are reported from Eocene to Pleistocene rocks in central and southern Europe (Beu, 1998b), from Middle Miocene rocks in southern Australia, and from Late Miocene onward in New Zealand and Japan. Specimens also are reported here from Late Miocene and Pliocene rocks of tropical America, especially northern Venezuela, but including the Dominican Republic. There is no reported fossil or living record of *C. lampas* in the tropical Indo-West Pacific (other than at Tuléar and in New Caledonia and the Philippines) or in the eastern Pacific. However, the widespread occurrence of adult individuals demonstrates that *C. lampas* can metamorphose and grow to adulthood almost anywhere in the warm temperate and tropical ocean, although it is the only one of the "Pacific fringe" species that has not been reported from Hawaii.

***Charonia seguenzae* (Aradas & Benoit, 1870)**

?*Tritonium nodiferum* var. *glabra* Weinkauff, 1868: 75 (*nomen nudum*).

Tritonium seguenzae Aradas & Benoit, 1870: 90; 1876: 275, pl. 4, fig. 1; Kobelt, 1889: 19, pl. 35, fig. 1, pl. 36, fig. 1, pl. 37, fig. 1.

Triton seguenzae. Tryon 1880: 10, pl. 5, fig. 26.

Tritonium seguenzae vars. *minor* and *major* Pallary, 1938: 29.

Charonia variegata. Clench & Turner, 1957: 193 [in part not *C. variegata* (Lamarck, 1816)]; Barash & Danin, 1992: 117.

Charonia seguenzae. Priolo, 1964: 533; Parenzan, 1970: 156, fig. 614; Magne & Vergneau-Saubade, 1973: 6, fig. 2; Gofas & Beu, 2002: 96.

Charonia tritonis variegata. Beu, 1970b: 209, pl. 2, figs 5, 7; 1985: 57; Henning & Hemmen, 1993: 44, pl. 7, fig. 2; Piech, 1995: 16 [in part not *C. variegata* (Lamarck, 1816)].

Remarks.—Clench & Turner (1957: 193) included the name *Tritonium seguenzae* in the synonymy of *Charonia variegata*, and have been followed by all subsequent authors, including me. Gofas and I (2002: 96) pointed out that *C. seguenzae*, isolated in the eastern Mediterranean Sea, is unlikely be conspecific with *C. variegata*. *Charonia seguenzae* replaces *C. lampas* in the eastern Mediterranean; they overlap only in the Sicily Straits, including at Malta (Russo *et al.*, 1990; Cachia *et al.*, 1996). Eastern Mediterranean specimens that I have examined differ from Atlantic specimens of *C. variegata* in having a markedly taller, narrower and more weakly sculptured shell with a duller, more brownish-purple coloration, with less of the paler red color seen in *C. variegata*. The apertural coloration and sculpture are similar in both species, but the outer lip of *C. seguenzae* is still more prominently ridged and less flared outward than in *C. variegata*. It therefore seems likely that Mediterranean specimens belong to a distinct species that has been isolated in the eastern Mediterranean for a considerable time, perhaps as a result of the Messinian desiccation of the Mediterranean. The uncommon central and eastern Atlantic specimens of *C. variegata* apparently constitute pseudopopulations recruited as planktotrophic larvae from the western Atlantic, as is usual among western Atlantic tonnoideans (as distinct from the endemic eastern Atlantic ones). It seems likely to me that *Charonia seguenzae* is a distinct eastern Mediterranean species. It therefore is not included in the synonymy of *C. variegata*. Few data are provided here for *C. seguenzae*, because it is outside the scope of this report. I have also only recently realized that it is likely to be distinct.

Dimensions.—GNS WM17493, Bodrun, Turkey: H 307.7, D 124.5 mm; WM15353, Gökovo, 50 km E of Bodrun: H 283.2, D 118.7 mm; WM17676, SW Cyprus: H 188.0, D 76.1 mm.

Types.—According to Priolo (1964: 533) and Stefano Palazzi (pers. comm. to P. Bouchet, MNHN, 2004), the holotype of *Triton seguenzae* is in the Museo Civico di Scienze Naturale di Milano; not seen. The type locality is the Golfo di Catania, Sicily.

Other material examined.—Recent: E Mediterranean:

sponge fishermen, 20 m, off of Bodrun, SW Turkey (GNS WM17493, 1; WM17467, 3; WM17494, 1); sponge divers, 20–30 m, Gökovo, 50 km E of Bodrun, Turkey (GNS WM15353, 1); weed-covered rocks, 4 m, SW Cyprus (GNS WM17676, 1); 3 m, Paradise Bay, Rhodos, Greece (GNS WM17496, 1 juvenile); 8 m, off Haifa, Israel (GNS WM15359, 1); beach, Shiqmona, South Haifa, Israel (GNS WM14877, 1); Ras al Nakura, Israel (GNS WM14470, 1); Aci-Trezza, near Catania, Sicily (SMF 306882, 1; original of Kobelt, 1890, pl. 37, fig. 1); Syrian coast (SMF 306826, 1).

Distribution.—*Charonia seguenzae* is limited in the Recent fauna to the eastern Mediterranean, east of Malta and the Straits of Sicily. Pallary (1938: 29) discussed localities for this species in the easternmost Mediterranean, recording specimens from Beirut (in the port, 2–3 m, “not rare”), “Jounieh, Fadaousse, Batroun, Tripoli, and Rouad.” The only two fossil specimens of which I am aware are: Université de Bordeaux, no. inv. 9-2-15, specimen figured by Magne & Vergneau-Saubade (1973: fig. 2), from Salles (Largileyre), Aquitaine Basin, SW France, Serravallian, Middle Miocene (one, quite severely abraded); Noaillan (Cachac), Aquitaine Basin, SW France, Burdigalian, late Early Miocene (one large, in collection of Jean-François Lesport, Bordeaux). Magne & Vergneau-Saubade (1973: 6) also recorded specimens from several “Sallomacien” (Tortonian, Late Miocene) localities in the Départements Gironde and Landes, Aquitaine Basin, SW France (Salles-Largileyre, Mios-Lalande, Saucats-Cazenave rive droite, and Marsan). They regarded these as the earliest known fossil localities for this species (although the Noaillon specimen is older), and of course the Aquitaine localities lie well to the west of all modern occurrences, and date from a time when there was presumably one Atlantic-Mediterranean population. The Aquitaine fossils are not well preserved, and it is possible that they represent *C. variegata* rather than *C. seguenzae*, but that seems unlikely in view of their narrow shape. The lack of a mention of a species of the *C. tritonis* group, by any name, by Bellardi (1873), Sacco (1904), or any other Italian paleontologist of which I am aware, testifies either that the segregation of *C. seguenzae* in the eastern Mediterranean is relatively recent, or that it has been segregated there since before the Italian Miocene and Pliocene rocks were deposited – an unlikely scenario in view of the Aquitaine Basin occurrences.

Charonia tritonis (Linnaeus, 1758)

Murex tritonis Linnaeus, 1758: 754; 1767: 1222; Gmelin, 1791: 3459; Dillwyn, 1817: 727.

Tritonium tritonis. Röding, 1798: 125 (in part); H. & A. Adams, 1853: 102; 1858: pl. 11, fig. 1c.

Triton marmoratum Link, 1807: 122 (in part).

Triton tritonis. Montfort, 1810: 587 (in part); Mörch, 1853: 108;

- Kobelt, 1878: 242; Tryon, 1880: 9, pl. 1, fig. 1, pl. 3, fig. 16.
Septa tritonis Perry, 1810: signature D5, pl. 6 (Matthews & Iredale, 1912: 10; Petit, 2003: 53).
Lampusia tritonis. Schumacher, 1817: 250.
Triton variegatum. Lamarck, 1822: 178 (in part not *T. variegatum* Lamarck, 1816); Kiener, 1842: 28, pl. 2; Hutton, 1873: 12; Coulon, 1933: 124 (in part).
Triton variegatus. Reeve, 1844a: pl. 2, fig. 3b (in part; not fig. 3a); Küster & Kobelt, 1871: 172, pls 48-49 (in part); Melvill & Standen, 1895: 110.
Triton imbricatus W. H. D. Adams, 1868: 268, fig. 1; Beu, 1971: 102, fig. 1.
Septa tritonis. Suter, 1913: 304, pl. 42, fig. 1.
Charonia tritonis. Iredale, 1913: 55; Oyama & Takemura, 1959: *Charonia* pl., figs 4-4a; Kira, 1962: 56, pl. 22, fig. 12; Wilson & Gillett, 1971: 76, pl. 52, fig. 1; Kay, 1979: 215, fig. 77F; Okutani, 1986: 115, bottom center fig.; 2000: 291, pl. 145, fig. 41; Lai, 1989: 119, fig. 14; Emerson, 1989: 13, figs 1-3; Osorio, 1991: 75, figs 1-2; Finet, 1991: 270; Wilson, 1993: 243, pl. 41, fig. 14; Kaiser, 1997: 32; Beu, 1998b: 66, fig. 20a; Zhang & Ma, 2004: 108, text-fig. 69; Beu, 2005: 71, fig. 186; Beu & Segers in Poppe, 2008: 638, pl. 264, figs 1a-b.
Charonia tritonis tritonis. Beu, 1970b: 208, pl. 1, figs 1-4; 1985: 57; Kilias, 1973: 61, fig. 48; 1981: 701; Kilburn, 1984: 8; Springsteen & Leobrer, 1986: 112, pl. 30, fig. 11; Henning & Hemmen, 1993: 43, pl. 7, fig. 1; Piech, 1995: 16.

Remarks.—*Charonia tritonis* is easily recognized by (a) its very large size, (b) its tall, narrow spire, (c) its smooth, polished exterior with very low, weakly rounded spiral cords, (d) its bright red-brown color pattern of crescentic bars on the cords, (e) its dark brown inner lip conspicuously barred with wide, white transverse ridges, and (f) its flared, weakly sculptured outer lip. Differences from *C. lampas* and *C. variegata* are discussed above.

Charonia tritonis only just qualifies as an eastern Pacific species, on the basis of a single specimen from Cocos Island, Costa Rica, and two specimens collected alive in the Galápagos Islands (all summarized by Emerson, 1989). Despite this, there are no records from the Marquesas Islands in far eastern French Polynesia (Beu, in prep.). An authentic, live-collected Brazilian specimen (with operculum) is illustrated excellently in color on a webpage (<http://www.femorale.com.br/shell-photos>, last accessed 28 April 2006), but this is the single record of which I am aware from the western Atlantic.

Dimensions.—*Charonia tritonis* is one of the largest known gastropods; Prigent (1989: 23) recorded a specimen from New Caledonia 464 mm H, and it is reputed to reach 500 mm H (e.g., Skoglund, 1992).

Types.—I designated (Beu, 1998b) the specimen in Linnaeus' collection housed by the Linnean Society of London as the lectotype of *Murex tritonis* and as the neotype of both *Triton marmoratum* and *T. imbricatum*. The type locality was designated as Ambon Island (Amboina), Indonesia.

Linnaeus (1758: 754) cited also for *M. tritonis* illustrations by Buonanni (1681: fig. 188), Rumphius (1705: pl. 28, fig. B), and Gualtieri (1742: pl. 48, fig. A). The illustration by Gualtieri (1742) shows *Charonia variegata*, but no specimens of this species remain in Gualtieri's collection, examined by me during January 2000 in the Museo di Storia Naturale e del Territorio, Università di Pisa, in the Certosa di Calci, outside Pisa.

Other material examined.—**Recent: E Pacific:** None examined. Shasky (1983) illustrated the specimen that he collected at Cocos Island, and Emerson (1989) illustrated the two specimens that have been collected alive at the Galápagos Islands. There is no fossil record in the region, but I identified (Beu, 1998b; 2005: 71, fig. 186) K. Martin's unfigured "*Triton* sp. 3" from Preangerian (Miocene) rocks of T'ji Boerial (Ciburial), Java, Indonesia, as *Charonia tritonis* (RGM 9810), so *C. tritonis* has a fossil record from the Miocene in the central western Pacific, as does *C. lampas* in the western Atlantic and around the Pacific fringes, in Australia, New Zealand, and southern Japan.

Distribution.—*Charonia tritonis* ranges very widely throughout the tropical Indo-West Pacific province and into the western fringes of the eastern Pacific. Records range from the eastern African coast and the Red Sea eastward as far as Hawaii (Kay, 1979), Pitcairn Island (Beu, 1998b), Easter Island (Osorio, 1991), the Galápagos Islands and Cocos Island (Emerson, 1989), and from southern Kyushu, Japan, southward to New Caledonia, to Dongara, Western Australia (Wilson, 1993: 243), and to southern Queensland, Lord Howe Island, and possibly to northernmost New Zealand. As noted above, a single specimen has also been collected alive in Brazil.

Charonia variegata (Lamarck, 1816)

Pl. 30, Figs 1-2

- Murex tritonis* Linnaeus, 1758: 754 (in part, reference to Gualtieri, 1742, only).
Triton marmoratum Link, 1807: 122 (in part).
Triton variegatum Lamarck, 1816: pl. 421, figs 2a-b, "Liste des objets": 5; 1822: 178 (in part); Blainville, 1825-1827: 399, pl. 18, figs 3-3a; Kiener, 1842: 28, pl. 2; Deshayes, 1843: 623; Chenu, 1859: 151, fig. 684.
Triton atlantica "Montfort" Bowditch, 1822: pl. 10, fig. 4.
Triton variegatus var. β Reeve, 1844a: pl. 2, fig. 3a only (not fig. 3b).
Triton nobilis Conrad, 1848: 121; 1849a: 212.
Triton variegatus. Küster & Kobelt, 1871: 172, pl. 48, 49 (in part); Guppy, 1876: 522.
Triton (Buccinatorium) marmoratum. Mörch, 1877: 26 (not *Triton marmoratus* Link, 1807, = *Charonia tritonis* Linnaeus).
Triton (Buccinatorium) nobilis. Mörch, 1877: 27.
Triton commutatus "Dunker" Küster & Kobelt, 1876: 224 (*nomen*

nudum).

Triton tritonis var. *nobilis*. Tryon, 1880: 10, pl. 4, figs 21, 26.

Tritonium tritonis. Gabb, 1881: 352 (not *Murex tritonis* Linnaeus, 1758).

Septa tritonis var. *nobilis*. Dall & Simpson, 1901: 416.

Tritonium tritonis var. *nobilis*. Dall, 1903b: 132.

Triton tritonis. Trechman, 1933: 39; 1937: 355 (not *Murex tritonis* Linnaeus, 1758).

Charonia nobilis. Piele, 1926: 80.

Charonia tritonis var. *nobilis*. Bayer, 1933: 57; Bellatante, 1954: 70.

Charonia tritonis nobilis. Morretes, 1949: 92; Abbott, 1954: 197, pl. 5, fig. f.

Charonia variegata. Clench & Turner, 1957: 193, pl. 111, figs 1-2, pl. 113, fig. 1, pl. 114, figs 1-2 [in part, = *C. sequenzae* (Aradas & Benoit, 1870)]; Olsson & McGinty, 1958: 15; Warmke & Abbott, 1961: 99, pl. 1, fig. a; 1974: 166, pl. 7, fig. 1776; Work, 1969: 660; Rios, 1970: 70; 1975: 78, pl. 21, fig. 314; Kaufmann & Götting, 1970: 370, fig. 81; Humfrey, 1975: 120, pl. 12, figs 8-8a; Nordsieck & Garcia-Talavera, 1979: 124, pl. 27, figs 2-3; Okutani, 1983: 262, illus.; H. Vokes & E. Vokes, 1983: 23, pl. 11, fig. 11; Bandel, 1984: 97, fig. 155, pl. 9, figs 1-2; Jensen & Harasewych, 1986: 428, illus.; de Jong & Coomans, 1988: 68; Lipe & Abbott, 1991: 10-11, illus.; Gofas & Beu, 2002: 95, fig. 4D; Ardovalini & Cossignani, 2004: 127, 2 upper figs.

Charonia tritonis variegata. Beu, 1970b: 209, pl. 2, figs 5, 7; 1985: 57; Kilias, 1973: 68, fig. 50; 1981: 701; Rosewater, 1975: 16; van Regteren Altena, 1975: 38; Gibson-Smith, 1976: 5, pl. 1, fig. 6; Coelho *et al.*, 1981: 113, fig. 1; Rios, 1985: 74, pl. 26, fig. 325; 1994: 90, pl. 30, fig. 355; Calvo, 1987: fig. 76 (radula); Henning & Hemmen, 1993: 44, pl. 7, fig. 2; Diaz & Puyana, 1994: 173, fig. 646; Vega-Luz & Vega-Luz, 1995: 7; Piech, 1995: 16; Cachia *et al.*, 1996: 116, pl. 12, fig. 1; Guerreiro & Reiner, 2000: 104; Macsotay & Campos Villarroel, 2001: 68, pl. 9, figs 2, 4; Redfern, 2001: 63, pl. 32, figs 265A-B.

Remarks.—*Charonia variegata* is moderately common at some localities in the western Atlantic at present, and is widely distributed, from North Carolina to southern Brazil. It is therefore not surprising to find that it is considerably more common than *C. lampas* in the fossil record in the western Atlantic region. Differences from *C. lampas* and *C. tritonis* are pointed out above; *C. variegata* is shorter and more coarsely sculptured than *C. tritonis*, many specimens have more shouldered whorls than in *C. tritonis*, the inner lip has much narrower, white transverse ridges than does that of *C. tritonis*, and the outer lip is much less strongly flared than in *C. tritonis* and has prominent, white transverse ridges on a dark brown background that is absent from *C. tritonis*. Almost all of the fossil specimens of *C. variegata* that I have seen are small to half-grown specimens, easily distinguished from *C. lampas* by their very much taller and narrower shape and their much smaller, more constricted aperture with much more prominent transverse ridges on both the inner and outer lips. Specimens are illustrated excellently in color on a webpage (<http://www.femorale.com.br/shellphotos>, last accessed 28 April 2006).

Although there have been few records of *C. variegata* as a fossil in the western Atlantic (Gabb, 1881: 352, from Limón, Costa Rica, latest Pliocene/Early Pleistocene; Gregory, 1895: 288, from Barbados, Pleistocene; Gibson-Smith, 1976, from Isla La Tortuga, Venezuela, Pleistocene), several specimens are present in the collections examined here from a wide range of localities. It occurs uncommonly in the Dominican Republic and commonly at Limón, Costa Rica (Robinson 1991, 1993). Gabb (1881: 352) recorded a fragment 30 cm H from Limón, Costa Rica. I pointed out (Beu, 1998b) reasons for regarding *C. variegata* as a species distinct from *C. tritonis*.

Dimensions.—The largest Recent specimen recorded by Clench & Turner (1957) is 331 mm H, but it probably reached more than 350 mm. Largest complete fossil seen (USGS 8544, Río Gurabo, Dominican Republic): H 105.2, D 47.5 mm (Pl. 30, Fig. 1), but a slightly incomplete specimen in the collection of Bernard Landau is 153.6 mm H (from TU 1210). Figured specimen, NMB H 17924, from NMB 19008 (TU 1240), Limón, Costa Rica: H 64.0, D 27.1 mm.

Types.—Following the monograph by Clench & Turner (1957), the name for this species has been stabilized as *Charonia variegata*, but few of the early synonyms are actually based on type specimens. Clench & Turner (1957: 196) merely stated that “according to Kiener the type of *T[riton] variegata* Lamarck is in the Paris Museum.” Link’s (1807) name *T. marmoratum* was in danger of replacing *T. variegatum* for this species, but Clench & Turner (1957) restricted Link’s name to the Gmelin (1791) reference cited by Link (1807: 122). As noted above, I designated (Beu, 1998b) the lectotype of *Murex tritonis*, in Linnaeus’ collection in London, as the neotype of *T. marmoratum*. *Triton variegatum*, 2 syntypes MHNG 1495/53 and MHNG 1099/70, both specimens of *Charonia variegata* of this report, both labelled “Oc. Indien.” The larger specimen (MHNG 1495/53) bearing a Lamarck label “*Triton variegatum*” inside the aperture, a medium-sized specimen agreeing in detail with the illustrations by Lamarck (1816: pl. 421, figs 2a-b), is here designated the lectotype of *T. variegatum*. Clench & Turner (1957: 196) designated the type locality as St. Thomas, Virgin Islands, West Indies. No type specimens are known to me from the work by Bowditch (1822), and so the lectotype of *T. variegatum* is also here designated the neotype of *T. atlantica*. *Triton nobilis*, lectotype ANSP 42537, from “West Indies,” designated by Clench & Turner (1957: 196).

Other material examined.—**Recent: W Atlantic:** Most material of this common, widespread species has not been listed; 32 lots at GNS. Specimens have been examined from the Bahamas (New Providence, LACM 18754, 1; Sales Cay, GNS WM15357, 1), Bermuda (*ex* Kobelt collection, SMF 306828, 1), Florida, E Honduras, E Costa Rica, E Panama, Jamaica, Cayman Islands, Cuba, Haiti, Dominican Republic, Puerto

Rico, Antillean islands (St. Thomas, St. Martin, St. John, Tortolo, Grenada, Guadeloupe, Tobago, Barbados), Aruba, Curaçao, E Colombia, Venezuela, Guiana, and Brazil (Aracate, GNS WM17675, 1; fishing boats, Pina, Pernambuco, GNS WM17669, 3). **E Atlantic: Mauretania, W Africa:** close to beach, off of Mauretania (GNS WM17668, 1); dredged, 80 m, off of Nouakchott, Mauretania (GNS WM17667, 1). **Cape Verde Islands:** beach, Porto Novo, Santo Antão Island, 1978 (R. von Cosel collection, MNHN, 1). **Canary Islands:** fishermen's nets, Punta de las Nieves, near Agaete, Gran Canaria (R. von Cosel collection, MNHN, 1); 55 m, La Palma, coll. Delpeut, March 1969 (LACM 29666, 2); escollera [protection wall] of Playa de las Teresitas, Tenerife (TFMC, 1 large, tall and narrow, resembling *C. seguenzae* but red-brown, not purplish, and with normal *C. variegata* aperture); and one smaller, normal short shape (TFMC 168, 1); Tenerife sur, 8 m (TFMC 166, 1 good, larger than above, normal shape); Tenerife (TFMC 171, 1 small and narrow, smooth, like off-shore Honduras specimens); Sardinia, Gran Canaria (GNS WM17665, 3); 15 m, Caleta Abado, Gran Canaria (GNS WM17674, 1). **Azores Islands:** fishermen's nets, Vilo do Porto, Santa Maria Island, pres. D. Pomba (GNS, WM15950, 1). **St. Helena:** Rupert's Bay, 10 m, dived F. Garcia-Talavera, August 1983 (TFMC, 1 dead and faded, moderately large, tall *seguenzae*-like form).

Fossils: Barbados: Pleistocene: USGS 18382 (1); Coral Rock, C. T. Trechman (BMNH Palaeontology Department, GG 10767, 1; GG10727, 1); low-level reefs, Bishopscourt (BMNH Palaeontology Department, G10896, 2); post-Coral Rock, Oistin Bay, C. T. Trechman (BMNH Palaeontology Department, G69028, 1; specimen listed by Trechman, 1937: 355). **Atlantic Costa Rica: Latest Pliocene-Early Pleistocene,** Moín: NMB 18079 (1); 18113 (1); 18276 (1); 18278 (3); TU 953 (GNS WM18832, 1 juvenile); 1240 = NMB 19008 (6, one illustrated, NMB H 17924, Pl. 30, Fig. 2); 1307 (GNS WM16939, 3); USGS 20468 (1); 21035 (1); 21051 (1); TU 1240, Moín Fm, Los Corales, Puerto Limón, collection of Bernard Landau (4); basal Moín Fm mudstone (Late Pliocene), Rte. 32, 3 km W of Puerto Limón, coll. J. A. Todd, February 1998 (BMNH Palaeontology Department, 1). Recorded also from the Moín Fm by Robinson (1991, 1993) in three Tulane University collections that I have not examined (TU 954, 1; 1240, 1; 1489, 3). **Atlantic Panama: Pleistocene:** NMB 18743, Swan Cay (1). **Colombia: Pleistocene:** terrace ca. 10 m above high tide, La Cieba, Departamento de Atlantico (UCMP S-46, 3); playa of Tierra Bomba, near Cartagena, Departamento de Bolívar (CAS loc. 295, 1). **Cuba: Pleistocene** raised terrace: USGS 3318 (1). **Haiti: Late Miocene:** USGS 9604 (USNM 482109, 1). **Dominican Republic: Late Miocene:** Cercado Fm: NMB 15893 (1, small internal mold). **Late Miocene/**

Early Pliocene: Gurabo Fm: TU 1231 (GNS WM18836, 1); USGS 26277 (1); 26281 (1). **Early Pliocene:** Gurabo Fm: NMB 15850 (1); 15864 (1, incomplete spire, H 94 mm); TU 1210 (GNS WM18834, 1); 1211 (GNS WM18833, 1); 1227 (GNS WM18835, 1); 1354 (GNS WM16941, 1 large incomplete spire, H 113 mm); USGS 8544 (1, illustrated, Pl. 30, Fig. 1); 8549 (1 large); Yaque River, St. Domingo, coll. T. S. Heneken (BMNH Palaeontology Department, GG20378, 1); TU 1210, Gurabo Fm, Río Gurabo, collection of Bernard Landau (1, largest seen); 1215, Gurabo Fm, Río Gurabo, collection of Bernard Landau (1). **Guadeloupe: Miocene:** NMB 10630 (1). **Trinidad: Middle-Late Miocene:** NMB 10220 (2 internal molds). **Venezuela: Pleistocene:** Punta Piedras Member, La Tortuga Fm, Isla La Tortuga (University of Venezuela Geology collection no. 4337, 2; one illustrated by Gibson-Smith, 1976: pl. 1, fig. 6).

Distribution.—As noted above, *Charonia variegata* lives now from North Carolina (Porter, 1970) south to Santos, São Paulo State, southern Brazil (Clench & Turner, 1957), including Bermuda, the Bahamas, and throughout the Caribbean. In the eastern Atlantic, it occurs uncommonly from southern Spain south to at least Ghana. Specimens are recorded also from most of the Atlantic islands, from St. Helena and Ascension as far north as the Azores. There are few records of it occurring sympatrically with *C. lampas*, but it does so at the Azores (Gofas & Beu, 2002: 95), the Canary Islands, and Madeira, although actual syntopical specimens seem not to be recorded, and the two are segregated by depth in the Canary Islands. Pleistocene fossils are recorded from several localities on the eastern Atlantic islands (Tenerife, Canary Islands: Garcia-Talavera *et al.*, 1978; Garcia-Talavera, 1990b; Cape Verde Islands: Garcia-Talavera, 1999). The first specimen is recorded here from St. Helena, collected by F. Garcia-Talavera. Fossils of *C. variegata* are recorded also from throughout the Atlantic part of the tropical American study area, from Costa Rica and the Dominican Republic to the northern coast of Venezuela, where they occur in Early Miocene to Pleistocene and Holocene rocks. I have seen no fossil records from Florida, and other than the three specimens of *C. tritonis* listed above, there are no reports of *Charonia* from the eastern Pacific, fossil or living.

Genus *CRASSICYMATIUM* n. gen.

Type species: *Crassicymatium crassicordatum* n. sp., Oligocene-Early Miocene fossils reworked into Late Miocene-Early Pliocene rocks, Matanzas, Chile.

Diagnosis.—Ranellidae of ovate-fusiform shape, with moderately tall spire, rather short, straight, open siphonal canal, and varices at about each 200-210° around whorls, *i.e.*, about half-

way between usual alternatives of aligned up opposing sides of spire (every 180°), as in Ranellinae, and three in every two whorls (every 240°), as in Cymatiinae. Sculpture of juvenile of three low, spiral folds, of which only uppermost shows on spire whorls, marked sulcus between uppermost and second folds coinciding with suture; spiral folds increasing in prominence rapidly down shell to form high swellings on last 3-4 whorls; low, wide, weakly nodulose, and weakly defined for first half of each intervariceal interval, coinciding with area of preceding whorl above aperture at each growth pause, increasing in prominence dramatically over second half of each intervariceal interval to form very prominent, gently round-topped cinguli as high as they are wide, with sharply undercut sides, at abapertural face of succeeding varix. Much of teleoconch surface of juvenile sculptured with low, wide, spiral cords, spaced so closely as to be seen as grooves in uniform surface rather than discrete cords; cords weakening down spire to form low, weak, faint threads on adult last whorl. Adult outer lip not seen; juvenile with lightly thickened, sinuous, weakly flared outer lip bearing five pairs of short, narrow nodules on interior; inner lip narrow, lightly callused, margin extending down siphonal canal, bearing two narrow, transverse parietal ridges very high up, and one row of short, low ridges on base of columella and top of siphonal canal.

Remarks.—The new genus and species *Crassicymatium crassicordatum* is proposed for a very unusually sculptured species from the Miocene of Chile. Unfortunately, the available material is imperfect, and the protoconch and the adult aperture are not preserved, but enough characters are shown by the available, exceedingly distinctive material for it to be recognized with ease when it is collected again. The complete juvenile paratype has an inflated-fusiform shape with a rather short spire, evenly rounded whorls and an unusually straight canal, giving it very much the appearance of a generalized cymatiine, similar to that of a *Monoplex* species, rather than a ranelline. The new genus and species has two unique characters, the huge, undercut cinguli resembling those of *Ecphora*, and the variceal position. The variceal position is the more surprising of the two, because all other ranellids that I have encountered with normal, evenly inflated whorls (*i.e.*, as distinct from a few strongly dorsoventrally compressed taxa) have their varices conforming to one or the other of the standard alternatives, each 180° or each 240°. It appears that this strange shell might have been forced to adopt a shorter growth interval than other Cymatiinae in order to allow the relatively weakly sculptured, early half of each growth interval to be positioned above (adapical to) the aperture of the succeeding whorl, where it could rest on the dorsum of the extended, creeping animal, rather than having the exceedingly prominently sculptured second half of each intervariceal interval resting on the creeping animal.

Etymology.—The generic name (Latin, *crassum*, heavy, coarse; + *Cymatium*) refers to the very prominent, wide, high spiral cords that are the most distinctive character of the genus. Gender neuter.

***Crassicymatium crassicordatum* n. sp.**

Pl. 30, Figs 3-5, 8

Cymatiinae gen. et sp. nov. Nielsen, 2003: 95, pl. 17, figs 13-16.

Description.—Shell moderately large (incomplete adult 65 mm H, originally *ca.* 90 mm), ovate-fusiform, very coarsely sculptured, with apparently rather thin varices (flared, lightly thickened edges of former outer lips) at each 200-210° down entire teleoconch. Juvenile sculptured with low, wide spiral folds, uppermost fold forming wide, moderately steeply sloping, convex sutural ramp; ramp forming all of visible spire whorls; sulcus between sutural ramp and second spiral fold coinciding with suture; suture becoming narrowly and shallowly channeled low on large specimens; below spiral sulcus, juvenile with 3 weakly elevated spiral folds, markedly narrower than fold forming sutural ramp, decreasing regularly in width down shell; 5 further low, closely spaced cords on canal. Surface of sutural ramp and between main cords below sulcus sculptured with shallow, narrow grooves (grooves between low, wide, very closely spaced spiral cords), 6-7 grooves on sutural ramp, 4 in next two succeeding spiral interspaces, 2-3 in lowest interspace. Sculpture strengthening down shell with growth, adult with low, rounded, weakly defined spiral folds following each varix on last 2-3 whorls, situated above (adapical to) aperture on last whorl, folds strengthening rapidly across second half of each intervariceal interval to form 3 exceedingly prominent cinguli at abapertural face of succeeding varix, each cingulum with height approximately equal to width, a gently rounded crest, and sides sharply undercut; fourth low, narrow, rounded cingulum present below third. Axial sculpture absent except for 4-5 very low, rounded nodules on each low fold over earlier half of each intervariceal interval, nodules aligned in vaguely axial rows. Shell surface of adult apparently almost smooth, sculptured with very low, narrow, rounded, obscurely defined, widely spaced, spiral ridges, at least in interspaces between cinguli over earlier half of each intervariceal interval, fading out in floor of cingular interspaces over second half of each intervariceal interval. Aperture of juvenile elongate-oval, relatively large, with narrow, lightly flared lips, outer lip weakly sinuous in conformity with spiral folds; interior of outer lip bearing 5 pairs of small, rounded nodules on inner edge of flare, situated interior to sutural ramp and to the 4 succeeding spiral interspaces; inner lip smooth, lightly callused, with 2 short, narrow parietal ridges and 6 short, very low transverse ridges on base of columella and top of canal. Outer lip of

adult lacking in available material; 3 long, narrow ridges on parietal callous pad; inner lip smooth, strongly thickened over neck, above cinguli of preceding whorl; base of inner lip not seen. Protoconch not present in available material.

Dimensions.—Holotype: H 64.8, D 39.0 mm; juvenile paratype, SGO.PI 5841: H 23.4 mm (Nielsen, 2003: caption to pl. 17).

Types.—Holotype SGO.PI 5839 (Pl. 30, Figs 4, 8), from Navidad Fm (Oligocene-Early Miocene fossils displaced into Late Miocene-Early Pliocene rocks; Nielsen *et al.*, 2003; Finger *et al.*, 2007), coastal cliff and wave-cut platform in front of Matanzas village, coast 4 km SW of Navidad, SW of Santiago, central Chile, coll. V. Covacevich & D. Frassinetti, 15 September 1976; with one complete juvenile paratype, SGO.PI 5841 (Pl. 30, Figs 3, 5) and two fragmentary paratypes (SGO.PI 5840, 5842). An incomplete paratype is also present at SMF (SMF 333438), collected by S. Nielsen from his locality RAP, coastal cliffs N of the mouth of Río Rapel, a few km N of the type locality. I have seen only the type material. Nielsen (2003: pl. 17, figs 13-16) illustrated the holotype and the complete juvenile paratype.

Remarks.—*Crassicymatium crassicordatum* n. gen., n. sp. differs from all other evenly inflated taxa of Ranellidae of which I am aware by its bizarre, enormously developed spiral cinguli with undercut edges, resembling the cinguli of the well-known American muricid genus *Ecphora*, and by its varices being positioned at each 200-210° around the spire, intermediate between the 180° or 240° of all other evenly inflated Ranellidae. A few strongly laterally compressed species of Cymatiinae, such as *Reticutriton elmerensis* (English, 1914) (see below), have their varices placed much more nearly together at the “sides” of the shell than in their evenly inflated relatives, because their marked compression allows them to produce varices only toward the edges of the strongly compressed shell, and leaves the wide dorsal and ventral surfaces free of varices, but this is a very different situation from the evenly inflated *Crassicymatium crassicordatum* n. gen., n. sp.

Distribution.—*Crassicymatium crassicordatum* n. gen., n. sp. is recorded only from the Navidad Fm (Oligocene-Early Miocene fossils displaced into Late Miocene-Early Pliocene rocks) at Matanzas and the coastal cliffs N of the mouth of Río Rapel, near Navidad, central Chile.

Etymology.—As with the generic name, the specific name (Latin, *crassum*, heavy, coarse; + *cordum*, a rope, used for a rib or ridge) refers to the very prominent spiral cords of this species.

Genus *CYMATIUM* Röding, 1798

Cymatium Röding, 1798: 129. Type species (by subsequent designation, Dall, 1904: 133): *Murex femorale* Linnaeus, 1758,

Pleistocene and Recent, western Atlantic.

Lotorium Montfort, 1810: 583. Type species (by monotypy): *Lotorium lotor* Montfort, 1810 (= *Murex femorale* Linnaeus, 1758).

Tritocurrus Lesson, 1842: column 65. Type species (by subsequent designation, Emerson & Old, 1963a: 3): *Trito currus (sic) amphitridis* Lesson, 1842 (= *Triton tigrinum* Broderip, 1833), Pleistocene(?) and Recent, Panamic western America. [The proposal of the new genus and species *Tritocurrus amphitridis* implies that the type species was selected by monotypy, but Lesson (1842) mentioned *Cymatium femorale* (Linnaeus, 1758) and *Lotoria lotoria* (Linnaeus, 1758) in his description (repeated below under *C. tigrinum*) and could be considered to have included them in the new genus, so the type species is regarded as selected by subsequent designation].

Luterium Herrmannsen, 1846: 631. Emendation of *Lotorium* Montfort, 1810.

Nyctilochus Gistel, 1848: xi. Type species (by subsequent designation, Beu, 1970b: 206): *Triton tigrinum* Broderip, 1833.

Remarks.—I have recently (Beu, 1998b) reviewed the subgenera of *Cymatium* and their defining characters, and this classification is essentially followed here, although the subgenera are ranked here as genera. I have long vacillated between ranking these taxa as either subgenera (influenced by the more conservative American tradition, particularly Clench & Turner (1957), and by the narrow distinction between some groups) and the narrower “Iredalean” tradition of Australasia and Japan in which they have usually been ranked as full genera. Recently a number of colleagues have expressed an opinion to me that the subgenera of *Cymatium* are similar to the increasingly narrower subdivisions ranked as genera in larger families such as the Muricidae and Buccinidae. Geerat Vermeij (University of California, Davis, pers. comm., April 2007) also pointed out that ranking groups as subgenera of another group expresses a phylogenetic hypothesis about their relationships that for the most part cannot be proven, and that narrower taxa are more likely to be monophyletic than broader ones. Narrow genera of Cymatiinae are therefore adopted here.

Cymatium contains species with large shells (140-250 mm H), a very large, capacious last whorl that tapers gradually toward the anterior to produce a triangular shell shape, a short spire, a relatively short anterior siphonal canal, a small, narrow, almost vestigial operculum (much smaller than the aperture) with an anterior terminal nucleus, and a tall, narrow protoconch with whorls lightly angled near the center of their height. In all other species of genera related to *Cymatium* for which the operculum has been described, it seals the entire aperture when the animal is retracted. Similarly, all other closely related taxa for which the protoconch has been described have a similarly tall protoconch (although it is relatively short in some *Ranularia*, *Septa*, and *Turritriton* spp.), but with evenly convex whorls. Four of the five species referred to *Cymatium*

occur in the tropical American region.

The species referred to *Cymatium* are:

- *femorale* (Linnaeus, 1758), Pliocene-Recent, western Atlantic & Cape Verde Islands.
- *praefemorale* (Maury, 1917), Late Miocene and Early Pliocene, Caribbean.
- *raderi* D'Attilio & Myers, 1984 (= *etcheversi* Macsotay & Campos Villarroel, 2001), Recent, western Atlantic.
- *ranzanii* (Bianconi, 1850), Recent, East Africa and Gulf of Arabia.
- *tigrinum* (Broderip, 1833), Pleistocene and Recent, western America and Galápagos Islands.

***Cymatium femorale* (Linnaeus, 1758)**

Pl. 30, Figs 6-7, 9-12; Pl. 31, Figs 2, 5-7

Murex femorale Linnaeus, 1758: 749; 1767: 1217; Gmelin, 1791: 3533.

Lotorium lotor Montfort, 1810: 583, illus.

Septa triangularis Perry, 1811: pl. 14, fig. 6.

Triton lotorium Lamarck, 1816: pl. 415, fig. 2, "Liste des objets": 4; 1822: 182; Deshayes, 1843: 631 (junior secondary homonym of *Murex lotorium* Linnaeus, 1758).

Triton femorale. Kiener, 1842: 10, pl. 10, fig. 1 (as *T. lotorium* in caption); Reeve, 1844a: pl. 7, fig. 22.

Tritonium femorale. Krebs, 1864: 23; Coomans, 1963: 64, 80.

Triton femoralis. Guppy, 1876: 522.

Triton (Cymatium) femorale. Mörch, 1877: 31; Tryon, 1880: 18, pl. 10, fig. 70.

Tritonium (Cymatium) femorale. Gabb, 1881: 352.

Lotorium femorale. Dall, 1889: 132; 1903b: 132; Dall & Simpson, 1901: 417.

Nyctilochus femorale. Maury, 1922: 116.

Cymatium femorale. Piele, 1926: 80; Morretes, 1949: 92; Abbott, 1954: 195, pl. 5, fig. d; 1974: 163, pl. 7, fig. 1751; Rios, 1970: 70, pl. 17; 1975: 78, pl. 21, fig. 315; 1985: 75, pl. 26, fig. 326; 1994: 87, pl. 29, fig. 339; Kaufmann & Götting, 1970: 371, fig. 86; Calvo, 1987: fig. 77 (radula); Leal, 1991: 114; Lipe & Abbott, 1991: 10, illus.; Guerreiro & Reiner, 2000: 113-114.

Triton (Lotorium) femorale. Coulon, 1933: 128, 134.

Cymatium (Cymatium) femorale. M. Smith, 1948: p. 1, pl. 2, fig. 13; Clench & Turner, 1957: 232, pl. 110, fig. 1.; pl. 112, figs 9-10, pl. 113, fig. 11 (in part only, not pl. 129, figs 2-3); Warmke & Abbott, 1962: 102, pl. 2, fig. c; Kiliass, 1973: 113, fig. 82; van Regteren Altena, 1975: 37; Beu, 1985: 58; Henning & Hemmen, 1993: 50, pl. 10, fig. 1; Piech, 1995: 8; Macsotay & Campos Villarroel, 2001: 64, pl. 12, fig. 5; Redfern, 2001: 60, pl. 30, figs 256A-D.

Remarks.—*Cymatium femorale* is a large (to ca. 210 mm H), spectacular shell, unique among the Recent ranellids of the western Atlantic (other than the very similar *C. raderi*) for its very large, wide, triangular last whorl, with the varices protruding strongly at large shoulder nodules to give the triangular

shape, with a moderately wide, gently sloping, concave sutural ramp, and with a short, stepped spire. However, most specimens are markedly smaller than *C. raderi* (ca. 120-150 mm H, compared with 200-225 mm in most adult *C. raderi*). The aperture is most unusually wide and elongate, tapering gradually into the anterior canal, and the operculum of living specimens is only about a fifth of the aperture length. *Cymatium ranzanii* (Bianconi, 1850), from the western Indian Ocean (as far south as Durban, South Africa) and Gulf of Arabia (Bosch *et al.*, 1995: 96, fig. 349), reaches a larger size than *C. femorale*, has a more narrowly triangular shape and still more massive varices, but has much weaker spiral sculpture than that of *C. femorale*, and has larger nodules inside the outer lip than any other *Cymatium* species and a large, distinctive black area on the outer parietal part of the inner lip. Its strongly angled periphery bears large, rounded nodes similar to those of *C. tigrinum*, but they are more strongly antero-posteriorly compressed than in *C. tigrinum*. Differences from the apparently distinct western Atlantic species *C. raderi* are discussed under *C. raderi*. Specimens of both *C. femorale* and *C. raderi* are illustrated excellently in color on a webpage (<http://www.femorale.com.br/shellphotos>, last accessed 28 April 2006).

Dimensions.—NMB 17692, Recent, largest seen, from Islas Chimanas, Estado Anzoategui, E. Venezuela, coll. J. d'Esposito, J. & W. Gibson-Smith collection: H 211, D 127 mm; figured specimen, NMB H 17925, from NMB 17512, Mare Fm (Late Pliocene), Cabo Blanco, Venezuela: H 78.7, D 48.0 mm; GNS WM18427, sand flat, 5 km off Marathon Key, Florida: H 159.2, D 67.5 mm; GNS WM17563, Harbour Island, N Eleuthera, Bahamas: H 151.3, D 76.7 mm; GNS WM17564, Baie de Robert, Martinique: H 143.3, D 69.0 mm; GNS WM9236, Key West, Florida: H 136.0, D 66.1 mm.

Types.—Linnaeus' collection, housed at the Linnean Society of London, includes one box containing three small, immature specimens (Pl. 30, Figs 6-7, 9-12) of the species known to all authors as *Cymatium femorale*; i.e., there is no question that any of them might be *C. raderi*. The largest of these three syntypes (H 62.2 mm, D 34.6 mm; Pl. 30, Figs 7, 9) is an abraded specimen with the spire apex and anterior end of the anterior canal missing, marked "531" inside the aperture in Linnaeus' handwriting; 531 is the species number of *Murex femorale* in the 12th edition of *Systema Naturae* (Linnaeus, 1767: 1217), demonstrating that this is a genuine syntype of *M. femorale*. The next-largest specimen (H 60.0 mm, D 31.0 mm; Pl. 30, Figs 11-12) is a fresh, unabraded specimen of *C. femorale*, marked "531" twice inside the aperture. The smallest syntype is a very small, unmarked shell (Pl. 30, Figs 6, 10). Clench & Turner (1957: 232) designated the type locality as Jamaica. According to Wallin (1993: 76), 3 further syntypes of *M. femorale* are present in Uppsala University Zoological

Museum, UZZM 695, UZZM 896, and UZZM 982. Two of these (UZZM 695 and 982) were identified as *Cymatium femorale* by the well-known malacologist Nils Odhner, but the third apparently is a specimen of "*Murex lampas*" Linnaeus [which could be intended for either *Charonia lampas* or *Tutufa bubo* (Linnaeus, 1758)]. Because the identifications were made by Odhner long before the similar species *C. raderi* was named, there is no guarantee that the specimens identified as *C. femorale* are not *C. raderi*. Because of the specimen of another genus (*Charonia* or *Tutufa*) and doubts over the identity of the other syntypes, the medium-sized syntype (H 60.0 mm) in Linnaeus' collection in London, marked "531" twice inside the aperture (Pl. 30, Figs 11-12) is here designated the lectotype of *M. femorale*. Because no type material is known today from the works of Montfort (1810) or Perry (1811), the lectotype of *M. femorale* is here designated the neotype of both *Lotorium lotor* and *Septa triangularis*. Emerson & Old (1963b: 2-3) repeated Perry's (1811: pl. 14, fig. 6) colored drawing of *S. triangularis*, and agreed with previous authors (Dodge, 1957; Clench & Turner, 1957) that this rather undiagnostic drawing probably was intended to represent *C. femorale*, but it is important to designate a neotype for it to be certain that it cannot threaten other, later names such as *C. raderi*, *C. ranzanii*, or *C. tigrinum*. Although Lamarck (1816: pl. 415, fig. 2) clearly published the name *Triton lotorium* for this species, his material in MHNG is now labelled "*Triton femorale* Lamk." [the species now known as *C. lotorium* (Linnaeus, 1758) was named *T. rhinoceros* by Lamarck (1922)]. Evidently this specimen has been relabelled since Lamarck owned the collection, along with several other species in his collection; the three lots with this label all are assumed to be syntypes of *T. lotorium*. MHNG 1099/90 is a single moderate-sized specimen, labelled "Antilles"; MHNG 1099/91 consists of three smaller specimens, again labelled "Antilles", and of these MHNG 1099/91/2 is clearly the specimen illustrated by Lamarck (1816: pl. 415, fig. 2) and by Kiener (1842: pl. 10, fig. 1), and is here designated the lectotype of *T. lotorium*. MHNG 1099/92 is a single large specimen, labelled by Lamarck inside the aperture.

Other material examined.—Recent: I have not recorded most material examined of this common species; the list almost certainly includes some specimens of *Cymatium raderi*; localities include South Carolina (Isle of Palms, LACM. H-654, 1 large), Bermuda (BMNH 1911.12.21.614, 1), Bahamas, Florida, Cuba, Haiti, Dominican Republic, Puerto Rico, Aruba, Curaçao, Barbados, Antillean islands (St. Croix, Guadeloupe, Martinique, St. Barthelemy, St. Kitts, St. Eustatius, St. Martin, Antigua; Mayreaux Island, Grendines), E Honduras, Venezuela, and Brazil (Medo Island, Salvador, Bahia, GNS WM14014, 1; 20-25 m, off of Alcobaça, southern Bahia, GNS WM17258, 2).

Fossils: Atlantic Costa Rica: Late Pliocene-earliest Pleistocene: Specimens were recorded from the Moín Fm at Limón, Atlantic coast of Costa Rica, by Gabb (1881: 352, "a couple of fine specimens") and by Robinson (1991: 315), 2 juvenile specimens, up to 18 mm H, from TU 954 and 1489, in Tulane University collections, which I have not examined. **Jamaica: Late Pliocene:** Bowden: NMB 11146 (1 small spire). **Colombia: Pleistocene:** terrace ca. 10 m above high tide, La Cieba, Departamento de Atlantico (UCMP S-46, 1 small). **Venezuela: Late Pliocene:** NMB 17512, Mare Fm (1, NMB H 17925; Pl. 31, Figs 6-7); Mare Fm, Cabo Blanco (CAS, 1 small).

Distribution.—*Cymatium femorale* lives now throughout the western Atlantic, from Bermuda and South Carolina, USA, throughout the Caribbean, south to Bahia, Brazil (Clench & Turner, 1957: 232-233; Coelho *et al.*, 1981: 128) and to Santa Catarina, Brazil, and Montague Seamounts (Rios, 1994: 87). Guerreiro & Reiner (2000: 113-114) recorded the first specimens from the eastern Atlantic, from São Vicente, Cape Verde Islands (on the basis of two empty shells, from "Fateixa e João D'Évora"). Their photographs clearly show specimens with the high, "hunched" shoulder nodules diagnostic of *C. femorale*. Like most of the other western Atlantic tonnoideans that, in small numbers, *almost* but do not quite reach the West African coast, these specimens presumably represent a pseudopopulation recruited from the western Atlantic, outside the normal breeding range of the species. If *C. femorale* proves to occur in the Cape Verde Islands, but *C. raderi* does not, it would provide strong evidence for the specific distinction of the two forms. Fossils are recorded from Late Pliocene and Pleistocene rocks only, in Jamaica and around the Atlantic coasts of tropical America.

Coulon (1933: 134) recorded three fossil specimens of "*Triton femorale* Lamk." from the Pliocene of Monastir, Tunisia, North Africa. It seems likely that this results from either a mislocalization or a misidentification, but in view of the record of Recent specimens from the Cape Verde Islands (Guerreiro & Reiner, 2000: 113-114), it is faintly possible that fossils could occur in Tunisia. Coulon's material (which I have not seen), presumably in the Musée d'Elbeuf, requires checking to verify this record.

Cymatium praeformale (Maury, 1917)

Pl. 31, Fig. 3; Pl. 33, Figs 1-9

Tritonium (*Cymatium*) *femorale*. Gabb, 1873: 211 (not *Murex femorale* Linnaeus, 1758).

Triton femoralis. Guppy, 1874: 438; 1876: 522 (not *Murex femorale* Linnaeus, 1758).

Lotorium praeformale Maury, 1917a: 270, pl. 17, fig. 3.

Cymatium praeformale. Pilsbry, 1922: 356; D'Attilio & Myers, 1984: 33, figs 5-6.

Cymatium (Cymatium) praefemorale. Pflug, 1961: 38, pl. 8, figs 3-4, 8-12.

Remarks.—Maury (1917a: 270) distinguished *Cymatium praefemorale* from *C. femorale* by the spire being “fusiform in the early stages,” not carinate or bearing a median row of nodules as in *C. femorale*, and by the aperture being ovate rather than “bi-angulate,” as in *C. femorale*. The differences between the two species are rather slight, but seem to be consistent. As noted by Maury (1917a), the spiral cords on early spire whorls of *C. praefemorale* are more numerous (6 or 7) and more uniform in height, width and spacing than in *C. femorale*, in which there are only three major cords on spire whorls, the one at the shoulder angle being the most prominent and the other two lying below that, so that there are no major cords on the sutural ramp and the shoulder angle is much more clearly defined than in *C. praefemorale*. The three spiral cords on the sutural ramp of early spire whorls of *C. praefemorale* are reduced in number progressively down the shell, so that large adults have only one low cord on the sutural ramp. The sutural ramp of adult *C. femorale* lacks major spiral cords, but most specimens have numerous, prominent, secondary spiral ridges on the ramp that are absent from *C. praefemorale*. The major spiral cords on the last whorl in *C. praefemorale* and the axial costae on the dorsum of nodulose specimens are lower, narrower, and more rounded, *i.e.*, less prominent than those of *C. femorale*. As was also pointed out by Maury (1917a), the aperture of *C. praefemorale* is smaller in proportion at all shell sizes than in *C. femorale*, both narrower and shorter, so that it is more evenly oval in shape. This is brought about partly by the top (posterior end) of the aperture not extending as far up onto the previous whorl as it does in *C. femorale*, and partly by the varices of *C. praefemorale* being less strongly shouldered and lacking the posteriorly directed shoulder nodule of *C. femorale*, so that the aperture is not drawn out to the right at the posterior end. Finally, the fine, slightly wavy axial ridgelets that are so characteristic of the external teleoconch surface of *C. praefemorale* are very much finer and less obvious in *C. femorale*. On the basis of its prominent, wavy axial ridgelets, fragments of a large specimen from the Early Pliocene Cayo Agua Fm of Atlantic Panama (Pl. 31, Fig. 3) are identified as *C. praefemorale*, the first record outside the Dominican Republic.

It seems feasible that *Cymatium praefemorale* was the direct ancestor of *C. femorale* and/or *C. raderi*. The other two species are also similar to *C. praefemorale*, and it is likely that *Cymatium* evolved and spread during Neogene time.

Dimensions.—Holotype of *Lotorium praefemorale*: H 81.3, D 50.2 mm; TU 1231, Río Gurabo: H 92.4, H 48.4 mm; figured specimen, NMB H 17927, from NMB 19023 (TU 1455), Dominican Republic: H 143.0, D 65.0 mm.

Types.—*Lotorium praefemorale*, holotype PRI 28759, “ex Gabb Coll.”; Maury stated the type locality to be “Zone F,” Río Gurabo at Los Quemados, Dominican Republic, Late Miocene, which suggests that the holotype was collected by Schmidt and Olsson. Evidently Maury used the poorly localized Gabb specimen as the holotype as better than later-collected material, and adopted the locality of the later one as the type locality.

Other material examined.—**Fossils: Atlantic Panama: Pliocene:** Cayo Agua Fm: NMB 17829, E coast Cayo Agua (2 frags from one large specimen, NMB H 17926; illustrated, Pl. 31, Fig. 3). **Dominican Republic: Late Miocene:** Cercado Fm: NMB 15899 (1); NMB 15905 (1); 16835 (1); 16838 (1, illustrated, NMB H 18329, Pl. 33, Figs 5-6); 16839 (1); 16982, Cercado Fm, Río Cana, collection of Bernard Landau (1); 15906, Río Gurabo, Cercado Fm, coll. M. Taviani (Zoological Museum, University of Bologna, 2); Gurabo Fm: NMB 16910 (1); TU 1280 = NMB 19014 (2; 1 illustrated, NMB H 18324, Pl. 33, Figs 1-2); USGS 8519 (3). **Late Miocene/Early Pliocene:** Gurabo Fm: TU 1225 (GNS WM18830, 1); 1231 = NMB 19006 (8; 2 illustrated, NMB H 18325, Pl. 33, Fig. 3; NMB H 18326, Pl. 33, Fig. 4; GNS WM16922, 1); 1250 (GNS WM18825, 3 frags); 1293 (GNS WM18828, 1); 1455 = NMB 19023 (1, illustrated, NMB H 17927; Pl. 33, Fig. 7); USGS 26275 (2). **Early Pliocene:** Gurabo Fm: NMB 15807 (1); 15836 (2); 15838 (1); 15864 (1); 15866 (1); 16818 (1); 16864 (1); TU 1210 = NMB 18578 (1, NMB H 18328, illustrated, Pl. 33, Figs 8-9); 1211 (GNS WM18829, 1); 1215 (GNS WM18695, 3); 1219 (GNS WM16915, 5); 1227 (GNS WM 18831, 1 frag); 1248 (GNS WM18826, 1); 1354 (GNS WM18828, 3); PRI, Maury’s loc. 207, Zone F, Río Gurabo (2, incomplete); 1215, Gurabo Fm, Río Gurabo, collection of Bernard Landau (6); 1219, Gurabo Fm, Río Amina, collection of Bernard Landau (2 large); 1354, Gurabo Fm, Cañada de Zamba, collection of Bernard Landau (1); Mao Fm: TU 1365 (GNS WM18824, 1 frag).

Distribution.—*Cymatium praefemorale* is recorded only from the Late Miocene-Early Pliocene Cercado to Mao Formations of the Dominican Republic (where it is moderately common; 47 specimens seen, plus the holotype) and from the Early Pliocene of Cayo Agua, Atlantic Panama (one specimen).

Cymatium raderi D’Attilio & Myers, 1984

Pl. 31, Figs 1, 4; Pl. 32, Figs 1-3

Cymatium femorale. Clench & Turner, 1957: pl. 129, figs 1-2 (in part not *Murex femorale* Linnaeus, 1758); Okutani, 1983: 255, illus.; Diaz & Puyana, 1994: 172, fig. 638.

Cymatium (Cymatium) femorale. Coelho *et al.*, 1981: 128, fig. 11; H. & E. Vokes, 1983: 22, pl. 11, fig. 2 (not *Murex femorale* Linnaeus, 1758).

Cymatium raderi D'Attilio & Myers, 1984: 33, figs 7-12.

Cymatium (Cymatium) raderi. Beu, 1985: 58; Henning & Hemmen, 1993: 50, pl. 10, fig. 2; Rios, 1994: 88, fig. 340; Lee, 2005: 3, figs 1-7.

Cymatium (Cymatium) etcheversi Macsotay & Campos Villarroel, 2001: 65, pl. 6, figs 14-15.

Remarks.—D'Attilio & Myers (1984) proposed *Cymatium raderi* for specimens differing from *C. femorale* in having a marked, triangular angle at the posterior end of the terminal varix, but no prominent, posteriorly directed nodule on the shoulder of each varix, so that the sutural ramp is flat and slopes weakly anteriorly, or even can be convex over the varices, rather than being concave as in *C. femorale*, in having lower spiral cords and very much weaker nodules or, in most specimens, no nodules at all on the spiral cords in the intervartical intervals, and in having lower and much less protruding nodules formed by the spiral cords around the outer edge of the terminal varix, but prominent, purplish red nodules inside the outer lip that are absent from *C. femorale*. Some of the characters of some specimens that they illustrated as *C. raderi* are the result of the specimens having lived in relatively deep water (e.g., the weakly sculptured specimen illustrated by D'Attilio & Myers, 1984: figs 9-10); the normal ranellid tendency for shells to become thinner, paler, and more weakly sculptured as they are collected progressively further offshore obviously affects *C. femorale* and *C. raderi* as much as other taxa. Many specimens of this complex examined since 1984 also seem to have the distinguishing characters weakly developed; while not exactly intermediate specimens, many can be difficult to place in one species or the other. Jack Gibson-Smith pointed out the possibility that the differences between these supposed species are due to sexual dimorphism; the "heavier" and more coarsely nodulose specimens are male, whereas the "lighter," less strongly nodulose ones are female, when collected alive, at least in one case that he observed in Venezuela. However, Brazilian colleagues insist that these two species consistently and easily are separable in Brazil, the consistently smaller *C. femorale* living in shallower water than the much larger *C. raderi*. *Cymatium raderi* recently has been redescribed under the name *C. etcheversi* by Macsotay & Campos Villarroel (2001: 65, pl. 6, figs 14-15), lending support to its separability from *C. femorale*.

I remain unsure of the status of the form named *Cymatium raderi*, because the differences are less than those between (e.g.) conspecific forms in *Crossata ventricosa* and *Priene scabrum*. Only molecular techniques will resolve the question of its status with certainty, but it seems likely to be a species distinct from *C. femorale*. I have few data on the range and variation of *C. raderi*, because until recently, I assumed that it is a synonym of *C. femorale*. Several illustrations in earlier works show *C. raderi* rather than *C. femorale*; even the illus-

trations by Clench & Turner (1957: 129, figs 1-2) show *C. raderi*, as was pointed out by Lee (2005). I have endeavored to sort the synonymy list out to include illustrations that definitely show *C. raderi*. Lee (2005) pointed out that Bob Work had recognized this species distinction in the 1950s, and sent specimens of *C. raderi* to Bill Clench from Bear Cut, Miami, Florida which, however, Clench & Turner (1957: 129, figs 1-2) illustrated as *C. femorale*. Lee (2005) very clearly defined the differences between these two species, their distributions, and the history of their recognition. It is unfortunate that the very conservative species taxonomy of Tryon's (1880-1881) influential *Manual of Conchology* lingered for so long in North American molluscan taxonomy as to still affect the species recognized by Clench & Turner (1957). Their failure to recognize the distinction between *C. pileare* (Linnaeus, 1759) and *C. aquatile* (Reeve, 1844) is even more surprising, but is a direct hold-over from Tryon.

Dimensions.—*Cymatium raderi* holotype: H 185, D 90 mm; paratypes: H 136, D 59 mm, H 187, D 87 mm, H 196, D 87 mm; H 192, D 87 mm; and H 124, D 69 mm (D'Attilio & Myers, 1984: 34); *C. etcheversi* holotype: H 117, D 84 mm (Macsotay & Campos Villarroel, 2001: 65); GNS WM17275, Rio de Fogo, North Natal, Rio Grande do Norte, Brazil: H 224.2, D 94.9 mm; H 219.2, D 110.5 mm.

Type material.—*Cymatium raderi*, holotype SDNHM 81627 (D'Attilio & Myers, 1984: figs 7-8), with 5 paratypes (SDNHM 81628; AMNH 182782; 1 in collection of L. J. Bibbey; 2 in collection of J. Rader); holotype and most paratypes from fishermen, collected off the east coast of Honduras; paratype AMNH 182782 from Tobago Island, West Indies (none seen). *Cymatium etcheversi*, holotype at Museo de Biología del Instituto de Zoología Tropical, Universidad Central de Venezuela, Caracas, Venezuela, catalogue no. MBUCV-XIV-4719, with 1 paratype, MBUCV-XIV-4692, from Margarita platform, N and NE of Isla Margarita, E Venezuela (Macsotay & Campos Villarroel, 2001: 65) (not seen).

Other material examined.—**Recent:** The following few lots have been examined during the last few years. **Bahamas:** Cherokee Sound (GNS WM16216, 1). **Honduras:** 50 m, trawled off NE Honduras (GNS WM13264, 2; WM13595, 3); trawled, 30-45 m, between Punta Patuca and Punta Castilla (GNS WM18429, 1). **Suriname:** dredged by shrimp fishers, off of Suriname, 50-60 m (RMNH, 3); ca. 100 m, Japanese shrimpers off Paramaribo (GNS WM16219, 1). **Guiana:** 50 m, off of French Guiana (GNS WM17020, 1). **Brazil:** Ilha Itaparica, Bahia (RMNH 912, 1); 25 m, off Rio Grande do Norte (GNS WM17113, 1); 30-50 m, off of Ceará (GNS WM18428, 1); Recife, Pernambuco (GNS WM15224, 1; WM16218, 1); 15 m, Itamaracá, Pernambuco (GNS WM17562, 2); lobster divers, on coral reef at 10-20 m, Rio de

Fogo, North Natal, Rio Grande do Norte (GNS WM17257, 2); lobster traps, 10-20 m, off of Tutóia, Maranhão State (GNS WM17256, 2).

Distribution.—*Cymatium raderi* has been collected in small numbers as far north as Florida, USA, and the Bahamas (Clench & Turner, 1957: pl. 129, figs 1-2; Lee, 2005). Records also extend from the western Gulf of Mexico and the southern Lesser Antilles and, in particular, off the coast of Venezuela, south to Brazil (Ceará to Bahia; Rios, 1994: 88). Most of the material in museums and collections is from Brazil. *Cymatium femorale* is correspondingly uncommon to rare in these same areas where *C. raderi* is common, although cases are known of their living closely nearby each other; Lee (2005) illustrated specimens of both species collected in Florida, the Bahamas, and Jamaica. I am not aware of fossil specimens of *C. raderi*.

***Cymatium tigrinum* (Broderip, 1833)**

Pl. 34, Figs 1, 4

?*Triton femorale* var. G. B. Sowerby I, 1825: 66; Mörch, 1860: 82.
Triton tigrinum Broderip, 1833: 5; Reeve, 1844a: pl. 8, fig. 27.
Tritocurrus amphytridis Lesson, 1842: column 65.
Triton (Lotorium) tigrinum. Chenu, 1859: 152, fig. 695.
Triton (Cymatium) tigrinum. Mörch, 1860: 82.
Triton (Cymatium) tigrinus. Tryon, 1880: 18, pl. 10, figs 71-72.
 ?*Cymatium* sp. aff. *tigrinus*. Dall & Ochsner, 1928: 97.
Triton (Lotorium) tigrinus. Coulon, 1933: 128.
Cymatium (Cymatium) tigrinum. M. Smith, 1948: 1, pl. 2, fig. 15;
 Clench & Turner, 1957: 233, pl. 130, figs 1-2; Keen, 1971:
 504, fig. 953; Kilias, 1973: 120, fig. 88; Beu, 1985: 58, fig. 12;
 Henning & Hemmen, 1993: 52, pl. 10, fig. 4; Piech, 1995: 8;
 López de la Fuente & Ramos, 2004: 85.

Remarks.—*Cymatium tigrinum* is a rare species that has been mentioned little in the literature, and its distribution and habitat are poorly known. It is a large (ca. 150-180 mm H), wide shell resembling *C. femorale* in shape, at least in a general way. It differs from *C. femorale* and *C. raderi* in having weaker spiral sculpture over the last whorl or two, so that although there are 8 or 9 spiral cords and numerous interstitial spiral threads on the last whorl, they are lower and less clearly defined than those of *C. femorale* and *C. raderi*. However, early spire whorls are much more strongly sculptured than in *C. femorale*, with a wide, flat, steeply inclined sutural ramp bearing three widely spaced, prominent spiral cords, a prominent, wide peripheral keel bearing two closely spaced, prominent, smooth spiral cords, and one relatively narrow, smooth cord visible below the keel; there is no obvious axial sculpture other than the 5-6 large, angling nodules per whorl. Only the last 2 or 3 varices are obvious on large adults. Most specimens produce two closely spaced, fringed axial blades of periostracum at each varix, so on some large shells, the three strongly angled ridges each consist of two axial blades, and in some specimens these

are aligned to form ridges down the last 2-3 whorls. Several specimens that I have examined have three sets of paired, closely spaced varices, each coinciding with an axial periostracal ridge. The shoulders of the varices are low and rounded, not extended into the extreme, posteriorly directed nodules of *C. femorale*, so that the sutural ramp is slightly convex and the aperture is more oval than in *C. femorale*. The interior of the outer lip is smooth, and weakly folded in conformity with the exterior cords, but lacks the nodules of *C. femorale* and, in particular, *C. raderi*. The dorsum of the exterior lacks the prominent, nodulose axial costae of *C. femorale*, but instead many specimens of *C. tigrinum* have 2 or 3 large, swollen, spirally elongate nodes, much wider than a spiral cord, around the periphery in each intervariceal interval on the last whorl. This species is distinct enough from the Atlantic species *C. femorale* and *C. raderi* to suggest that it has been separate from them since at least Pliocene time, rather than forming a geminate species pair, in the sense of speciating after uplift of the CAI. Specimens are illustrated excellently in color on a webpage (<http://www.femorale.com.br/shellphotos>, last accessed 28 April 2006).

Because the original description of *Tritocurrus amphytridis* Lesson (1842: column 65) is in a rare scientific “news” journal, the rather long French description is worth quoting in full here [followed by translation]:

“Ce magnifique triton appartient au même groupe que les *triton femorale* et *lotorium* de Lamarck. C’est une coquille que attient jusqu’à 16 centimetres de longueur sur 8 de largeur, turriculée et à spire courte, les sept tours sont déprimés et aplatis sur les côtés, saillant et anguleux en dessus, aplatis en dessous, ce qui donne à cette coquille une forme triangulaire. Le dernier tour est beaucoup plus grand que tous les autres réunis; il a en dessus une forte éminence gibbeuse, d’où semblent s’irradier de grosses côtes, mais qui ne sont en peu apparentes que sur le rebord du lèvre, et qui se manifeste dans le haut, où un autre éminence s’élève sur le côté. Ces côtes sont nulles chez les jeunes sujets qui n’ont que la grosse côte supérieure et mamelonnée, partant de ce point culminant du test. Les derniers tours ont des stries transversales plus manifestes et assez serrées et comme cordonnées, saillantes et mamelonnées dans le milieu de chaque tour. La surface inférieure est plane, masquée de quatre côtes peu en relief. Sa coloration est un jaune orangé brunâtre.

L’ouverture est ovulaire-allongée, blanche au fond, jaune orangé avec larges macules brun marron espacées sur le rebord droit. Celiu-ci est large, excessivement épais, lisse et légèrement sinueux, mais sans nodosités. La columelle est concave, jaune orangé, marquée au milieu et en dedans de deux dents, don’t une très-forte. Le canal est allongée, légèrement tordu, et la columelle, en s’atténuant à la naissance de ce canal, laisse paraître l’ouverture ombilicale qui a la forme d’une scissure

qui va s'élargissant.

Un épiderme épais, rouge brun, couvre le test; mais cet épiderme forme des franges longues et abondantes sur les côtés des tours, sur leurs angles et sur le rebord de l'ouverture. Cette coquille est une des plus belles espèces du genre."

Translation: This magnificent triton belongs to the same group as *Triton femorale* and *lotorium* of Lamarck. It is a shell that reaches up to 16 cm H and 8 cm D, turriculated and with a short spire, the seven whorls are depressed and flattened on the sides, projecting and angled on the dorsum, flattened below, giving this shell a triangular shape. The last whorl is larger than all the others combined; it bears a large gibbous prominence on the dorsum, from which the wide ribs seem to radiate, but which are only a little apparent except on the edge of the outer lip, and which are obvious on the top where another prominence is raised on the side. These ribs are not present on young specimens, which have only the wide, mammillate uppermost rib, radiating from this culminating point of the shell. The last whorls have more manifest and serried transverse [spiral or axial?, unclear] ribs like cords, projecting and mammillated in the center of each whorl. The interior surface is flat, masked by four ribs with little relief. Its color is a brownish orange-yellow.

The aperture is elongate-oval, white inside, orangish yellow with large brown-maroon maculations widely spaced on the inner lip. This is wide, excessively thick, smooth, and lightly sinuous, but without nodules. The columella is concave, orangish yellow, marked in the middle and inside by two teeth, of which one is very prominent. The canal is elongate, lightly twisted, and the columella, which reaches to the beginning of this canal, leaves an umbilical opening visible that has the shape of an enlarging slit.

A thick red-brown epidermis covers the shell; but this epidermis forms long, abundant fringes on the sides of the whorls, on their angles and on the varix of the aperture. This shell is one of the most beautiful species of the genus. [End of translation; right and left lip usage follows the spire-down Continental convention, the opposite of the Anglophone spire-up convention, and has been reversed in the translation.]

The height of 16 cm, the similarity to "*Triton femorale* and *lotorium*," the description of the triangular shape, the last whorl much larger than all the others combined, the smooth interior of the outer lip lacking nodules, the large maroon-brown maculations on the inner lip, the reddish brown periostracum bearing many fringes, and the statement that "this shell is one of the most beautiful species in the genus" leave no doubt that this is a description of the species that Broderip (1833: 5) previously had named *Triton tigrinum*. The full text is cited here; there is no locality information other than in the title, and the location of the specimen is not stated (as was

usual at the time) and remains unknown.

Dimensions.—The maximum recorded height is 194 mm (Skoglund, 1992); Montijo Bay, W Panama, GNS WM17500: H 177.0, D 103.6 mm; Palo Seco, Canal Zone, W Panama, GNS WM13366: H 163.6, D 83.3 mm; syntypes, BMNH 1950.8.28.21: H 166.2, D 90.1 mm, H 142.3, D 79.9 mm, H 140.9, D 71.6 mm.

Types.—*Triton tigrinum*, 3 syntypes BMNH 1950.8.28.21; from "Guacomayo," Central America. As pointed out by Clench & Turner (1957), this name appears not to be in current use; it is probably more misinformation by Hugh Cuming. The illustrated syntype is here designated the lectotype of *T. tigrinum*. Because the locality "Guacomayo" is unknown, the type locality of *T. tigrinum* is also designated as Corinto, Nicaragua. *Tritocurrus amphytridis*, location of type material not known, not in MNHN; Lesson gave no locality other than in the title, "Realejo (Center-Amérique)." This refers to Corinto, Pacific coast of Nicaragua (Morton & Keen, 1960: 27). The lectotype of *T. tigrinum* figured here (Pl. 34, Figs 1, 4) is here designated the neotype of *T. amphytridis*.

Other material examined.—**Recent: Pacific Costa Rica:** Guanacaste (LACM. HH-706, 1); 3-15 m, 2.5 km E of Punta Ballena, Bahia Ballena, Puntarenas Province, *Searcher* sta. 431-432 (LACM 72-42, 1); 2-15 m, head of Golfo Dulce, ca. 2 km NW of Rincon de Osa, Puntarenas Province, *Searcher* sta. 499 (LACM 72-71, 1). **Pacific Panama:** intertidal, Venado Island (LACM-A. 9334.70, 1, live-collected; LACM. B-387, 2); Venado Beach (LACM 20896, 1; LACM 21543, 1); Panama Bay (LACM 23253, 2); Palo Seco, Canal Zone (GNS WM13366, 2); low tide, Pedro Gonzales Island (GNS WM16221, 1); W Panama (GNS WM10116, 1; WM16220, 1); Veracruz, intertidal, -1.4 tide, *ex* A. R. Arthur collection (GNS WM17499, 1 juvenile); trawled, Montijo Bay, *ex* A. R. Arthur collection (GNS WM17500, 1); trawled, 30 m, off of Pedro Gonzales Island, *ex* A. R. Arthur collection (GNS WM17501, 1).

Fossils: I have not seen any fossils of *Cymatium tigrinum*, but Dall & Ochsner (1928: 97) listed "*Cymatium* sp. *aff. tigrinus* Broderip" from their loc. B2, "upper zones," Indefatigable Island, Galápagos Islands, Pleistocene. Garcia-Talavera (1993: 33) also recorded "*Cymatium* cf. *tigrinum*" as a Pleistocene fossil from Isla de Santa Fe, Galápagos Islands so, although this species apparently has not been recorded in the living fauna of the Galápagos Islands, it evidently lived there in the past.

Distribution.—*Cymatium tigrinum* was reported by Keen (1971: 504) to range from La Paz, Gulf of California, western Mexico, south to Panama. Most material seen is from Panama Bay. Kilius (1973: 88) illustrated a specimen said to be from "Punta Arenas, Chile," but this is clearly an error for Puntarenas Province, western Costa Rica. It seems likely that this species occurs at least as far south as Ecuador, and pos-

sibly to northern Peru, but it definitely does not occur as far south as the cold waters of Punta Arenas, on the Straits of Magellan. There appear to be no records of Recent specimens from the Galápagos Islands, although the only fossils are reported from there. Although many specimens seem to have been collected in the intertidal zone, others were trawled in up to 30 m of water.

Genus **GELAGNA** Schaufuss, 1869

Lagena "Klein" Mörch, 1853: 110. Type species (by subsequent designation, Dall, 1904: 139): *Triton clandestinum* Lamarck, 1816 (= *Murex succinctus* Linnaeus, 1771), Miocene to Recent, Indo-West Pacific and eastern and western Atlantic (junior homonym of *Lagena* Walker & Boys, 1784, Foraminifera, of *Lagena* Röding, 1798, and of *Lagena* Schumacher, 1817).

Gelagna Schaufuss, 1869: 3. Type species (by subsequent designation, Iredale, 1917: 325): *Triton clandestinum* Lamarck, 1816 (= *Murex succinctus* Linnaeus, 1771).

Paralagena Dall, 1904: 132. Replacement name for *Lagena* Mörch, 1853, preoccupied.

Remarks.—The genus *Gelagna* is distinguished by its strongly and evenly convex whorls and deeply impressed suture, by its prominent, smooth spiral cords and almost complete lack of axial sculpture, by most specimens developing only a terminal varix, and by its oval operculum with a subcentral nucleus near its columellar edge. Only two species are known at present, *G. succincta* (Linnaeus, 1771), occurring throughout the Indo-West Pacific province and, rarely, throughout the tropical Atlantic, and *G. pallida* (Parth, 1996), occurring only in the western Indian Ocean.

Gelagna succincta (Linnaeus, 1771)

Pl. 34, Fig. 5

Murex succinctus Linnaeus, 1771: 551; Hanley, 1855: 456.

Buccinum caudatum var. β Gmelin, 1791: 3471.

Neptunea doliata Röding, 1798: 116.

Triton clandestinum Lamarck, 1816: pl. 433, fig. 1, "Liste des objets": 8; 1822: 187; Kiener, 1842: 35, pl. 11, fig. 2; Deshayes, 1843: 639.

Murex clandestinus. Dillwyn, 1817: 723.

Triton clandestinus. Reeve, 1844a: pl. 4, fig. 13; Küster & Kobelt, 1871: 184, pl. 52, figs 5-6.

Ranularia (Lagena) clandestinus. Mörch, 1853: 110.

Triton (Lagena) clandestinum. Chenu, 1859: 154, fig. 702.

Tritonium (Gelagna) clandestinum. Schaufuss, 1869: 29.

Triton (Linatella) clandestinus. Tryon, 1880: 15, pl. 9, fig. 58.

Triton confinis Brancsik, 1896: 211, pl. 5, figs 1a-b.

Argobuccinum succinctum. Hedley, 1908: 456.

Triton (Lagena) clandestinus. Coulon, 1933: 131.

Gelagna clandestina. Habe, 1961: 45, pl. 22, fig. 12; 1964: 72, pl. 22, fig. 12.

Gelagna succincta. Rippingale & McMichael, 1963: 63, pl. 6, fig. 28; Salvat *et al.*, 1988: 103, pl. 13, fig. 5; Lai, 1989: 126, fig. 52.

Gelagna cynocephala. Habe & Kosuge, 1966a: 61, pl. 24, fig. 5 (not *Triton cynocephalum* Lamarck, 1816).

Cymatium (Linatella) clandestinum. Kiliyas, 1973: 125, fig. 91; Kay, 1979: 220, fig. 79A; Bernard, 1981: 17, right fig.

Cymatium (Linatella) succinctum. Bernard, 1984: 60, pl. 22, fig. 94.

Linatella (Gelagna) succincta. Beu, 1985: 60, fig. 26; Beu & Cernohorsky, 1986: 257, figs 28-33; Rios, 1985: 77, pl. 27, fig. 338; 1994: 91, fig. 357; Springsteen & Leobrera, 1986: 112, pl. 30, fig. 15; Henning & Hemmen, 1993: 110, pl. 20, figs 5-6; Piech, 1995: 17; Kaiser, 1997: 32.

Linatella succincta. Finet, 1991: 270; Kubo in Kubo & Kurozumi, 1995: 76, fig. 8; Ardovini & Cossignani, 2004: 130, central left fig.

Cymatium (Gelagna) succinctum. Wilson, 1993: 244, pl. 41, fig. 3; Beu, 1998b: 79, figs 23e, 24a-c; 1999: 13, figs 21-23; 2005: 73, fig. 186; Okutani, 2000: 291, pl. 144, fig. 37; Beu & Segers in Poppe, 2008: 640, pl. 265, fig. 3.

Gelagna cf. *succincta* (sic). Guerreiro & Reiner, 2000: 115.

Cymatium succinctum. Lee & Chao, 2003: 41, pl. 4, fig. 101.

Remarks.—This highly distinctive species is easily recognized by its strongly and evenly convex whorls, and by its sole sculpture consisting of prominent, smooth, polished spiral cords, which are a much darker brown than the rest of the shell in Recent specimens. *Gelagna succincta* has long been a well-known shell in the tropical Indo-West Pacific, and it is rather surprising that so striking a shell should be discovered in the Atlantic only in the 1980s. The first Atlantic record of which I am aware was by Bernard (1981), from Gabon, West Africa, and a short time later it was reported from Bahia, Brazil, by Rios (1985: 77; 1994: 91).

Dimensions.—GNS WM15008, Mactan Island, Cebu, Philippine Islands: H 62.3, D 31.8 mm; reaching at least 101 mm in height (Parth, 1996: fig. 1a).

Types.—Lectotype of *Murex succinctus*, designated by me (Beu, 1998b: 80, figs 24a-c) in Linnean Society of London; I designated (Beu, 1998b) the type locality as Bohol Island, Philippine Islands. The lectotype of *M. succinctus* was also designated by me (Beu, 1998b) as the neotype of *Neptunea doliata*. *Triton clandestinum*, lectotype MHNG 1100/16/2, designated by me and Cernohorsky (1986: 258), with two paralectotypes (MHNG 1100/16/1, 1100/16/3). Brancsik (1896) stated that his material is in "Musei budapestini"; type material of *Triton confinis* not seen; from Astrolabe Bay, Papua New Guinea. Brancsik's (1896: pl. 5, figs 1a-b) illustrations leave no doubt that this is a synonym of *Gelagna succincta*.

Other material examined.—**Recent: Atlantic:** Guadeloupe, West Indies, from local fishermen (1, collection of D. Lamy; Pl. 34, Fig. 5); also, the illustrations by Bernard (1984: pl. 22, fig. 94) of specimens from Gabon, and by Rios (1985: 77, pl. 27, fig. 338; 1994: 91, pl. 30, fig. 357) of a specimen from

northeastern Brazil, leave no doubt of the identity of their specimens. **E Pacific:** Shasky (1989) and Emerson (1991: 68) recorded a specimen from the Galápagos Islands in the eastern Pacific, and Shasky (1996: 38, fig. 4) illustrated a juvenile specimen, 10.4 mm high, from Isla de Coco, off the coast of Costa Rica (collected alive under a slab at 13 m, at Bahia Weston, 13 April 1983).

Distribution.—*Gelagna succincta* occurs uncommonly throughout the Red Sea and the entire Indo-West Pacific province, from East Africa (as far south as Conducia Bay, Mozambique; 3 specimens in NMP) to Hawaii, and from Okinawa south to Barrow Island, Western Australia (Wilson, 1993: 244), to New Caledonia and to Fitzroy Island, southern Queensland; one specimen was recorded from the Galápagos Islands by Emerson (1991), and Shasky (1996) recorded a specimen from Isla de Coco. In the Atlantic, there are few records other than those by Bernard (1981, 1984) from Gabon, and by Rios (1985, 1994) from Bahia, Brazil. Guerreiro & Reiner (2000: 115) recorded a small specimen from São Vicente, Cape Verde Islands, and Dominique Lamy (Guadeloupe) has a magnificent specimen from Guadeloupe, lesser Antilles. Although fossils are reported from Miocene and Pliocene rocks in the Indo-West Pacific, there are no fossil records in either the Atlantic or the eastern Pacific.

Genus *GUTTURNIUM* Mörch, 1853

Gutturnium Mörch, 1853: 109. Type species (by subsequent designation, Dall, 1904: 133): *Triton tuberosum* Lamarck, 1822 (= *Distorsio muricina* Röding, 1798), Miocene to Recent, Indo-West Pacific and eastern and western Atlantic.

Afrocanidea Connolly, 1929: 178. Type species (by original designation): *A. gemma* Connolly, 1929 [supposedly a terrestrial snail, but a larval shell of *G. muricinum* (Röding, 1798); Beu, 1998b: 80, fig. 25].

Remarks.—The genus *Gutturnium* contains only the single species *G. muricinum*, an unusual species that resembles *Ranularia* species in its strongly callused aperture and moderately long anterior canal, but differs from them in having an anterior terminal opercular nucleus, whereas in *Ranularia*, the nucleus is situated near the center of the columellar edge, as in *Bufonaria* and the phaliine cassids — although it is a little nearer to the opercular center (situated inside the margin) in some species of *Ranularia*. The protoconch of *G. muricinum* also is shorter and wider and with a more weakly indented suture and less inflated whorls, producing a distinctive, wider and more inflated protoconch than those of most other species of Cymatiinae. The distinction between *Gutturnium* and *Monoplex* is slight, and molecular study is required to confirm or deny the status of *Gutturnium*, but the *status quo* is maintained at present.

Gutturnium muricinum (Röding, 1798)

Pl. 34, Figs 2-3

Distorsio muricina Röding, 1798: 133.

Tritonium nodulus Link, 1807: 122.

Triton tuberosum Lamarck, 1822: 185; Kiener, 1842: 12, pl. 14, fig. 2; Deshayes, 1843: 635.

Ranella gyriata Risso, 1826b: 203, pl. 8, fig. 115; Arnaud, 1978: 119.

Triton antillarum Orbigny, 1841a: 161, pl. 23, fig. 20; Krebs, 1864: 22; Mörch, 1877: 31.

Triton tuberosus. Reeve, 1844a: pl. 1, fig. 1a, b; Ávila *et al.*, 1998: 499.

Triton crispus Reeve, 1844a: pl. 17, fig. 68; 1844c: 118.

Triton pyriformis Conrad, 1849a: 211.

Litiopa obesa C. B. Adams, 1850a: 71 (larval shell).

Triton productum Gould, 1851: 240; Johnson, 1964: 132.

Triton (Gutturnium) antillarum. Chenu, 1859: 153, fig. 697.

Triton albocingulatus Deshayes, 1863: E113.

Tritonium (Ranularia) nodulus. Tapparone-Canefri, 1881: 35 (making available a pre-Linnean name).

Tritonium (Gutturnium) tuberosum. Martin, 1884: 129.

Ranularia tuberosa. Dall, 1903b: 132; Morretes, 1949: 92.

Cymatium tuberosum. Piele, 1926: 80.

Afrocanidea gemma Connolly, 1929: 178 (larval shell).

Triton (Lampresia [sic]) tuberosum. Coulon, 1933: 125.

Ranularia (Gutturnium) tuberosa. Trechman, 1933: 39.

Cymatium (Gutturnium) muricinum. Clench & Turner, 1957: 225, pl. 112, figs 5-6, pl. 113, fig. 8, pl. 126, figs 1-3, pl. 127; Warmke & Abbott, 1962: 101, pl. 18, figs h, f [not *C. parthenopeum*]; Andrews, 1971: 103, fig. p. 104; Abbott, 1974: 165, pl. 7, fig. 1764; Andrews, 1977: 130, illus.; Kay, 1979: 217, fig. 77E; H. & E. Vokes, 1983: 23, pl. 11, fig. 8; Beu, 1985: 58, fig. 13; 1998b: 81, figs 23d, 25; 1999: 15, fig. 25; Rios, 1985: 75, pl. 27, fig. 327; 1994: 88, fig. 341; Springsteen & Leobrera, 1986: 112, pl. 30, fig. 12; Garcia-Talavera, 1987: 252, pl. 1, fig. 6; Lai, 1989: 119, fig. 16; Henning & Hemmen, 1993: 53, pl. 11, figs 4-5; Wilson, 1993: 244, pl. 41, fig. 6; Piech, 1995: 9; Kaiser, 1997: 32; Okutani, 2000: 289, pl. 143, fig. 24; Macsotay & Campos Villarroel, 2001: 66; Redfern, 2001: 60, pl. 31, fig. 257A, B; pl. 109, fig. 257C; Zhang & Ma, 2004: 132, text-fig. 82; Beu, 2005: 74, figs 188-189; Beu & Segers in Poppe, 2008: 640, pl. 265, figs 1-4.

Gutturnium muricinum. Habe, 1961: 45, pl. 22, fig. 10; 1964: 72, pl. 22, fig. 10; Wilson & Gillett, 1971: 78, pl. 53, figs 4-4a.

Cymatium muricinum. Work, 1969: 663; Hinton, 1972: 12, pl. 6, figs 12-14; Salvat & Rives, 1975: 306, fig. 174; Hinton, 1978: 29, fig. 5; Garcia-Talavera, 1983: 111, pl. 4, fig. 3; Bandel, 1984: 99, pl. 10, fig. 1; Drivas & Jay, 1988: 64, pl. 17, fig. 6; de Jong & Coomans, 1988: 69; Jensen & Harasewych, 1986: 428, illus.; Emerson, 1991: 68, table 1; Finet, 1991: 270; Lipe & Abbott, 1991: 12, illus.; Vega-Luz & Vega-Luz, 1995: 7; Kubo in Kubo & Kurozumi, 1995: 76, fig. 6; Hickman & Finet, 1999: 72, fig. 64.

Cymatium (Ranularia) muricinum. Kilius, 1973: 243, fig. 105; 1981: 705.

Ranularia (Gutturium) muricinum. Kilburn, 1984: 3, pl. C, fig. 1.

Remarks.—*Gutturium muricinum* is easily recognized by its rather small size (reaching ca. 70 mm H, but Atlantic specimens rarely exceeding 50 mm), moderately tall spire and moderately long anterior canal, by the gray-brown exterior of most specimens, sculptured with low, wide, rounded, roughly and irregularly nodulose spiral cords and several prominent varices and, in particular, by its heavily and smoothly callused aperture with widely flared, out-turned lips, covering the face of the terminal varix and much of the ventral surface of the whorl alongside the inner lip, and with prominent, rounded transverse ridges inside both lips. The aperture and callus are white, and the interior of the shell is a deep brownish red in most specimens. The short, stout protoconch with very weakly impressed sutures is also distinctive. *Gutturium muricinum* occurs in two color forms, uniformly gray or brownish gray, with a narrow, peribasal, medium-brown spiral band on some specimens, or with the anterior half of the last whorl or even the entire shell uniform medium to dark brown, in some specimens with a narrow, paler, grayish spiral peribasal band. It is this latter color form that was named *Triton albocingulatus* by Deshayes (1863). Many specimens with a brown teleoconch have a markedly darker protoconch than those with a gray teleoconch.

Gutturium muricinum is one of the most abundant species of shallow-water Cymatiinae throughout the Indo-West Pacific province, rivalled perhaps only by *Monoplex nicobaricus*, and is moderately common in the western Atlantic, so it is not surprising to find there are several records of young fossils in the western Atlantic area.

Dimensions.—GNS WM18388, Apia, W Samoa: H 65.6, D 31.5 mm; GNS WM18380, 8-12 m, Fort de France, Martinique: H 53.0, D 28.1 mm; GNS WM16230, Cuba: H 43.8, D 24.1 mm; GNS WM17008, Guadeloupe: H 40.3, D 23.0 mm.

Types.—The synonyms and types were reviewed by me (Beu, 1998b). *Triton tuberosum*, lectotype MHNG 1100/4/2, designated by me (Beu, 1998b), the original of Kiener (1842: pl. 14, fig. 2), with two paralectotypes (MHNG 1100/4/1, 1100/4/3). The lectotype of *T. tuberosum* was also designated the neotype of *Distorsio muricina*, of *Tritonium nodulus*, and of *Triton productum*. I designated (Beu, 1998b) the type locality as Ambon Island (Amboina), Indonesia. *Ranella gyri-nata*, supposedly from the Mediterranean, lectotype designated by Arnaud (1978: 119) at MNHN, a typical specimen of *Gutturium muricinum*. *Triton crispus*, holotype BMNH 196739, a small specimen of *G. muricinum*. *Triton antillarum*, lectotype BMNH 1854.10.4.406/1, the specimen illustrated by d'Orbigny (1841a: pl. 23, fig. 20), designated by me (Beu, 1998b), with one paralectotype, labelled "Martinique." *Triton*

pyriformis, no type material known. *Litiopa obesa*, holotype MCZ 186594, a larval shell of *G. muricinum* (Turner, 1956: 136). *Triton albocingulatus*, lectotype (designated by me; Beu, 1998b) and two paralectotypes in MNHN, from "Bourbon" (Réunion), three specimens of the dark brown color form of *G. muricinum* with a pale peribasal band. *Afrocanidea gemma*, holotype BMNH 1937.12.30.4936 (Beu, 1998b: figs 25a-b), a larval shell of *G. muricinum*, discussed by Bouchet (pers. comm. in Beu, 1998b: 80); supposedly a land snail from the Shimbi Hills, Kenya, but evidently mislocalized.

Other material examined.—**Recent:** Western Atlantic lots have not been listed for this abundant species; 12 lots at GNS, from Bahamas, Cuba, Tortola, Bequia, Martinique, Guadeloupe (5 lots, including GNS WM17008, 31), Trinidad, Bonaire, and Margarita Island, Venezuela. **E Atlantic: Canary Islands:** 6 m, off of Tenerife (GNS WM15183, 1); Santa Cruz de La Palma (GNS WM15184, 1). **Cape Verde Islands:** "Îles du Cap Vert," coll. Bouvier, ex Fischer collection (MNHN, 1).

Fossils: Bermuda: Pleistocene (or Holocene?): USNM, unnumbered, south shore of Bermuda (1). **Cuba: Pleistocene:** USGS 7943 (1); 12103a (1); 12103b (1). **Dominican Republic: Pleistocene:** La Isabella Fm, El Castillo, La Isabella, collection of Bernard Landau (5). **Barbados: Pleistocene:** NMB 10118 (1; figured, NMB H 18051); USGS 18381 (3); 18382 (2). **Venezuela: Pleistocene:** NMB 17541 (1).

Distribution.—*Gutturium muricinum* occurs commonly throughout the entire Indo-West Pacific province, including the Red Sea, from eastern South Africa to Hawaii (Kay, 1979) and eastern French Polynesia, and from Kii Peninsula, Honshu, Japan (Habe, 1964: 72) to Shark Bay in Western Australia (Wilson, 1993: 244) and to southernmost Queensland in eastern Australia. It is recorded rarely in the eastern Pacific, at the Galápagos Islands (Emerson, 1991: 68; Hickman & Finet, 1999) and a single specimen has been collected on the mainland, at Isla Gobernadora in Panama Bay (Emerson, 1983: 119, figs 15-16). In the western Atlantic, it is recorded from Bermuda and from Jupiter Inlet, Florida, USA, south to Paraná, Brazil (Rios, 1985: 75; 1994: 88). In the eastern Atlantic, it has been recorded only from the Azores (MacAndrew, 1856, cited in Ávila *et al.*, 1998: 499), the Canary Islands (García-Talavera, 1983: 111; TFMC 1443, Santa Cruz de La Palma, 2 specimens; TFMC 2976, Tenerife, 1; TFMC 1468, Dázena comercial, Santa Cruz de Tenerife, 2; TFMC 1467, alive in 5 m, Club Nautico, Santa Cruz de Tenerife, 1), and the Cape Verde Islands (one specimen in MNHN, "Îles du Cap Vert, coll. Bouvier, ex Fischer collection"). Fossils are recorded quite widely in the western Atlantic, but (as with *Bursa granularis*, *Monoplex mundus*, and *M. nicobaricus*) only in Pleistocene deposits. Gregory (1895: 288) and Trechman (1933: 39) recorded Pleistocene fossils

from Barbados, and Rutten (1931: 664) recorded fossils (as *Triton antillarum*) from Pleistocene rocks of Curaçao, citing two earlier publications that I have not seen.

Genus *LINATELLA* Gray, 1857

Linatella Gray, 1857: 39. Type species (by monotypy): “*L. cingulata*” (= *Cassidaria cingulata* Lamarck, 1822; = *Buccinum caudatum* Gmelin, 1791), Miocene to Recent, Indo-West Pacific and eastern and western Atlantic.

Remarks.—Although Beu & Cernohorsky (1986) treated *Linatella* as a full genus of Cymatiinae, I removed (Beu, 1998b) “*Linatella*” *wiegmanni* (Anton, 1838) to the subgenus *Cymatium* (*Monoplex*), leaving only one species in *Linatella*, which was then reduced to a subgenus of *Cymatium*. Along with the other former subgenera of *Cymatium*, *Linatella* is recognized as a full genus again here. Beu & Cernohorsky (1986) also revised the synonyms and type specimens of *L. caudata* and “*L. wiegmanni*”, so much of this need only be summarized here.

I noted (Beu, 1998b: 84) that, as a result of reducing *Linatella* to a subgenus of *Cymatium*, two unrelated species both bore the name *C. caudatum* (Gmelin, 1791): *C. (Ranularia) caudatum*, a well-known name for which no obvious synonym is available, and *C. (Linatella) caudatum*, for which Lamarck provided not one but two younger synonyms. As first reviser, I adopted the name *Cymatium (Ranularia) caudatum* as the senior homonym to be used by all authors who regard the secondary homonyms *C. (Ranularia) caudatum* and *C. (Linatella) caudatum* as congeneric. The next available synonym, *Fusus cutaceus* Lamarck, 1816, was therefore adopted for the species also known as *C. (Linatella) caudata*. However, Gary Rosenberg (ANSP; pers. comm., 2001) pointed out to me that Clench & Turner (1957: 198) listed the name *F. cutaceus* in the synonymy of this species, and replaced it with the next name of which they were aware, *C. poulsenii* (Mörch, 1877), because they thought that *F. cutaceus* was a junior secondary homonym of the Mediterranean species usually known as *Cabestana cutacea* (Linnaeus, 1758). Because *F. cutaceus* was replaced because of secondary homonymy before 1961, it is permanently unavailable (ICZN Article 59.3) and the next available name must be used. The next name, *Cassidaria cingulata* Lamarck, 1822, was therefore adopted, and *C. (L.) cingulatum* was used as the valid name for this species by me (Beu, 1999, 2001, 2005; Beu & Segers in Poppe, 2008). Now that I recognize *Linatella* again as a full genus, the two names *Murex caudatum* Gmelin, 1791 (now *Ranularia caudata*) and *Buccinum caudatum* Gmelin, 1791 (now *L. caudata*) are no longer secondary homonyms, and although these alternating name changes are most undesirable, the latter name must be

reinstated, because *L. caudata* has been used as the valid name after 1899, and was replaced because of secondary homonymy after 1961 (ICZN Article 59.4).

Linatella caudata (Gmelin, 1791)

Pl. 34, Figs 6-10; Pl. 63, Figs 8, 11

Buccinum caudatum Gmelin, 1791: 3471.

Fusus cutaceus Lamarck, 1816: pl. 427, figa 4a-b, “Liste des objets”: 6 (unavailable; replaced because of secondary homonymy before 1961).

Cassidaria cingulata Lamarck, 1822: 216.

Fusus voigtii Anton, 1838: 77.

Triton undosum Kiener, 1842: 44, pl. 6, fig. 2 (not *T. undosum* Lamarck, 1816, = *Buccinum undosum* Linnaeus, 1758).

Ranularia (Lagena) rostratus “Martini” Mörch, 1853: 110 (adoption of a name now ruled non-binominal).

Triton (Linatella) poulsenii Mörch, 1877: 33.

Triton (Linatella) rostratum. Mörch, 1877: 33.

Tritonium (Cabestana) verbeeki Boettger, 1883: 37, pl. 1, figs 10a-b.

Purpura (Polytropa) bantamensis Martin, 1899: 135, pl. 21, figs 310, 310a, 311.

Cassis (Semicassis) tegalensis Martin, 1899: 156, pl. 24, fig. 363.

Dolium losariense Martin, 1899: 163, pl. 24, figs 377-378.

Cymatium (Linatella) krenkeli Cox, 1930: 118, pl. 12, figs 20-21b.

Cymatium (Linatella) floridanum Mansfield, 1930: 94, pl. 12, fig. 10; Petuch, 1994: pl. 39, fig. K.

Cymatium (Linatella) cingulatum peninsulum M. Smith, 1937: 113, pl. 1, fig. 2, pl. 44, fig. 5.

Cymatium (Linatella) poulsenii. Clench & Turner, 1957: 198, pl. 111, figs 7-8, pl. 113, fig. 2, pl. 115, figs 1-3; Warmke & Abbott, 1962: 100, pl. 18, fig. e; Andrews, 1971: 105, illus.; van Regteren Altena, 1975: 36, fig. 14; Coelho *et al.*, 1981: 116; Macsotay & Campos Villarroel, 2001: 66, pl. 11, fig. 23.

Linatella neptunia Garrard, 1963: 43, pl. 7, figs 7-8.

Cymatium poulsenii. Coomans, 1963: 81.

Cymatium (Linatella) cingulatum. Kiliyas, 1973: 122, fig. 89; 1981: 704; Abbott, 1974: 164, pl. 7, fig. 1761; Andrews, 1977: 132, illus.; H. & E. Vokes, 1983: 22, pl. 11, fig. 6; Okutani, 1983: 258, illus.; Hu, 1992: 763, pl. 125, figs 33, 35; Beu, 1999: 16, figs 27-30; 2001: 712, fig. 2; 2005: 75, figs 190-197; Beu & Segers in Poppe, 2008: 640, pl. 265, figs 2, 5, 6.

Linatella (Linatella) caudata. Kilburn, 1984: 3, pl. C, fig. g; Beu, 1985: 60, fig. 24; Beu & Cernohorsky, 1986: 244, figs 1-2, 5-22 (with further synonymy); Henning & Hemmen, 1993: 107, pl. 20, fig. 3; Rios, 1994: 90, fig. 356; Piech, 1995: 17.

Cymatium cingulatum. Lipe & Abbott, 1991: 12, illus.

Neptunea szukouensis Hu & Tao, 1991: 340, pl. 60, figs 1-2; Tao & Hu, 1992: 1446, pl. 250, figs 7, 9.

Cymatium andoi. Tao & Hu, 1992: 1441, pl. 249, figs 19-20 only (in part not *Cymatium andoi* Nomura, 1935, = *Murex pilearis* Linnaeus, 1758).

Cymatium (Linatella) cutaceum. Wilson, 1993: 244, pl. 41, fig. 7; Beu, 1998b: 83; Okutani, 2000: 291, pl. 144, fig. 38; Zhang & Ma, 2004: 158, text-figs 98a-b.

Linatella caudata. Vega-Luz & Vega-Luz, 1995: 7.

Linatella cingulata. Guerreiro & Reiner, 2000: 110.

Cymatium cutaceum. Lee & Chao, 2003: 41, pl. 4, fig. 96.

?*Linatella* cfr. *caudata*. Ardovini & Cossignani, 2004: 130, bottom left fig.

Remarks.—*Linatella caudata* is recognizable by its *Tonna*-like shape and sculpture, with a rather low spire, although obviously taller than in *Tonna* species, a short, widely open anterior siphonal canal, lightly shouldered but otherwise strongly and evenly inflated whorls, sculpture of low, wide, rounded, closely spaced spiral cords, and only a weak terminal varix developed on most specimens. Many but by no means all specimens have low nodules around the shoulder angle. The prominence of the shoulder angle is highly variable. The width and prominence of the spiral cords is also highly variable, from wide, closely spaced, even cords, to alternating wide and narrow ones, and some specimens have narrow spiral interspaces between the cords, whereas they are equal in width to one cord on most others. The operculum is oval, with the nucleus near the center of the columellar margin. Despite these distinctive characters, *L. caudata* has been misidentified by more authors than any other tonnoidean of which I am aware. Martin (1899, 1919) in his monographs of Javanese fossils provided three synonyms (in Tonnidae, Cassidae, and Muricidae) and even during the 1990s, authors have continued to misidentify it as a variety of other gastropods (e.g., Hu & Tao, 1991; Tao & Hu, 1992). Brazilian specimens are illustrated excellently in color on a webpage (<http://www.femorale.com.br/shellphotos>, last accessed 28 April 2006).

Dimensions.—Largest specimen seen, USGS 26552, Florida State Rte. 68, NW of Lake Okeechobee, Elderberry, Florida, probably from Pinecrest Fm: H 96.7, D 60.5 mm; holotype of *Cymatium (Linatella) floridanum*, USNM 370465: H 25.0, D 17.1 mm; presumed holotype of *Triton (Linatella) poulsenii*, in ZMC: H 46.7, D 33.7 mm.

Types.—Neotype of *Buccinum caudatum* and lectotype of both *Fusus cutaceus* and *Cassidaria cingulata* (all designated by Beu & Cernohorsky, 1986), Lamarck type collection, MHNG 1100/74/1; type locality here designated as Bohol Island, Philippines. The location of the lectotype of *Fusus voigtii* is unknown (the specimen illustrated by Philippi, 1842-1851: *Fusus* pl. 1, fig. 1). Schniebs (1997, 2000) listed and illustrated several of Anton's types, at the Staatliches Museum für Tierkunde, Dresden, but although the holotype of *F. wiegmanni* is present (Schniebs, 2000: figs 8a-b), that of *F. voigtii* evidently is not. It could well be in Philippi's collection, at the National Museum of Natural History, Santiago, Chile, but, because no type material of either *Tritonium contabulatum* Anton, 1838, or *T. munsteri* Anton, 1838, evidently is present in Dresden, all three types might simply be lost. *Triton (Linatella) poulsenii*, presumed holotype in ZMC, labelled "*Linateria (sic) Poulsenii* Mörch, Panama, Swift [from] Riise,

no. 498," and with another label reading "*Triton chemnitzii*, Swift. — Swift thinks it's from Panama," although if so the type locality must be on the Atlantic coast of Panama, near Colon. *Tritonium (Cabestana) verbeeki*, holotype SMF XII/2881a (Beu, 2005: figs 194-195), "Eburnamergel von Pfahl 65 (Druchst. von Kampai), Seluma, Sumatra, Verbeek," late Miocene. *Cassis tegalensis*, holotype RGM 9979 (Beu, 2005: figs 190-191), Pangkah, Residence of Tegal, Java, Pliocene; an abraded half-shell, anterior missing; its wide, flat-topped spiral cords and narrow axial ridges indicate that this is probably *Linatella caudata*. *Dolium losariense*, figured syntype RGM 10038 (Beu, 2005: figs 192-193), Menengteng Gorge, Waled, Java, Pliocene, a spire of *L. caudata*; syntype RGM 10039, Junghuhn's locality L, Java, Preanger (Priangan), a very poor, distorted mold of *L. caudata*; 2 syntypes RGM 10037 (Beu, 2005: figs 196-197), Menengteng Gorge, Cheribon (Cirebon), Java, Pliocene, one of them figured by Martin; incomplete but undoubted specimens of *L. caudata*. *Purpura (Polytropha) bantamensis*, lectotype (designated by Beu & Cernohorsky, 1986), RGM 9726, from "Tji Keusik (Cikusik), Java," with 2 paralectotypes, all from the Pliocene Bantam Fm. *Cymatium (Linatella) krenkeli*, holotype (S4456) and 3 paratypes in Hunterian Museum, University of Glasgow, from Pliocene of Mombassa Island, Kenya, East Africa (not seen). *Cymatium (Linatella) floridanum*, holotype USNM 370465 (Pl. 34, Fig. 6), from the Pliocene Jackson Bluff Fm (Choctawhatchee Group), Florida. *Cymatium (Linatella) cingulatum peninsulum*, holotype (not seen) in Florida Museum of Natural History, Gainesville (Clench & Turner, 1957: 199), presumably the specimen illustrated by M. Smith (1937: pl. 1, fig. 2), from Lake Worth, Florida. *Linatella neptunia*, holotype AMS C.62552, from 55 m, off of Southport, Queensland; with 4 paratypes. *Neptunea szukouensis*, holotype (an incomplete but normal specimen of *L. caudata*) in National Museum of Natural Sciences, Taichung, Taiwan, NMNS 0568, from Si-gou layer (Pleistocene), Heng-chun terrace, Heng-Chun Peninsula, Taiwan (not seen; synonymy based on illustration by Hu & Tao, 1991: pl. 60, figs 1-2).

Other material examined.—**Recent.** **W Atlantic:** 39 lots examined, in ANSP, GNS, LACM, NMB, RMNH, SMF, USNM; from Georgia, USA (*Pelican* sta. 179-5, 170 km ESE of Altamaha Island, McIntosh Co, USNM 486555, 1), Florida, Texas, E Mexico, E Panama, Colombia, Haiti, Virgin Islands, Venezuela, French Guiana, and Brazil (25 m, under dead coral, off of Fortaleza, Ceará, GNS WM17455, 1). **E Atlantic.** **W Africa:** Conakry, Guinée, 20-30 m (MNHN, 1); dredged, 20-30 m, off of Conakry, Guinea, M. Pin (GNS WM14952, 3 large); *Canap III* sta. 3.129, Tydeman Madeira-Mauritania Expedition 1978, 32 m, off of Mauritania, 18°56'N, 16°27'W (RMNH, 9 small). **Canary Islands:** from fishermen's nets, Punta de las Nieves, near Agaete, Gran

Canaria, coll. R. von Cosel (MNHN, 15; SMF, 27); Las Nievas, Agaete, Gran Canaria (RMNH, 4; GNS WM16270, 1; WM18210, 4); San Andrés, Tenerife, from fishermen's traps in *ca.* 25 m, with pagurids (TFMC, several hundred; GNS WM15189, 1; WM 17700, 16).

Fossils: **Florida: Pliocene:** the holotype of *C. floridanum* (Pl. 34, Fig. 6) is from the Jackson Bluff Fm (Choctawhatchee Group), USGS 11732; 26552, Pinecrest Fm (middle Pliocene), 4.8 km W of Indian Prairie Canal, Lake Okeechobee, Elderberry (1, largest specimen seen, illustrated, Pl. 34, Figs 8, 10); Petuch (1994: pl. 39, fig. K) also illustrated a specimen [as *Cymatium (Linatella) floridanum*] from Petuch unit 7, APAC pit, Sarasota, Florida. **Atlantic Costa Rica: Pliocene:** USGS 5882A (7); 5883A (3). **Pacific Costa Rica: Miocene:** NMB 17764 (1). **Atlantic Panama: Miocene:** Valiente Fm: USGS 8326, two cays off Bluefields Point, Valiente Peninsula (1). **Pliocene:** Cayo Agua Fm: NMB 18735, coast W of Punta di Nispero, Cayo Agua (1). **Pacific Panama: Pleistocene:** NMB 17442, Armuelles Fm, Río Rabo de Puerco, Burica Peninsula (5, well-preserved to rather abraded small juveniles; one illustrated, NMB H 18343, Pl. 63, Figs 8, 11). **Colombia: Miocene:** Fault Peak, SE of Agua Viva, N of Usiacuri, Departamento de Atlantico (UCMP S-7396, 1, large). **Trinidad: Early Pliocene:** USGS 18634 (1); Springvale Fm (Early Pliocene; Donovan, 1994), Springvale Quarry (UCMP S-7959, 2). **Venezuela: Early Pliocene:** NMB 12045, collection described by Rutsch (1934) (2); NMB 12865 (1); 13892 (1); 17531 (4); Cerro Negro Member, Cubagua Fm (Early Pliocene), *ca.* 400 m SW of house at Las Calderas, Cubagua Island, Nueva Esparta (UCMP S-122, 2; 1 illustrated, Pl. 34, Fig. 7); Río Sabanita traverse, Falcón (UCMP S-150, 1). **Pleistocene:** NMB 17541 (1).

Distribution.—Although nowhere very common (except off of San Andrés, Tenerife, and Agaete, Gran Canaria, both in the Canary Islands, where empty shells are collected in large numbers in fishing nets), *Linatella caudata* occurs widely throughout the Indo-West Pacific province from East Africa and the Red Sea east to Hawaii (Kay, 1979) and from southern Japan (quite common in Yamaguchi and Wakayama Prefectures, southern Honshu; Beu, 1999; Koyama, 2004; Toki *et al.*, 2005) to northern New Zealand (one authentic record; Beu & Cernohorsky, 1986). The southernmost South African material seen is from Knysna Lagoon, southern Cape Province, South Africa, on intertidal sand flats (NMP E.6331, 1 small); other rather surprising intertidal material from South Africa includes Kosi Bay estuary, Zululand, intertidal on eastern shore, alive among *Pinna* (NMP D.9735, 5). I did not report specimens from New Caledonia, although this was among the species that I (Beu, 1998b: 17) thought “eventually might be found” in New Caledonia; two specimens from New Caledonia now have been recognized at MNHN.

In the western Atlantic, it occurs from Chincoteague Inlet, Virginia (Merrill & Porter, 1966), south to Río de Janeiro, Brazil (Rios, 1994: 90). In the eastern Atlantic, *L. caudata* is abundant off the Canary Islands (hundreds of specimens from fishermen's nets shown to me by F. Garcia-Talavera and A. de Vera, TFMC; reported also by Nordsieck & Garcia-Talavera, 1979: 118; Saunders, 1980: 7), and a specimen is present at CASIZ from the Cape Verde Islands. Fossils are widespread but uncommon throughout the Indo-West Pacific as well, from the Pliocene of Zanzibar (Cox, 1930), Pleistocene of Taiwan (Hu & Tao, 1991) and the Miocene-Pliocene of Java (Martin, 1899; Beu, 2005) to New Zealand (Pleistocene specimens reported by me; Beu, 1976a: 308, figs 4-7; many more since collected; two Early Pliocene specimens also now have been recognized in New Zealand). In the Caribbean area, fossil specimens are again widespread but uncommon, in Miocene to Pleistocene rocks throughout the Atlantic part of the study area.

The record of *Linatella caudata* from the eastern Pacific is patchy but surprisingly long. One specimen is recorded above from the Late Miocene Punta Judas Fm at Punta Judas, Pacific Coast Rica, and five small Pleistocene fossils are recorded from the Burica Peninsula, Panama (NMB 17442). This raises a biogeographical puzzle, however; Miocene transport through the Central American seaway is feasible and reasonable, whereas Pleistocene transport through Panama seems impossible at first thought, in view of the generally accepted Pliocene (*ca.* 3-3.5 Ma) closure of this seaway. Although it is possible that these specimens resulted from larval transport from the western Pacific, this seems unlikely in view of the lack of Recent records in the eastern Pacific (Emerson, 1991), or anywhere in the Pacific east of Hawaii (Beu, in prep.). It is suggested under “Biogeography” that they provide evidence that a seaway through Central America reappeared during earliest Pleistocene interglacial periods of high sea-level (see also Beu, 2001).

Genus *MONOPLEX* Perry, 1810

Monoplex Perry, 1810: signature M7; no included species; Perry, 1811: explanation to pl. 9 (see Petit, 2003: 21). Type species (by subsequent designation, Dall, 1904: 134): *Monoplex australasiae* Perry, 1811 (= *Murex parthenopeus* von Salis Marschlin, 1793), Early Miocene to Recent, Mediterranean, eastern and western Atlantic, South Africa, East Africa, northern Indian Ocean, Red Sea, Australia and New Zealand to the Kermadec Islands and New Caledonia, Hawaii, southern Japan-Taiwan.

Lampusia Schumacher, 1817: 350. Type species (by subsequent designation, Herrmannsen, 1847: 575): *Murex pilearis* Linnaeus, 1758, Miocene to Recent, Indo-West Pacific.

Cabestanimorpha Iredale, 1936: 307 (unavailable, no definition, published after 1931); Allan 1950: 114. Type species (by original

monotypy): *Cabestanimorpha exarata* (combined description of genus and species), i.e., *Triton exaratus* Reeve, 1844, Pleistocene-Recent, Australia, New Zealand, New Caledonia, Hawaii, Japan, Red Sea; western Atlantic?

Cymatriton Clench & Turner, 1957: 210. Type species (by original designation): *Tritonium nicobaricum* Röding, 1798, Pleistocene-Recent, Indo-West Pacific and eastern and western Atlantic.

Remarks.—*Monoplex* is the most speciose genus of Cymatiinae (although not much more so than *Ranularia*), containing all the generalized, broadly to narrowly fusiform species with a tall, narrow protoconch, a moderate-sized, oval aperture, a more-or-less equally long spire and anterior canal, and an operculum with an anterior terminal nucleus. This is the group for which many authors earlier in the 20th century customarily used the name *Lampusia*, and for which Clench & Turner (1957) adopted the name *Septa* Perry, 1810. Although I earlier followed Clench & Turner's usage of *Septa* for this genus, more recently I have shown (Beu, 1987, 1998b) that *Septa* should be reserved for the group of brightly colored, relatively small species related to *S. rubecula* (Linnaeus, 1758). The genus *Turritriton* Dall, 1904 (= *Tritoniscus* Dall, 1904, = *Particymatium* Iredale, 1936) similarly is reserved for the small species with spiral sculpture of crisp, narrow, fasciculate cords, i.e., bearing a main, central thread and a less elevated thread on each side, anterior and posterior to the central one. This allows the inclusion of only the *T. labiosus* (Wood, 1828), *T. gibbosus* (Broderip, 1833), and *T. tenuiliratus* (Lischke, 1873) species groups in *Turritriton*, and all other more generalized species that have been included in *Turritriton* in the past merely because of small adult teleoconch size are here included in *Monoplex*. *Septa* and *Turritriton* are therefore reasonably certainly monophyletic groups, whereas the larger, more diverse genus *Monoplex* is much less certainly so.

I have assumed that the gender of the several *Monoplex*, *Biplex*, *Triplex*, *Hexaplex*, *Polyplex*, etc., names proposed by Perry (1810, 1811) is masculine, as usually used for such names as *Murex*.

Monoplex amictus (Reeve, 1844)

Pl. 32, Figs 4-5; Pl. 35, Figs 1-5, 7

Triton amictum Reeve, 1844a: pl. 15, fig. 62.

Triton (Gutturnium) amictus. Tryon, 1880: 22, pl. 40, fig. 188.

Cymatium corrugatum var. *tremperi* Dall, 1907a: 85.

Cymatium corrugatum tremperi. Oldroyd, 1927: 243.

Cymatium amictum. Strong & Hertlein, 1937: 172, pl. 34, figs 17-18; Shasky, 1960: 22.

Cymatium (Monoplex) corrugatum tremperi. M. Smith, 1948: 10.

Cymatium (Gutturnium) amictum. Keen, 1958: 344, fig. 319; Emerson & Old, 1963b: 19.

Cymatium (Gutturnium) amictoideum Keen, 1971: 505, fig. 954.

Cymatium (Septa) amictum. Kiliyas, 1973: 163, fig. 119.

Cymatium (Septa) amictum tremperi. Abbott, 1974: 464.

Cymatium (Monoplex) corrugatum amictum. Beu, 1985: 58; Piech, 1995: 10; Kaiser, 1997: 32.

Cymatium amictoideum. Finet, 1991: 270.

Cymatium (Monoplex) amictum. Henning & Hemmen, 1993: 60, pl. 12, fig. 3.

Cymatium corrugatum amictum. Emerson, 1995: 15 (table).

Remarks.—The original locality for *Triton amictum* given by Reeve (1844a) was "Philippine Islands." However, all of the very extensive dredging and netting for shells by fishermen there for more than 150 years since has not brought anything resembling Reeve's type specimen to light, and there can be no doubt that this is another of Hugh Cuming's misremembered localities. Strong & Hertlein (1937: 172, pl. 34, figs 17-18; specimen at CASIZ) recognized the species in the eastern Pacific fauna and, despite doubts by Keen (1971), who renamed the eastern Pacific species, comparison with Reeve's type shows that the eastern Pacific is indeed the correct location of *Monoplex amictus*. Extensive lots at the Allan Hancock (LACM) and other collections examined are listed below, to show the range of this still poorly known species. Meanwhile, Dall (1907a) did not realize that he had the long-lost *M. amictus* before him, and named a particularly large, fine specimen from off of San Pedro, southern California, as *Cymatium corrugatum* var. *tremperi* — a telling name when seeking the relationships of this species.

I previously have been impressed with the similarities between *Monoplex amictus*, *M. krebsii* (Mörch, 1877) in the western Atlantic, and *M. corrugatus* (Lamarck, 1816) in the Mediterranean-West African region. In the published catalogue of Ranellidae (Beu, 1985), I expressed this similarity by ranking these as three geographical subspecies of *M. corrugatus*. I now feel, though, that the relationship is not as close and the time of separation not as recent as that ranking seems to express, and that these three taxa are separate species. Also, Garcia-Talavera (1983: 107, pl. 4, fig. 1; 1987: 249) has recorded *M. krebsii* living sympatrically with *M. corrugatus* in the Canary Islands, eastern Atlantic, demonstrating their distinction. *Monoplex amictus* and *M. krebsii* both differ from *M. corrugatus* in reaching a much smaller maximum size — little more than half of the height of a large Mediterranean specimen — and in having weaker spiral sculpture. The greatest similarity between these three species is seen in the apertural armature; prominent, narrow teeth inside the outer lip are similar in all three, although those of large specimens of *M. corrugatus* are much the largest, and those of *M. krebsii* are rather longer (closing off more of the aperture) but narrower than in either *M. corrugatus* or *M. amictus*; those of *M. amictus* are the least prominent of the three. The inner lips of *M. corrugatus* and *M. amictus* each bear many similar low, closely spaced, weakly anastomosing transverse ridges.

One of the most distinctive characters of *M. krebsii* is that the transverse ridges on the inner lip are not all low and uniform, but vary markedly in prominence down the lip and between specimens, and in general they are all more prominent than in either of the other two species, and a few (two, in most specimens) of the ridges low on the columella protrude very strongly into the aperture. Specimens of *M. krebsii* also vary greatly in height, ranging from very tall, narrow shells, even narrower than most *M. corrugatus* and *M. amictus*, to very short, squat shells with a short spire and almost no anterior canal. In contrast, almost all specimens of *M. corrugatus* are tall and narrow, and almost all specimens of *M. amictus* are a little shorter-spined than *M. corrugatus*, but with a longer anterior canal. The spiral cords are most subdued in *M. amictus*, intermediate in *M. krebsii*, and most prominent in *M. corrugatus*. A further important character is the nodules around the shoulder angle, which are large and prominent on most specimens of *M. krebsii*, giving it a strongly stepped spire, whereas they are much smaller and less prominent, if present at all, on most specimens of both *M. corrugatus* and *M. amictus*. Finally, the varices of most specimens of *M. amictus* are significantly higher and narrower than in both *M. krebsii* and *M. corrugatus*. Overall, specimens of *M. amictus* have a shorter spire, a longer anterior canal, much weaker spiral cords, a flatter anterior variceal face, smaller apertural ridges, and a paler, more uniform coloration than in *M. krebsii*.

Dimensions.—*Triton amictus*, holotype: H 35.0, D 16.7 mm; *Cymatium corrugatum* var. *tremperi*, holotype: H 83.8, D 38.2 mm; *Cymatium amictoideum*, holotype: H 53.6, D 22.9 mm; LACM 55054, Perlas Islands, Panama Bay (Pl. 35, Figs 5, 7): H 57.8, D 24.5 mm; MCZ 259867, San Lorenzo Island, Gulf of California: H 76.1, D 33.0 mm; ANSP 340995, trawled near Guaymas, W Mexico: H 60.7, D 26.3 mm; specimen illustrated by Strong & Hertlein (1937: 172, pl. 34, figs 17-18): H 48.6, D 22.5 mm.

Types.—This seems to be the one species named by Reeve (1844a) that was not described subsequently by him (1844c). *Triton amictum*, holotype BMNH 1967650 (Pl. 35, Figs 1, 4), from "Philippine Islands" (incorrect); the type locality is here designated as off of Isla San José, Perlas Islands, Panama Bay. *Cymatium corrugatum* var. *tremperi*, holotype USNM 210824 (Pl. 35, Figs 2-3), from 77 m, off of San Pedro, California. *Cymatium (Gutturium) amictoideum*, holotype CASIZ, SU 10043, from 27-55 m, off of the NW end of Isla San José, Perlas Islands, Panama Bay.

Other material examined.—**Recent: California:** the holotype of *Cymatium corrugatum* var. *tremperi* seems to be the only specimen recorded from California; from off of San Pedro. **W Mexico:** 120 m, off of Norillaro, Sinaloa (MCZ 259909, 1); W side of San Lorenzo Island, Gulf of California (MCZ 259867, 1); Puerta Refugia, N end of Angel de la

Guardia Island, Baja California (AMNH 77288, 1); 100 m, Arena Bank, Gulf of California (AMNH 94093, 6); Espiritu Santo, Baja California (AMNH 131071, 1); trawled, 60 m, near Topolobampo, Sinaloa (AMNH 181313, 1); Baja California (AMNH 75818, 2); 90 m, Gorda Banks (AMNH 94092, 2); trawled near Guaymas, Sinaloa (ANSP 340955, 1); dredged, 15 m, near Topolobampo, Sinaloa (ANSP 340956, 1); dredged, 80 m, Punta Coyote, S of La Paz, Baja California (ANSP 340959, 1); outside harbor, San Bartolome Bay, Baja California, USBF (USNM 266912, 1); near Cedros Island (CAS 27596, 1); dredged off of W Mexico, 23°03'-06'N, 109°36'-31'W (CAS 27584, 4); 100-120 m, Gorda Banks (CAS 17760, 2); outside Ballandra Bay, Carmen Island, 50-70 m (CAS 34680, 1); 110 m, Arena Bank (CAS 17692, 1); off of central Mexico, 14°52'N (CAS 27568, 2); 80 m, Santa Inés Bay (CAS 17731, 2); 40 m, Kellett Channel, S of Cedros Island, *Searcher* sta. 251 (LACM 71-159, 1); 100 m, off of Rompiente Point, *Searcher* sta. 264-266 (LACM 71-167, 1); 100 m, off of Rompiente Point, *Searcher* sta. 265 (LACM 71-168, 1); 30-60 m, Puerto Refugio, Angel de la Guardia Island (LACM-AHF 542-36, 1); 35 m, Los Angeles Bay (LACM-AHF 702-37, 1); 130 m, Puerto Refugio, Angel de la Guardia I (LACM-AHF 544-36, 2); 10 m, sand, Concepcion Bay (LACM-AHF 687-37, 1); 120 m, Puerto Refugio, Angel de la Guardia Island (LACM-AHF 708-37, 1); 110 m, N of Granite Island, Angel de la Guardia Island (LACM-AHF 1055-40, 3); 50 m, N of Coyote Point (LACM-AHF 1753-49, 1); 70-90 m, off of Boca Flor de Malva, SE of Punta Tosca (LACM 71-16, 1); 80 m, W of Isla Partida (LACM-AHF 560-36, 2); 25 m, off Concepción Bay (LACM-AHF 682-37, 2); 80-180 m, off of W side of gap between Isla Partida & Espiritu Santo Islands (LACM 60-6, 1); 80-140 m, N of Angel de la Guardia Island (LACM-AHF 546-36, 2); 50 m, San Lorenzo Channel (LACM-AHF 607-36, 1); 40 m, between Isla Partida & Angel de la Guardia Islands (LACM-AHF 555-36, 1); 80 m, San Cristobal Bay (LACM-AHF 1949-50, 1 large); 30 m, off of E coast of Angel de la Guardia Island (LACM-AHF 270-36, 1); 180 m, off of Cabo Haro, near Guaymas, Sonora (LACM 60-3, 1); shore, Sulphur Bay, Clarion Island (LACM-AHF 141-34, 1); near Cedros Island, Baja California (CAS 27595, 1); dredged off of Mexico, 23°03'-06'N, 109°36'-31'W, 40-440 m, Templeton Crocker Expedition (CAS 27584, 4); 100-120 m, Gorda Banks (CAS 17760, 2); 110 m, Arena Bank (CAS 17692, 1); outside Ballandra Bay, Carmen Island, 50-70 m (CAS 34680, 1); off of central Mexico, 14°52'N (CAS 27568, 2); 73 m, Gulf of California, 29°20.0'N, 113°00.2'W (ZMC, 2); dredged, 30-60 m, off of Danzanti Island, Gulf of California (GNS WM 13368, 2; WM17509, 1); dredged, 100 m, off of Tetas de Cabras, Sonora (GNS WM17510, 1); dredged, 100 m, SE of Punta San Antonio, Sonora (GNS WM13757, 1; WM16318, 1); dredged 100 m, off of Sonora

(GNS WM16319, 1). **Pacific Panama:** NE Tobago Island, 1967 (ANSP 314697, 1); dredged, 25-40 m, N of Pedro Gonzales Island, Perlas Islands (ANSP 340960, 1); 60-70 m, off Medidor Island, Bahia Honda (LACM-AHF 948-39, 1); Perlas Islands, Panama Bay (LACM 55054, 1 large); 97 m, SW of Isla San José, Pearl Islands, T. Mortensen (ZMC, 1); dredged, 30-60 m, Bay of Chiriqui, W Panama (GNS WM16317, 2); dredged, 53-60 m, off of Canal de Afuera Island, W Panama (GNS WM18588, 1). **Cocos Island:** Costa Rica: 60-100 m, off of Nuñez Island (LACM-AHF 772-38, 1); 80-95 m, Chatham Bay (LACM-AHF 780a-38, 1). **Galápagos Islands:** Jervis Island (AMNH 110470, 1); 20 m, Rabida Island (AMNH 111857, 1); 20-50 m, Jervis Island (AMNH 157266, 1); 30 m, Jervis Island (ANSP 340953, 1); dredged, 80 m, N of Santa Cruz Island (ANSP 350954, 1); dredged, 200 m, off of S coast of Santa Cruz Island (ANSP 340957 (2); 170-200 m, S of Academy Bay, Santa Cruz Island (ANSP 340958, 2); dredged, 30 m, James Bay, Santiago Island (ANSP 340961, 1); 78 m, N of Cabo Barrington, Isla Isabella, *Anton Bruun* cruise 18B, sta. 795 (LACM 66-211, 1); 30 m, Tagus Cove, Albemarle Island (LACM-AHF 328-35, 1); 90 m, Tagus Cove, Albemarle Island (LACM-AHF 324-35, 2); 60 m, off James Bay, James Island (LACM-AHF 182-34, 5); 160-180 m, Tagus Cove, Albemarle Island (LACM-AHF 431-34, 3); 25 m, Tagus Cove, Albemarle Island (LACM-AHF 329-35, 1); 10-40 m, Sullivan Bay, James Island (LACM-AHF 177-34, 2); 20-35 m, Tagus Cove, Albemarle Island (LACM-AHF 157-34, 2); 60 m, Tagus Cove, Albemarle Island (LACM-AHF 147-34, 1); 34 m, 1.8 km W of James Bay, Isla San Salvador, *Anton Bruun* cruise 18B, sta. 794-E (LACM 66-210, 1); 30 m, Tagus Cove, Albemarle Island (LACM-AHF 322-35, 1); 100-150 m, off of Barrington Island (LACM-AHF 810c-38, 1). **Colombia:** R. von Cosel's material in SMF: sandy bottom, 50 m, NE of Isla Gorgona (1). **Peru:** off of Tumbes, between Caleta la Cruz and Puerto Pizzaro, Tumbes Province, 3°28'S, 80°36'W, shrimp boat *Maria Elena* (LACM 72-83, 1).

Fossils: **California:** **Pliocene:** LACMIP loc. 305, San Diego Fm, K Ranch, hills S of Tijuana River, San Diego Co (1 small). **Ecuador:** **Pliocene:** NMB 12822 (2, incomplete); loc. CRB 284, Onzole Fm, Quebrada Camarones, 20 km E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town (BMNH Palaeontology Department, 1 good; Pl. 32, Figs 4-5).

Distribution.—*Monoplex amictus* lives in the eastern Pacific from San Pedro, southern California, USA, to northern Peru (LACM 72-83), and at the Galápagos Islands, Cocos Island, and the Revillagigedo Islands (Emerson, 1991). Most material in museum collections is from the Gulf of California, Panama, or the Galápagos Islands. The only recorded fossils are from Pliocene rocks of southern California State and the

Early Pliocene Onzole Fm of Ecuador.

***Monoplex aquatilis* (Reeve, 1844)**

Pl. 35, Figs 6, 8-16; Pl. 36, Figs 1-2

Triton aquatilis Reeve, 1844a: pl. 7, fig. 24; 1844c: 114.

?*Triton (Simpulum) aquatile occidentale* Mörch, 1877: 19 (*nomen nudum*).

Triton (Simpulum) pilearis var. *aquatilis*. Kobelt, 1878a: 245.

Triton (Simpulum) pileare. Tryon, 1880: 12, pl. 6, figs 34-35 (in part).

Tritonium aquatile. Tapparone-Canefri, 1881: 25.

Triton (Lampresia [sic]) aquatilis. Coulon, 1933: 126.

Cymatium (Lampusia) aquatilis. Morretes, 1949: 92.

Cymatium (Septa) pileare. Clench & Turner, 1957: 216 (in part); Warmke & Abbott, 1962: 101 (in part); Kiliyas, 1973: 182 (in part).

? *Cymatium pileare* var. *cruzana* Nowell-Usticke, 1959: 60.

Cymatium (Septa) pileare martinianum. Weisbord, 1962: 257, pl. 24, figs 11-12.

Cymatium (Lampusia) cf. *pileare*. Olsson, 1964: 173, pl. 30, fig. 3 (not *Murex pilearis* Linnaeus, 1758).

Cymatium (Septa) aquatile. Wolfe, 1975: 6, fig. 3 left, fig. 5 right; Kay, 1979: 220, figs 76E, 77A; Kilburn, 1984: 2, pl. B, figs j-k; Springsteen & Leobrero, 1986: 112, pl. 30, fig. 16.

Cymatium bayeri. Popenoe & Kleinpell, 1978: pl. 5, fig. 61 (not *Cymatium bayeri* van Regteren Altena, 1942, = *Triton pfeifferianus* Reeve, 1844).

Cymatium krebsii. Bandel, 1984: 99, text-fig. 154, pl. 9, fig. 5 (not *Triton krebsii* Mörch, 1877).

Cymatium (Monoplex) aquatile. Beu, 1985: 58; 1998b: 85, fig. 34a; Beu, 2005: 78, figs 198-200; Beu & Kay, 1988: 197, figs 1, 12-16, 21-32; Lai, 1989: 123, fig. 34; Henning & Hemmen, 1993: 61, pl. 14, fig. 5; Wilson, 1993: 245, pl. 41, fig. 2; Piech, 1995: 10; Bosch *et al.*, 1995: 98, fig. 353; Okutani, 2000: 287, pl. 142, fig. 18; Redfern, 2001: 61, pl. 31, figs 258A-B; Zhang & Ma, 2004: 137, text-fig. 84; Beu & Segers in Poppe, 2008: 642, pl. 266, fig. 1.

Cymatium pileare. Jensen & Harasewych, 1986: 428, fig.; Lipe & Abbott, 1991: 12, illus. (in part).

Cymatium martinianum. de Jong & Coomans, 1988: 69, pl. 36, fig. 379 (not *Triton martinianum* d'Orbigny, 1841).

Cymatium aquatile. Vega-Luz & Vega-Luz, 1995: 7; Kubo in Kubo & Kurozumi, 1995: 76, fig. 2; Ardovini & Cossignani, 2004: 127, bottom left fig.

Remarks.—Since the opinions of Tryon (1880) and Clench & Turner (1957) that *Monoplex pilearis*, *M. intermedius*, and *M. aquatilis* all are variants of a single widespread species, these species have been confused by most authors. A more critical approach began when Wolf (1975) pointed out the differences between Hawaiian specimens of these three species; Kay (1979) followed Wolfe's usage. Beu & Kay (1988) pointed out several rather subtle differences between a number of species in this "*Monoplex pilearis* complex" that pre-

viously had been confused. Most of these species occur in the study area. Examination of further collections in recent years has shown that Beu & Kay (1988) were too enthusiastic in subdividing this "complex." Collections of *M. pilearis* from the western Indian Ocean, particularly the material from Madagascar and Mozambique in TFMC shown to me by Francisco Garcia-Talavera and Alejandro de Vera, are intermediate in shape, color, and size between western Pacific material of *M. pilearis* and the Atlantic form that I have previously identified as *M. martinianus*, and there is little doubt that this is one, clinally varying species, *i.e.*, the form that I have called *M. martinianus* in the Atlantic is conspecific with *M. pilearis*. Also, Dominique Lamy (Guadeloupe) has shown me a narrow specimen of *M. pilearis*, 102 mm H, trawled off of French Guiana, shaped and colored exactly as in western Pacific specimens. *Monoplex aquatilis* occurs in both the Indo-West Pacific and the eastern and western Atlantic, with a few records from the eastern Pacific, and is easily distinguished from all the other members of the group by its more coarsely nodulose appearance and much higher (more widely extended) varices, its paler exterior (orange or yellow, in most specimens), and consistently almost uniform pale orange aperture, in many specimens with two rows of nodules inside the outer lip. *Monoplex pilearis*, formerly thought to be restricted to the Indo-West Pacific province, is now known to have the same range as *M. aquatilis*. It is the largest of the group, with western Pacific specimens reaching at least 125 mm H (although the mean height decreases fairly regularly westward from there through the Indian Ocean to the western Atlantic), and is easily distinguished by its tall, narrow shape, its deep red or yellow-brown exterior with bluish gray tones in places, and its bright-scarlet to deep-red aperture, with the ridges inside of the outer lip extending far back into the aperture. Specimens occur fairly commonly in the western Atlantic but only rarely in the eastern Atlantic. Atlantic specimens are smaller than western Pacific ones, and most specimens have a wider, more oval shape, and the interior of the outer lip is a markedly paler red and bears shorter transverse ridges than western Pacific specimens. *Monoplex macrodon* (Valenciennes, 1832) is limited to the eastern Pacific and is very similar to Atlantic specimens of *M. pilearis* in most characters; it is distinguished by its slightly finer exterior sculpture, its darker red exterior, its consistently taller and narrower spire and the brighter red, in most specimens salmon-red, color inside the outer lip. Finally, *M. intermedius* is limited to the Indo-West Pacific province, where it is rare other than in the Hawaiian Islands and French Polynesia. It resembles *M. aquatilis* in most characters, but is much the smallest species in this group, has only a single row of nodules inside the outer lip, and has a dark brown columella with white transverse ridges, as in *M. pilearis*, rather than the pale orange one of *M. aquatilis*. Beu & Kay (1988)

also presented cumulative percentage curves that demonstrate the significantly different protoconchs of these species; these now indicate that the protoconch, as well as the teleoconch, of *M. pilearis* varies clinally in size and shape.

Monoplex aquatilis is one of the largest *Monoplex* species in the western Atlantic fauna, second only to *M. parthenopeus* (von Salis Marschlins, 1793) in height. The shell is broadly fusiform, with a moderately tall spire and a rather short anterior canal; many specimens have the anterior canal quite strongly twisted toward the dorsum or to the right, so that the siphonal fasciole is very prominent. The varices are the most prominent of all of the *Monoplex* species in the study area, high and rather thin, with a flat adapertural face but an excavated abapertural face, so that the spiral cords form buttresses where they cross the hollows. Most specimens have rather coarse sculpture of wide, rugose spiral cords, raised into a few large, prominent nodules in each intervariceal interval on the last few whorls; many specimens have one or two very large, strongly protruding nodules on the dorsum of the last whorl. The aperture displays the most diagnostic characters; the inner lip is closely covered with large, weakly anastomosing, transverse ridges, and is pale orange or pinkish, with the ridges only slightly paler than the background on Recent specimens; the interior of the outer lip consistently has two rows of short, prominent nodules ("teeth"), the inner row separated from the outer by a narrow smooth interval. The nodules inside the outer lip are a little paler than the background, yellow or pinkish on an orange ground. The exterior also is pale yellowish orange to dark orange in life on most specimens. The color provides immediate separation from the sympatric species *M. pilearis*, in which most specimens are medium to dark, dull red-brown on the exterior; the interior of the outer lip bears a single row of pink, moderately short transverse ridges on a pale to bright red background, and the inner lip is dark red to dark brown (black in some live-collected specimens) with white transverse ridges. *Monoplex pilearis* also reaches a significantly smaller maximum size than *M. aquatilis* in the Atlantic, although their relative sizes are reversed in the western Pacific. The protoconch of *M. aquatilis* is considerably larger and wider than that of *M. pilearis* and of all other species closely related to it (Beu & Kay, 1988: fig. 1; de Jong & Coomans, 1988: pl. 36, fig. 379, misidentified as *M. pilearis*; but note that this was identified as *M. martinianus* in the text).

Another form of uncertain status occurs in many populations of *Monoplex aquatilis* in the Indo-West Pacific. The exterior is paler (near white in many specimens) except for large, dark-brown areas on the varices and around the base, and the inner lip is a brighter red, with more obvious pink transverse ridges than in "typical" orange specimens of *M. aquatilis*. Many specimens also have even wider varices than "typical" specimens. It is possible that this apparently constant form is

a further species distinct from *M. aquatilis* but, as usual, only molecular analysis will clarify its status, and at present it seems best regarded as part of the variation of *M. aquatilis*. I have not seen Atlantic specimens of this color form.

All definite fossil records of *Monoplex aquatilis* from the western Atlantic are Pleistocene or Holocene, with a few possible Pliocene records, and one undoubted specimen is recorded from the Early Pliocene Onzole Fm of Ecuador. This probably indicates that *M. aquatilis* is one of the many species that entered the Atlantic from the Indian Ocean only during late Pliocene or Pleistocene time. The possibility that *M. longispira* n. sp. was directly ancestral to *M. aquatilis*, and that the Pacific population began as specimens entering the Pacific from the Atlantic before the Panama seaway closed, is discounted by the numerous records of *M. aquatilis* from the Miocene and Pliocene of Java (Beu, 2005). The specimen (RMNH 3759) from Santa Marta, Colombia, from which Bandel (1984: 88, text-fig. 154, pl. 9, fig. 5) extracted the radula attributed to *M. krebssii* has been examined, and is a specimen of *M. aquatilis*.

Dimensions.—Largest Atlantic Recent specimen seen, NMB 17675, Borburata, between naval base of Puerto Caballo and Playa Quizandal, Estado Carabobo, Venezuela, J. & W. Gibson-Smith collection: H 115.0, D 58.4 mm; *Triton aquatilis*, lectotype: H 111.4, D 52.4 mm, paralectotype: H 110.0, D 50.0 mm.

Types.—*Triton aquatilis*, lectotype BMNH 1967626, designated by me (Beu, 1998b: 86); with one paralectotype, from “Philippine Islands.” No type material is known for *T. aquatile occidentale*, a *nomen nudum*, or for *Cymatium pileare* var. *cruzana* Nowell-Usticke, from St. Croix, West Indies (Beu & Kay, 1988: 199; Faber, 1988: 76). One of the paralectotypes of *T. martinianus*, BMNH 1854.10.4.408, from St. Lucia, Caribbean (Pl. 35, Figs 8, 10) is a specimen of *M. aquatilis*.

Other material examined.—**Recent: W Atlantic:** Kay and I (Beu & Kay, 1988: 200) listed material that we examined. I have since seen 30 additional lots (Bahamas, GNS; Florida, GNS, 2 lots; Aruba, ZMA; Bonaire, ZMA; Curaçao, SMF, ZMA; St. Vincent, GNS; St. Martin, ZMA; St. Thomas, SMF; Guadeloupe, GNS, 4 lots; Puerto Rico, GNS; Tobago, GNS, 3 lots; Colombia: R. von Cosel’s material at SMF, 8 lots). **E Pacific: Mexico:** “Gulf of California, Mexico, Capt. Porter,” Hemphill collection (CASIZ 69686, 1); “Central America west coast,” W. S. Raymond collection (CASIZ 69685, 1); Cerros Island, Lower California, Veitch (USNM 484275, 1, abraded beach specimen). **Cocos Island:** Wafer Bay, Cocos Island, Costa Rica, leg. P. Slud, March–April 1963 (AMNH 107015, 1 abraded beach specimen; Pl. 35, Figs 1, 3) (Emerson & Old, 1964; Beu & Kay, 1988; Emerson, 1991). Only the records from Cocos Island are modern, well localized, and reliable ones, but there is no reason to doubt that

M. aquatilis occurs rarely on the western American mainland.

E Atlantic: Îles du Cap Vert, coll. Bouvier, *ex* Fischer collection (MNHN, 2; Pl. 35, Figs 12, 16; Pl. 36, Fig. 2); La Palma, Canary Islands, pres. F. Garcia-Talavera (GNS WM15201, 1); La Palma (TFMC, 1); 45 m, fish trap, El Socorro, Tenerife (TFMC, 1); Fuencaliente, La Palma (TFMC 281, 1).

Fossils: Mexico: Pliocene: TU 1046, Agueguexquite Fm, cutting on Mexico Hwy 180, Isthmus of Tehuantepec (GNS WM18888, 1 small frag, identity uncertain). **Atlantic Panama: Miocene:** Gatun Fm: TU 959, Colon (GNS WM18889, 1 frag, assigned tentatively). **Cuba: Pleistocene or Holocene:** Las Puercas Beach, Ensenada de Mora, Oriente, *ex* Johns Hopkins University (USNM, 4). **Dominican Republic: Pleistocene:** La Isabella Fm, El Castillo, La Isabella, collection of Bernard Landau (1). **Barbados: Pleistocene:** NMB 10118 (1; figured, NMB H 18049; Pl. 35, Fig. 11); USGS 18381 (1); 18382 (2); 18383 (1); Coral Rock (USNM 559575, 1). **Bonaire: Pleistocene,** Kralendijk, collection of Bernard Landau (1). **Venezuela: Pliocene:** La Salina Fm, W of Puerto Cabello (PRI 26189, 1; specimen illustrated by Weisbord, 1962: pl. 24, figs 11–12). **Ecuador: Pliocene:** USGS 23479, Onzole Fm, Punta Gorda (USNM 644045, 1; specimen illustrated by Olsson, 1964: pl. 30, fig. 3).

Distribution.—*Monoplex aquatilis* lives today throughout most of the tropical realm of the world, from eastern South Africa and the Red Sea throughout the Indo-West Pacific province to southern Japan and to the Capricorn Group, southern Great Barrier Reef, Queensland, and eastward throughout Hawaii and Polynesia, and rarely to Cocos Island and the western American mainland (Emerson, 1991). In the western Atlantic, it occurs from the Bahamas and southern Florida, USA, and throughout the Caribbean Sea to the northern coast of South America (many from Venezuela in Gibson-Smith collection, NMB). *Monoplex aquatilis* almost certainly occurs further south in the western Atlantic, at least to northern Brazil, but has not been recorded from Brazil (*e.g.*, Oliveira & Trinchao, 1993; Rios, 1994), probably because of continuing confusion with *M. pilearis*. In the eastern Atlantic, *M. aquatilis* is recorded only from the Canary and Cape Verde islands (Beu, 1998b). Ardovini & Cossignani (2004: 127, lower left fig.) illustrated a Canary Island specimen in color. Within the study area, most fossils are from Pleistocene deposits of the Caribbean area, but a single specimen is recorded from the Pliocene of Ecuador. Occasional pseudopopulations are still transported to the eastern Pacific, and survive to adulthood.

Monoplex cecilianus (Dall, 1916)

Pl. 36, Fig. 4

Cymatium cecilianum Dall, 1916: 507, pl. 85, fig. 10.

Remarks.—I am not aware of any published mention of *Monoplex cecilianus* since its description, and so the type is illustrated here for comparison with the tropical American fossils. The single small specimen has an unusual, finely pitted, apparently corroded surface, so the present sculpture might not represent the original condition. *Monoplex cecilianus* is a small, narrow, finely sculptured, generalized species of *Monoplex*, with thin varices described by Dall (1916) as “almost sharp ... irregularly disposed.” The sculpture is almost entirely of spiral cords, which are narrower, smoother and more widely spaced than in any other species considered here. There are a few narrow spiral threads in the interspaces. Unfortunately, the aperture is not preserved, so many of the characters that are critical for determining the relationships of *M. cecilianus* are not available. In a general way, the holotype resembles the small Chipola Fm specimen of *M. krebsii* figured here (Pl. 38, Fig. 8), but *M. cecilianus* is much more finely sculptured than *M. krebsii*.

Dimensions.—Holotype: H 25, D 14 mm (Dall, 1916: 507).

Types.—*Cymatium cecilianum*, holotype USNM 166727 (Pl. 35, Fig. 4), from USGS 7074, Hale landing, W bank of Flint River ca. 11 km SE of Bainbridge, Decatur Co, Georgia, USA, Oligocene; the only recorded specimen.

***Monoplex cercadicus* (Maury, 1917)**

Pl. 36, Figs 6-9, 11; Pl. 47, Fig. 16

Simpulum antillarum var. *cercadicum* Maury, 1917a: 270, pl. 17, fig. 2.

Cymatium (Monoplex) cercadicum. Beu & Kay, 1988: 214, figs 83-84.

Remarks.—*Monoplex cercadicus* was proposed by Maury (1917a: 270) as a variety of *Simpulum antillarum*, i.e., *Gutturium muricinum*, although Maury seems to have been confused about which species d'Orbigny's name applies to. *Monoplex cercadicus* is in fact a highly distinctive species of *Monoplex*, not well shown in Maury's (1917a: pl. 17, fig. 2) illustration, because the shell is turned too far to the right. Most medium-sized specimens of *M. cercadicus* have an unusual shape, with a rather short, strongly inflated last whorl, a moderately short spire, a rapidly contracted neck, and a rather long, narrow, straight anterior siphonal canal, and only the terminal varix is developed on almost all specimens; the holotype is unusual in having a penultimate varix developed as well. A moderately steep, flat to slightly convex sutural ramp is defined by a slightly raised spiral cord around the shoulder, bearing low, rounded nodules on most larger specimens. The spiral cords below the shoulder angle alternate regularly in height and prominence, and the whole shell surface is crossed by many narrow, closely spaced axial costellae. The most distinctive

characters are in the aperture. Both lips are prominently armed with many high, rather widely spaced, transverse ridges, particularly prominent on the narrow inner lip, and grouped into 7 pairs of short, very prominent ridges inside the outer lip, those of the upper two or three groups subdivided again by a median groove in most specimens, all prominently revealed on the strongly out-turned lip, which covers the inner half to two-thirds of the adapertural face of the terminal varix.

A fine specimen from the Río Mao, Dominican Republic, collected by Bernard Landau (Pl. 36, Figs 7-8), is important for understanding the relationships of this species, because it bears some similarity to *Monoplex wiegmanni* (Anton, 1838), suggesting that this living eastern Pacific species might have descended from *M. cercadicus*. Characters in common are the lightly shouldered whorls, the production of only the terminal varix in most specimens, the strongly out-turned, unusually prominently lirate outer lip, and the long, straight, narrow anterior canal. Many, but not all, specimens of *M. wiegmanni* also have the strongly ridged inner lip of *M. cercadicus*. *Monoplex wiegmanni* differs from *M. cercadicus* in its markedly larger size, in having much weaker exterior axial sculpture and in having lower, wider spiral cords and a longer last whorl that, in many specimens, has flatter, less inflated outlines below the shoulder than in *M. cercadicus*. There is little doubt that the real relationships of *M. wiegmanni* lie with *M. cercadicus* and similar *Monoplex* species such as *M. parthenopeus*, rather than with *Linatella caudata*, where it has usually been placed until recently.

Dimensions.—*Simpulum antillarum* var. *cercadicum*, holotype: H 44.3, D 26.2 mm; largest seen, TU 1379, Gurabo Fm, Río Mao, collection of Bernard Landau: H 57.4, D 32.8 mm; figured specimen, NMB H 17930, from NMB 16923, Dominican Republic: H 28.0, D 17.2 mm.

Types.—*Simpulum antillarum* var. *cercadicum*, holotype PRI 28758 (Pl. 36, Figs 6, 9), from Cercado de Mao, Maury's bluff 3, Río Mao, Dominican Republic, Cercado Fm, Late Miocene.

Other material examined.—**Fossils: Atlantic Panama: Middle Miocene:** BMNH Palaeontology Department, lower Gatun Fm, *ex situ*, Los Lomos quarry, Cativa, Colon (2 good, BMNH Palaeontology Department, GG22580 (illustrated, Pl. 47, Fig. 16, and GG22581). **Dominican Republic: Late Early Miocene:** Baitoa Fm: TU 1364 (GNS WM16943, 1 small). **Late Miocene:** Cercado Fm: NMB 16852 (1); TU 1230 (1); 1294 (GNS WM16938, 3); USGS 8525 (USNM 483443, 2); 26279 (1); 26280 (1); Gurabo Fm: NMB 16923 (2; one illustrated, NMB H 17930; Pl. 36, Fig. 11); NMB 17266 (1); TU 1358 (GNS WM18885, 1); 1379 (GNS WM16944, 8); 1379, Gurabo Fm, Río Mao, collection of Bernard Landau (1, illustrated, Pl. 36, Figs 7-8). **Late Miocene/Early Pliocene:** Gurabo Fm: TU 1231 (GNS WM18886, 1 frag); 1279 (many

small); 1293 (1); USGS 8528 (1); Maury's loc. 106, Cercado de Mao (PRI, 1). **Early Pliocene:** Gurabo Fm: TU 1215, Gurabo Fm, Río Gurabo, collection of Bernard Landau (1). **Venezuela: Late Early Miocene,** Cantaure: NMB 17516 (1); 17519 (1); 17520 (1). **Early Pliocene:** Cerro Negro Member, Cubagua Fm, Cañón de las Calderas, Cubagua Island, collection of Bernard Landau (1).

Distribution.—*Monoplex cercadicus* is recorded only from late Early Miocene to Early Pliocene rocks of the Dominican Republic, apart from a few specimens from the Middle Miocene lower part of the Gatun Fm of Panama, and the late Early Miocene Cantaure Fm and Early Pliocene Cubagua Fm of northern Venezuela. Only one specimen from the Dominican Republic is from the Pliocene part of the Gurabo Fm, and one specimen is from the Early Pliocene Cubagua Fm on Cubagua Island; all other records are Miocene.

Monoplex chlorostomoides (Maury, 1924)

Simpulum chlorostomoides Maury, 1924: 125, pl 6, fig. 13.

Cymatium (Septa [sic]) chlorostomoides. Simone & Mezzalana, 1994: 36, pl. 9, fig. 261 (copy of Maury's figure).

Remarks.—This is one of several species of *Monoplex* described by Maury (1924) from partial impressions in hard rock, from the Pirabas Fm (late Early Miocene, correlated with the Chipola and Baitoa Formations of the Caribbean-Florida area; Woodring, 1971; Ferreira, 1980; Távora & Fernandes, 1999) at Bahia Pirabas, Paraná, Brazil (see also *Monoplex infelix* (Maury, 1924), and *M. williamsi* (Maury, 1924)). For all of these taxa, such poor, stylized drawings were supplied that it is impossible to say much about their characters, their relationships, or their value as distinct taxa. Most or all of the type specimens were preserved in PRI when I visited there in 1985 as "plastotypes" (guttapercha or putty molds from the natural casts, the original material having been returned to Brazil) and these molds gave a slightly more useful impression of the shells than the original drawings (although they no longer seem to be present in PRI). It is still very difficult, though, to say much about these species, other than that they seem to represent *Monoplex* species at least superficially similar to *M. aquatilis* and *M. pilearis*. Vokes (1990a: 6, pl. 12, fig. 5, holotype; fig. 6, copy of Maury's fig.) has provided a new illustration and compared it with Maury's original for another species(?) from the same locality, *M. williamsi*, giving a good idea of the problems faced when trying to identify Maury's (1924) taxa. Better material is needed before useful characters of these species can be seen. Another species named by Maury (1924) in the same work, *Colubraria paraensis* Maury, 1924, has a relatively wide shell and might well also be a species of *Monoplex*, but to which family it belongs is not determinable

from the available illustration. Maury's (1924) illustrations all were repeated in the catalog by Simone & Mezzalana (1994), but add nothing to knowledge of these species.

Types.—Pirabas Fm (late Early Miocene) at Bahia Pirabas, Paraná, Brazil (Simone & Mezzalana, 1994). The type material is still the only recorded material.

Monoplex comptus (A. Adams, 1855)

Pl. 36, Figs 10, 14

Triton comptus A. Adams, 1855: 312; Tryon, 1880: 33.

?*Triton (Simpulum) thersites occidentale* Mörch, 1877: 30 (*nomen nudum*).

Triton ruidleyi E. A. Smith, 1890a: 489, pl. 30, fig. 1.

Lampusia gracile. Dall, 1889: 227, pl. 29, fig. 2 (not *Triton gracilis* Reeve, 1844, = *T. pfeifferianus* Reeve, 1844; Beu, 1998b: figs 42f-g; Dall, 1903b: 132).

Cymatium gracile. Maury, 1922: 116 (not *Triton gracilis* Reeve, 1844).

Cymatium comptum. Yen, 1942: 215, pl. 18, fig. 112.

Cymatium (Septa) gemmatum. Clench & Turner, 1957: 222, pl. 110, fig. 2, pl. 113, fig. 6, pl. 125, figs 1-2 (not *Triton gemmatum* Reeve, 1844).

Cymatium (Septa) vespacium. Warmke & Abbott, 1962: 101, pl. 18, fig. b; Kiliyas, 1973: 193, fig. 139; Abbott, 1974: 163, fig. 1754; Rios, 1975: 79, pl. 79, fig. 322; Kay, 1979: 223, fig. 79E (not 79F); Saunders, 1980: 5, upper fig.; Coelho *et al.*, 1981: 124, fig. 9 (not *Triton vespacium* Lamarck, 1822).

Cymatium vespacium. Matthews & Kempf, 1970: 28; Hinton, 1978: 30, fig. 9; Garcia-Talavera, 1983: 108, pl. 5, fig. 2; Cosel, 1982b: 54; Wellens & Wils, 1997: 79, fig. 14 (not *Triton vespacium* Lamarck, 1822).

Cymatium (Septa) comptum. Rios, 1985: 75, pl. 27, fig. 329; 1994: 89, pl. 29, fig. 345; Springsteen & Leobrera, 1986: 113, pl. 31, figs 3a-b.

Cymatium (Turritriton) comptum. Beu, 1985: 60; Garcia-Talavera, 1987: 253, pl. 2, fig. 5; Lai, 1989: 125, fig. 44; Henning & Hemmen, 1993: 99, pl. 21, fig. 5; Piech, 1995: 14; Redfern, 2001: 62, pl. 31, figs 263A-B, pl. 109, fig. 263C.

Cymatium comptum. Leal, 1991: 116; Kubo in Kubo & Kurozumi, 1995: 75, fig. 9.

Cymatium occidentale. Oliveira & Tostes, 1993: fig. 2, upper shell (not *Triton rubecula occidentale* Mörch, 1877).

Cymatium (Monoplex) comptum. Wilson, 1993: 245; Beu, 1998b: 86, figs 23i, 26a-k; 1999: 21, fig. 35; Okutani, 2000: 287, pl. 142, fig. 11; Zhang & Ma, 2004: 147, text-fig. 91; Beu & Segers in Poppe, 2008: 644, pl. 267, figs 1, 3-4, 7-8.

Cymatium comptum amphiatlanticum Garcia-Talavera & de Vera, 2003: 202, figs 1-5.

Remarks.—I distinguished (Beu, 1998b) the closely similar Recent species in the *Monoplex comptus*-*M. vespacium* group, discussed their ranges, provided data on the type material, and illustrated them all in color. Little of this need be repeated here. The species in this group are:

- *comptus*, Indo-West Pacific and eastern and western Atlantic.
- *exaratus* (Reeve, 1844), Australia-New Zealand, New Caledonia, South Africa, Hawaii, Japan, Red Sea; possibly in western Atlantic (see below).
- *norai* Garcia-Talavera & de Vera (2004: 19, figs 1, 3, 4d, 5a, 6b, 7b, 8a), western Indian Ocean.
- *penniketi* Beu, 1998, northwestern Indian Ocean.
- *thersites* (Reeve, 1844), Indo-West Pacific, but rare other than in northern Western Australia.
- *vespaceus* (Lamarck, 1816), Indo-West Pacific and, rarely, western Atlantic.

Of these, only *M. comptus*, *M. vespaceus*, and possibly *M. exaratus* occur in the study area, and these are discussed here in alphabetical order.

I pointed out (Beu, 1998b) that *Monoplex comptus* is much the more common of the small *Monoplex* species in the Atlantic identified by Dall (1899) and other early workers as *M. gracilis*, by Clench & Turner (1957) as *M. gemmatus*, and by Abbott (1974) and other recent authors as *M. vespaceus*. Reeve's (1844a) types of *Triton gracile* are juvenile specimens of *Reticutriton pfeifferianus* (Reeve, 1844) (*cf.* Beu, 1998b), *M. gemmatus* (Reeve, 1844) is a distinct species limited to the Indo-West Pacific (Emerson, 1991; Beu, 1998b), and *M. vespaceus* does occur in the Atlantic, but is a much rarer, distinct, larger, more coarsely sculptured and differently colored species (Piech, 1993; Beu, 1998b). The characters distinguishing *M. comptus* from *M. vespaceus* are (a) its more brightly colored shell (nearly uniform cream, orange, red, brown, through to almost black) with slightly darker varices, lacking the grayish tones and the brightly banded white and brown varices of *M. vespaceus*, (b) its thinner and more widely expanded varices, (c) its denticles inside the outer lip that are finer and more closely spaced and extend further into the aperture than in *M. vespaceus*, (d) its nodules around the shoulder angle that are markedly larger and fewer in number than in *M. vespaceus*, and (e) its spiral cords that are lower and much narrower than in *M. vespaceus* and remain completely undivided on all specimens, whereas in *M. vespaceus* the upper two spiral cords, at the shoulder angle and immediately below, are subdivided over the varices by a narrow groove, and in large specimens the groove can extend around the last whorl; finally, although their protoconchs are about the same height, that of *M. comptus* is markedly wider than that of *M. vespaceus*. Also, *M. comptus* is the smallest species in this complex, reaching ca. 40 mm H but rarely exceeding 33 mm, whereas *M. vespaceus* can be much larger, reaching ca. 65 mm and commonly exceeding 40 mm. The recently named *M. norai* (Garcia-Talavera & de Vera, 2004) differs from *M. comptus* in its wider shape, its lower varices, its shorter anterior siphonal canal, its more prominent axial ridgelets, and in having a row

of dark brown spots around the outer edge of the outer lip, between the spiral cords.

Garcia-Talavera & de Vera (2003) provided the name *Monoplex comptus amphiatlanticus* for Atlantic specimens of *M. comptus*, pointing out that most Atlantic material has only the terminal varix developed, whereas most Indo-West Pacific specimens have two or three varices. However, the two populations intergrade in this character – some Atlantic ones seen have more than one varix, and many small Indo-West Pacific specimens at GNS have only one varix. Most Atlantic material also is very pale, cream, or white, whereas Indo-Pacific material is much more variable in color. The material examined by Garcia-Talavera & de Vera (2003) also is all small, whereas Pacific material shows that varices before the terminal one are more likely to be present on large specimens. In my opinion, differences between Atlantic and Indo-West Pacific specimens are too trivial to be recognized taxonomically. A specimen at TFMC from Cuba is almost black in color, demonstrating that the dark color form occurs in both Atlantic and Pacific populations (TFMC 1266). Specimens from the beach at Borburata, Estado Carabobo, Venezuela (G. & W. Gibson-Smith collection, NMB 17675; 23 specimens), include a range of small, pale shells with only one varix each, some small specimens of entirely pale red-brown color, and several larger specimens with two varices each, and with red-brown maculations on the nodules and varices. A moderately large specimen from Florida (5 m, 1.6 km south of Boca Inlet, Boca Raton, GNS WM18249) is strongly varicate, colored bright orange-brown, and is identical to the many Philippine Islands specimens in GNS. Javier Lopez (Lanzarote, Canary Islands) has also shown me several Canary Islands specimens that closely resemble Indo-West Pacific specimens of *M. comptus* in size and color. In any case, the youthfulness of the fossil record in the Atlantic indicates that this is one of the species that have entered the Atlantic from the Indian Ocean via South Africa during or after Pleistocene time, so Atlantic and Indo-West Pacific specimens are likely to be one genetic population. Perhaps a slight but inconsistent difference in varix number results from a minor founder effect in the Atlantic as a consequence of an initially small population recruited to the Atlantic. Specimens of *M. comptus* are certainly uncommon in the eastern Indian Ocean, but a few have been seen (see below), and it is feasible that *M. comptus* entered the Atlantic recently from the Indian Ocean. The apparent protoconch differences illustrated by Garcia-Talavera & de Vera (2003: fig. 2) result from the specimen identified as *M. comptus amphiatlanticus* retaining its protoconch periostracum, whereas it has been lost entirely by the specimens identified as *M. comptus comptus*, giving the latter a narrower appearance than the former.

A more difficult question is the status of "*Guttarium grac-*

ile var. *gurabonicum*" Maury, 1917. I regarded (Beu, 1998b: 88) this Dominican Republic taxon as simply a synonym of *Monoplex comptus*, stating under the type data that the holotype of *M. gurabonicus* is "a nicely preserved, but slightly incomplete, Late Miocene fossil specimen of *M. comptus* from 'Los Quemados', Dominican Republic." Examination of a larger lot of material, assembled for the present report, showed that in fact the Dominican Republic fossils are consistently and significantly taller and narrower and still more finely sculptured than Recent specimens. *Monoplex gurabonicus* therefore is maintained as a separate species here.

Leal (1991: 115) considered *Triton ridleyi* E. A. Smith, 1890, to be an earlier name for *Ranularia rehderi* (A. H. Verrill, 1950), a distinctive, endemic, large Atlantic *Ranularia* species. However, E. A. Smith's type specimen (see below) is a very small specimen of *Monoplex comptus*.

Dimensions.—*Triton comptus*, lectotype: H 36.0, D 16.3 mm; *T. ridleyi*, holotype: H 18.3, D 10.0 mm; largest specimen seen, P. Bouchet and B. Marshall's airlifter sta. 5, Pointe Magnin, Lagon de Nouméa, New Caledonia, MNHN: H 38.5, D 20.2 mm; NMB 17670, Borburata, Venezuela: H (incomplete) 34.9, D 19.6 mm.

Types.—*Triton comptus*, lectotype (selected by Yen, 1942: 215, pl. 18, fig. 112) and 3 paralectotypes BMNH 1967684, from "China," ex H. Cuming collection. Yen's choice was appropriate, because this largest specimen (H 36 mm) is the only one that is *Monoplex comptus*; the largest paralectotype is a specimen of *Reticutriton pfeifferianus* (Reeve, 1844), and the smallest two paralectotypes are both *M. vespacum*. The lectotype probably really came from the Philippine Islands. *Triton ridleyi*, holotype BMNH 1888.6.27.42, from Fernando de Noronha Island, off of the coast of Brazil; a small (H 18.3 mm) specimen of *M. comptus* (Beu, 1998b: fig. 25f). *Cymatium comptum amphiatlanticum*, holotype and paratypes at TFMG (listed by Garcia-Talavera & de Vera, 2003: 203), holotype from off of Pompano Beach, Florida; paratypes 1-4 from 15 m, Cienfuegos, Cuba, including one paratype GNS TM8283; paratypes 5-7 from Ensenada de Maya, Cuba; paratype 8 from Los Roques, Venezuela; paratype 9 from La Habana, Cuba; and paratype 10 from Port Luis, Guadeloupe.

Other material examined.—**Recent: W Atlantic:** 127 lots examined at AMNH, ANSP, GNS, LACM, MCZ, NMB, RMNH, SMF, USNM, ZMA, from Bahamas, Florida. Grand Cayman Island, Dominican Republic, Puerto Rico, Aruba, Curaçao, Antillean islands (Barbados, Tobago, Trinidad, St. Croix, St. Thomas, Antigua, Grenada, Bequia, Grenadine Islands, Martinique, Barbuda), E Mexico, E Honduras, Belize, E Panama, Colombia, Venezuela, Guiana, and Brazil (off of Fortaleza, Ceará, MCZ 277386, 1; 25 m, off of Fortaleza, Ceará, AMNH 140135, 3; 50 m, off of Fortaleza, Ceará, ANSP 341065, 1; 10-15 m, off of Natal, Rio Grande do Norte, GNS

WM17266, 1). Also, the specimen from Itaparica, Bahia, Brazil, figured by Oliveira & Tostes (1993: fig. 2, upper specimen) clearly is *Monoplex comptus*. **Indian Ocean/Red Sea:** The few Indian Ocean records of which I am aware deserve listing here: Mauritius, J. Closel (GNS WM13867, 4); beach 19 km N of Mogadiscio, Somalia, Mrs. A. C. Davis (GNS WM10567, 1); Eilat, Red Sea, D. Peled (GNS WM13342, 1 large). **E Atlantic: Cape Verde Islands:** *Canap VI* sta. 6.103, Tydeman Cape Verde Islands Expedition 1982, 102 m, SW of Santa Luzia, 16°43'N, 24°46'W (RMNH, 1). **Canary Islands:** F. Garcia-Talavera (TFMG; pers. comm., 2005) stated that he has seen 2-3 specimens from Gran Canaria.

Fossils: Jamaica: Late Pliocene: Bowden: USGS 2580 [USNM 135295, 1; specimen mentioned by Woodring (1928: 298) as "*Cymatium (Lampusia)* species b"]. **Atlantic Costa Rica: Late Pliocene:** basal Moín Fm mudstone member, Rte. 32, 3 km W of Puerto Limón, coll. J. A. Todd, February 1998 (BMNH Palaeontology Department, 1). **Atlantic Panama: Pleistocene or Holocene:** USGS 5850, Mount Hope, Canal Zone (1).

Distribution.—*Monoplex comptus* occurs now throughout the Indo-West Pacific province, from East Africa and the Red Sea (rare records listed above) eastward at least as far as Hawaii (Beu, 1998b), and from southern Japan to New Caledonia and southern Queensland. In the western Atlantic, it is the common species previously known as *Cymatium gracile* or *C. vespacum*, ranging at least from the Bahamas and Florida (Clench & Turner, 1957, and list above), USA, to Brazil (Rios, 1985; 1994: 89, "Amapa to Espiritu Santo, Fernando de Noronha Is. and seamounts"). Matthews (1968) recorded specimens of "*Cymatium vespacum*" found uncommonly in the gut of the toadfish or "pacomon," *Amphychthys cryptocentrus*, caught off of Fortaleza, Ceará, Brazil, probably referring to *M. comptus*, because *M. vespacum* is very rare in the western Atlantic. In the eastern Atlantic, it is recorded only from the Cape Verde Islands (Saunders, 1980: 5; and record above) and the Canary Islands (Garcia-Talavera, 1983). Fossils are recorded in the western Atlantic only from Late Pliocene and younger rocks.

Monoplex exaratus (Reeve, 1844)

Pl. 37, Figs 1-4

?*Monoplex cornutus* Perry, 1811: pl. 3, fig. 1 (*nomen dubium*; Petit, 2003: 31).

Triton exaratum Reeve, 1844a: pl. 13, figs 50a-b; 1844c: 116; Lischke, 1869: 35; 1871: 30, pl. 2, figs 15-17; Küster & Kobelt, 1876: 231, pl. 64, figs 6-7.

Triton obscurus A. Adams, 1855: 312 (junior primary homonym of *T. obscurus* Reeve, 1844).

Litorium (Cymatium) kiiense G. B. Sowerby III, 1915: 165, pl. 10, fig. 7.

- Cymatium zimara* Iredale, 1929a: 346, pl. 38, fig. 11.
Cabestanimorpha exarata. Iredale, 1936: 307; Allan, 1950: 114, text-fig. 4.
Cabestanimorpha euclia Cotton, 1945: 252, fig. 2.
Cabestanimorpha tabulata. Iredale, 1949: 20 (not *Triton tabulatus* Menke, 1843).
Cymatium (Ranularia) sarcostomum (sic). Clench & Turner, 1957: 206, pl. 118, fig. 5 only (in part not *Triton sarcostoma* Reeve, 1844).
Turritriton loebbeckei. Habe, 1961: 45, pl. 22, fig. 9; 1964: 72, pl. 22, fig. 9 (not *Triton loebbeckei* Lischke, 1870).
Turritriton kiiensis. Kuroda *et al.*, 1971: 126, pl. 29, figs 8-9; Okutani, 1986: 112, illus. p. 113.
Cymatium (Turritriton) exaratum exaratum. Beu, 1985: 60; Piech, 1995: 14.
Cymatium (Turritriton) exaratum kiiense. Beu, 1985: 60; Piech, 1995: 14.
Cymatium (Monoplex) exaratum. Wilson, 1993: 245, pl. 42, figs 1a-b; Beu, 1998b: 89, figs 23n, 27a-k (with further synonymy); 1999: 22, figs 37-48; Zhang & Ma, 2004: 143, text-fig. 88, pl. 3, fig. 8.
Cymatium exaratum. Wellens & Wils, 1997: 77, fig. 21.
Cymatium (Turritriton) exaratum. Okutani, 2000: 289, pl. 143, fig. 25.
Cymatium tranquebaricum. Ardevini & Cossignani, 2004: 129 (in part, upper right fig. only).

Remarks.—*Monoplex exaratus* has not been reported previously from the western Atlantic, or from any other part of the study area, but is included here to point out two published figures that appear to show specimens of *M. exaratus* from the Atlantic. The characters, type material, synonymy and range were discussed by me (Beu, 1998b, 1999), and most need not be repeated here. The specimen illustrated by Clench & Turner (1957: pl. 118, fig. 5), as "*Cymatium (Ranularia) sarcostomum*," from St. Croix, Virgin Islands, Caribbean, clearly shows all the taxonomically important characters of *M. exaratus*. Also, a specimen from 80 m, off Dakar, Sénégal, illustrated in color by Ardevini & Cossignani (2004: 129, upper right fig.) under the name *C. tranquebaricum* appears to be another typical specimen of *M. exaratus*. Because these are the only records, fossil or living, of *M. exaratus* from western Atlantic of which I am aware, they clearly require confirmation from more material. If it does occur in the Atlantic, *M. exaratus* apparently is rare there, and both records possibly result from larval transport from South Africa.

Among the species of the *Monoplex comptus*-*M. vespaceus* species group, *M. exaratus* is distinguished by its large size, commonly exceeding 50 mm and reaching *ca.* 80 mm H, by its short, squat shape, by its nearly uniform yellow to pale orange-brown color, by its relatively strongly shouldered whorls and stepped spire and, principally, by at least the uppermost two major spiral cords, at the shoulder angle and immediately below, being deeply subdivided by a median groove down the

whole height of the shell; the next two cords below these are weakly subdivided in some specimens.

A helpful conclusion from examination of the NMP collection is that both *Monoplex exaratus* and *M. durbanensis* (E. A. Smith, 1899) occur at present along the southern coast of Africa. They are distinguished by the markedly smaller maximum size of *M. durbanensis* (rarely over 35 mm H, compared with commonly 60 mm and up to 80 mm in *M. exaratus*), the much taller and more straight-sided, more narrowly pointed protoconch of *M. exaratus* than of *M. durbanensis*, the markedly darker red-brown to purplish brown teleoconch exterior of *M. durbanensis* than of *M. exaratus* (which, as noted above, is pale yellow to pale orange-brown), and in the markedly more prominent, narrower, and more widely spaced spiral cords of *M. durbanensis* than of *M. exaratus*. The primary spiral cords on the last whorl, entering onto the terminal varix, also are entirely subdivided by an obvious median groove in *M. durbanensis*, at least where they cross the varices on all specimens, and around the whole teleoconch surface on many specimens, whereas only the uppermost two primary cords are strongly subdivided and, in some specimens, the next two below them are more weakly subdivided by a groove in *M. exaratus*. Also, both species extend southwestward to eastern Cape Province, but records of *M. durbanensis* extend northeastward to Inhaca Island, Mozambique, whereas those of *M. exaratus* extend only to northern Zululand. There is some evidence that *M. exaratus* tends to occur further offshore than *M. durbanensis*, which is a shallow-water species, dived and collected on beaches much more frequently than is *M. exaratus*. In contrast, most living specimens of *M. exaratus* have been dredged or trawled in *ca.* 20-150 m, with a few specimens dived in water as shallow as 10 m, in New Zealand, Australia, New Caledonia, and Japan, as well as in South Africa. Hayward *et al.* (2001: 64, fig. 8 lower center) listed specimens of *M. exaratus* collected alive on intertidal sand and seagrass flats near Paua, Parengarenga Harbor, in northernmost New Zealand, but this is the only intertidal occurrence of which I am aware.

Dimensions.—*Triton exaratus*, lectotype: H 46.9, D 28.3 mm; *Litorium kiiensis* G. B. Sowerby III, lectotype: H 36.2, D 18.8 mm; *T. obscurus*, lectotype: H 51.8, D 29.7 mm; BPBM 62160, Midway Island: H 29.3, D 18.7 mm; GNS RM 5551, off Tutukaka, northern New Zealand: H 62.4, D 35.1 mm; largest seen, Hummock Hill Island, Port Curtis, Queensland, LACM 52911: H 78.5, D 42.6 mm; Golden Beach, Hurghada, Red Sea coast of Egypt, in collection of E. Wils: H 43.3, D 25.0 mm; Lotus Bay, north of Safaga, Red Sea coast of Egypt, collection of E. Wils: H 40.0, D 24.1 mm; Salisbury Island dredgings, Durban, South Africa, NMP B.2528: H 34.2, D 20.6 mm.

Types.—Lectotype of *Triton exaratus*, designated by me (Beu, 1998b), BMNH 1967633/1, from "north coast of New

Holland," *i.e.*, Australia, probably from southern Queensland, where this species is particularly common. *Triton obscurus*, lectotype designated by me (Beu, 1971), BMNH 1967685, from "Sydney under stones Mr Strange," *i.e.*, Sydney Harbor, New South Wales. *Lotorium (Cymatium) kiiensis*, lectotype designated by Beu (1971), BMNH 1919.12.31.30, from "Kii, Japan." *Cymatium zimara*, holotype AMS C57849, from Sydney Harbor *Triton* dredgings, New South Wales. *Cabestanimorpha euclia*, holotype South Australian Museum D6515, from 100m, 16 km W of Eucla, southern coast of Western Australia. Other details were listed earlier by me (Beu, 1998b: 91).

Other material examined.—**Recent:** It is not necessary to list all of the material examined from New Zealand, Australia, New Caledonia, and southern Japan. I listed (Beu, 1998b: 91) 23 lots from the New Caledonian region, and later (Beu, 1999) listed material from Yamaguchi Prefecture, southwestern Honshu, Japan. The biogeographically interesting specimens are those few reported from outside of these areas where the species is moderately common, and the few known to me are listed here. **Hawaiian Islands:** Midway Island (Bernice P. Bishop Museum, Honolulu, BPBM 62160; 1; illustrated, Pl. 37, Figs 1, 3). **Red Sea:** Golden Beach, Hurghada, Egypt, collected by snorkeling, E. Wils, May 1991, collection of E. Wils, Brussels (1, specimen illustrated by Wellens & Wils, 1997: 77, fig. 21; Pl. 37, Fig. 4); fresh golden-brown (live-collected?) specimen, Lotus Bay, north of Safaga, Egypt, coll. E. Wils, May 1996, collection of E. Wils (1; illustrated, Pl. 37, Fig. 2). **South Africa:** 33 lots examined at NMP, ranging from Jeffreys Bay, eastern Cape Province (NMP 4645, 2) to northern Zululand (NMP sta. ZA41, NE of Kosi Bay, 49 m, 26°53.9'S, 32°55.3'E, NMP S.5671, 1), implying that *Monoplex exaratus* also occurs further north, in Mozambique. A Pleistocene fossil specimen also is present (9 m terrace, Brighton Beach, Algoa Bay, NMP D.4329). **W Atlantic:** The specimen illustrated by Clench & Turner (1957: pl. 118, fig. 8), identified as a juvenile specimen of "*Cymatium sarcostoma*," from St. Croix, Virgin Islands, Caribbean, clearly is a specimen of *M. exaratus*. I have not seen the specimen, which likely is in the G. D. Nowell-Usticke collection, AMNH, although it could not be recognized during recent searches. **W Africa:** The specimen illustrated in color by Ardovali & Cossignani (2004: 129, upper right fig.), from off Dakar, Sénégal, also clearly is a typical specimen of *M. exaratus* (H 45 mm).

Distribution.—In the western Pacific, *Monoplex exaratus* occurs in northeastern New Zealand, much of southern Australia from Geographe Bay, southern Western Australia (Wilson, 1993: 245) to central Queensland (particularly common in central and southern Queensland), at the Kermadec Islands, around New Caledonia and in the Coral Sea, at Midway in the Hawaiian Islands, and commonly in southern Japan to

Taiwan (Beu, 1998b). Wellens & Wils (1997: 77, fig. 21) recorded the first specimens from the Red Sea (examined AGB). Specimens are newly recorded here from South Africa, where it occurs from Jeffreys Bay to northern Zululand, and previously has been confused with *M. durbanensis* [43 lots of *M. durbanensis* examined at NMP, ranging from Blue Bend, Nahoon River mouth, eastern Cape Province (NMP A.687, 2) to Mozambique (10 m, N of Ponta do Ouro, 1, NMP; and Inhaca Island, NMP L.1552, 1)]. Pleistocene fossils are recorded from New Zealand, South Africa (above) and Japan. These records suggest that *M. exaratus* is very widespread throughout the Indo-West Pacific, including the Red Sea, and in the western Atlantic, but is rare other than in the south-west Pacific, in South Africa, and in southern Japan. Its close similarity to the European Miocene and Pliocene fossil species *M. heptagonus* (Brocchi, 1814) (Pl. 37, Fig. 5) suggests that *M. exaratus* had a similar Tethyan origin to those of *Charonia lampas*, *M. parthenopeus*, *M. pilearis*, *Turritriton tenuiliratus* (Lischke, 1873), and many other tonnoidean species. However, I illustrated (Beu, 2005) the unique holotype of *M. gembacanus* (Martin, 1884) from Miocene rocks of Java, and suggested that it possibly represents a Pacific Miocene record of *M. exaratus*. Certainly, *M. gembacanus* is still more nearly similar to *M. exaratus* than is *M. heptagonus*.

***Monoplex gatunicus* n. sp.**

Pl. 37, Figs 11, 15-17, 19-20;

Pl. 38, Figs 6-7; Pl. 53, Figs 9-12

Description.—Shell rather small for genus (most specimens 30-35 mm H, reaching 42 mm), moderately elongate, resembling *Monoplex lignarius* (Broderip, 1833) but with taller spire and longer anterior siphonal canal. Two varices present on most specimens, 3 on large specimens (including holotype); varices moderately wide and prominent, with weak hollow (shallow groove) on posterior face, weakly buttressed by raised primary spiral cords crossing groove. Spire and last whorl profile moderately tall, 3 or 4 primary spiral cords revealed on penultimate whorl. Spiral sculpture of low, moderately wide spiral cords with weakly convex crests, 7 or 8 primary cords on last whorl (passing onto terminal varix), 5 or 6 further primary cords and many secondary and tertiary cords on anterior canal, each spiral interspace above canal bearing 1 or 2 relatively narrow secondary cords, each secondary interspace filled by 1 or 2 low, narrow tertiary cords; crests of uppermost 2 or 3 primary cords weakly subdivided by shallow median groove where they cross varices. Axial sculpture of 3 or 4 low, widely spaced folds per intervariceal interval, each with crest narrowly rounded, interspaces weakly concave; entire surface crossed by low, narrow, closely spaced, axial ridgelets with clearly defined interstitial grooves and weakly convex crests, form-

ing obviously and regularly gemmate shell surface. Aperture small, elongate-oval, with weakly to very weakly excavated columella, both lips strongly thickened and strongly armed; interior of outer lip bearing 6 very prominent transverse nodules and a weak seventh (anterior) one, uppermost (posterior) 3 each subdivided by a weak median groove; inner lip bearing large, rounded parietal nodule and 6 or 7 large, wide transverse ridges, irregularly subdivided into short, rounded, prominent nodules, continuing weakly down upper part of left margin of anterior canal. Anterior siphonal canal moderately long, straight, inclined weakly to left (in conventional apertural view), with little deflection from axis of columella. Protoconch not seen.

Dimensions.—Holotype, H 42.0, D 22.3 mm; paratype, BMNH Palaeontology Department, GG22577, bed 8 of Todd, Los Lomos Suites, Cativa: H 31.5, D 20.0 mm (anterior siphonal canal incomplete); paratype, BMNH Palaeontology Department, GG22579, locality same as last: H 29.5, D 16.6 mm; figured paratype, NMB H 17941, from NMB 17643, Isla Payardi, Colon, Panama: H 26.9, D 16.7 mm.

Types.—Holotype, BMNH Palaeontology Department, GG22578 (Pl. 53, Figs 9, 12), lower Gatun Fm (Middle Miocene), bed 6 of Todd, quarry floor, Los Lomos Suites, Cativa, Colon Province, Atlantic Panama, coll. J. Todd, June-July 1999.

Other material examined.—**Fossils: Atlantic Panama: Miocene:** Gatun Fm: NMB 17643, Isla Payardi, Colon (1 paratype, illustrated, NMB H 17941; Pl. 38, Figs 6-7); 18261, as last (1 paratype); TU 960 = NMB 19029, near refinery gates, Colon (1 paratype); 962 = NMB 19027, as last (1 paratype); 961, Cativa, Colon, collection of Bernard Landau (1 paratype); USGS 22016, near Cativa (2 paratypes; 1 illustrated, Pl. 37, Fig. 11, USNM 542201); 22019, road to Payardi Island (1 paratype, illustrated, Pl. 37, Fig. 19, USNM 542200); CAS 60189, 1.5 km NW of Sabanita, Colon (1 paratype, illustrated, Pl. 37, Figs 15, 20); CAS loc. 9A-B2-407, hill due N of Sabanita, Colon (1 paratype, illustrated, Pl. 37, Figs 16-17, CAS Geology 70835); BMNH Palaeontology Department, GG22577, bed 8 of Todd, quarry floor, Los Lomos Suites, Cativa, Colon (1 paratype; illustrated, Pl. 53, Fig. 10); BMNH Palaeontology Department, GG22579, *ex situ*, Los Lomos quarry, Cativa, Colon (1 paratype; illustrated, Pl. 53, Fig. 11).

Remarks.—At first, material from the Gatun Fm of Panama was assigned to *Monoplex lignarius*, and was so listed by me (Beu, 2001). However, even the specimens available early in this study extended the boundaries of that species, because they have taller spires, longer anterior canals, and lower spiral cords than either eastern Pacific Recent or Caribbean fossil specimens of *M. lignarius*. The new material from the lower Gatun Fm at Los Lomos Suites, Cativa, contributed by Jon

Todd (BMNH), demonstrated that Gatun Fm specimens also reach a much larger size than any undoubted *M. lignarius* material that I have seen, when they become much more elongate than the smaller Gatun specimens. Despite the coarsely nodulose inner lip, not unlike that of *M. lignarius*, this is concluded to be a distinct species. So far, all material seen is from the Gatun Fm. The nodules on the inner lip of large specimens in fact are also larger and sparser than in *M. lignarius*. It seems likely that the new species *M. gatunicus* is a closely related (sister?) species to *M. lignarius*.

Distribution.—Recorded so far only from the Gatun Fm (Middle-Late Miocene) of Atlantic Panama.

Etymology.—The species name refers to the provenance of all material from the Gatun Fm.

Monoplex gurabonicus (Maury, 1917)

Pl. 36, Figs 12-13, 15-17

?*Triton gemmatus*. Guppy, 1876: 522 (not *Triton gemmatus* Reeve, 1844).

Guttarium gracile var. *gurabonicum* Maury, 1917a: 271, p. 17, fig. 10.

Cymatium (Monoplex) comptus. Beu, 1998a: 86 (in part not *Triton comptus* A. Adams, 1855).

Remarks.—*Monoplex gurabonicus* occurs moderately commonly in the Dominican Republic, and yet seems never to have been mentioned again after it was named. Maury (1917a: 271) distinguished it from "*Guttarium gracile*" (*i.e.*, presumably *M. comptus* of this report) by its "more prominent dorsal humps, shorter canal, and surface much more finely reticulated." She distinguished it also from "Gabb's *Triton domingensis*" by "that species" having "an elongate aperture and a straight canal while ours has a round aperture and a sharply twisted canal." *Monoplex gurabonicus* is indeed similar in size and shape to the syntopic species *Turritriton domingensis*, but the resemblance is superficial, because *T. domingensis* has three spiral threads on each spiral cord, as in all species of *Turritriton*. *Monoplex gurabonicus* is much more nearly similar to *M. comptus*, from which it differs in its consistently much taller and narrower shape, even though almost all of the fossil material lacks the anterior canal, in its narrower and more widely spaced major spiral cords and its more numerous and more prominent secondary spiral cords, and in its more even and consistently fine axial ridgelets, the two together producing, as phrased by Maury (1917a: 271), a "much more finely reticulate" surface than in *M. comptus*. Also, the aperture of *M. gurabonicus* has much less prominent transverse ridges on both the inner and the inside of the outer lips than in *M. comptus*, giving the aperture a smoother and more evenly oval appearance. The protoconch also is a little taller and wider than in *M. comptus*.

Dimensions.—*Guttarium gracile* var. *gurabonicum*, ho-

lotype: H 21.7, D 12.9 mm; largest seen, USGS 8547, Dominican Republic: H 28.9, D 16.8 mm; figured specimen, NMB H 17931, from NMB 18579 (TU 1210), Dominican Republic: H 23.7, D 12.7 mm.

Types.—*Guttarium gracile* var. *gurabonicum*, holotype PRI 28764 (Pl. 36, Figs 15-16), from Maury's zone D, Los Quemados, Río Gurabo, Dominican Republic, Early Pliocene.

Other material examined.—**Fossils: Dominican Republic:** **Late Early Miocene:** Baitoa Fm: TU 1226 (GNS WM18865, 1). **Late Miocene:** Cercado Fm: TU 1359 (GNS WM16940, 1); NMB 16982, Cercado Fm, Río Cana, collection of Bernard Landau (1); Gurabo Fm: NMB 15882 (1); TU 1412 (GNS WM18871, 1); unnamed formation of Vokes (1989: 21): NMB 17273 (1). **Late Miocene/Early Pliocene:** Gurabo Fm: TU 1225 (GNS WM18864, 2); 1231 (GNS WM18867, 1); 1246 (GNS WM16928, 1); 1250 (GNS WM18868, 2); 1277 (GNS WM18869, 2). **Early Pliocene:** Gurabo Fm: NMB 15839 (1); 15857 (1); TU 1210 = NMB 18579 (3; 1 illustrated, NMB H 17931; Pl. 36, Figs 13, 17); 1211 (GNS WM16910, 3); 1212 (GNS WM18863, 1); 1215 (GNS WM16897, 14); 1219 (GNS WM16914, 2); 1227 (GNS WM18866, 1); 1278 (GNS WM18870, 1); USGS 8547 (1, illustrated, Pl. 36, Fig. 12); Dominican Republic, *ex* Gabb collection (USNM 112201, 1); TU 1215, Gurabo Fm, Río Gurabo, collection of Bernard Landau (9); 1219, Río Amina, collection of Bernard Landau (1).

Distribution.—*Monoplex gurabonicus* is recorded so far only from the late Early Miocene to Early Pliocene rocks of the northern Dominican Republic.

Monoplex infelix (Maury, 1924)

Simpulum infelix Maury, 1924: 123, pl. 6, fig. 16.

Cymatium (Septra [sic]) infelix. Simone & Mezzalana, 1994: 36, pl. 9, fig. 262 (copy of Maury's illustration).

Remarks.—See above, under *Monoplex chlorostomoides*. Maury (1924: 123) felt that *Simpulum infelix* resembled *M. cercadicus*, "but its condition is too incomplete for any exact comparison." This understatement shows that even Maury had difficulty finding distinctive characters for the "species" she was naming. The figure shows a partial mold of the last whorl of a *Monoplex* species, similar to species of the *M. aquatilis-M. pilearis* species group, but cannot be compared without much better material.

Types.—Known only from the type material, from Pirabas Fm (late Early Miocene) at Bahia Pirabas, Paraná, Brazil (Simone & Mezzalana, 1994).

Monoplex jackwinorum n. sp.

Pl. 37, Figs 6-9

Description.—Shell small (to 40 mm H), broadly fusiform, with rather short, weakly stepped spire of slightly convex outline, strongly and very evenly convex last whorl, and short to moderately long siphonal canal inclined weakly to left. Only terminal varix developed on all specimens seen, very high, thick and prominent, slightly convex on adapertural face, slightly excavated on abapertural face, weakly buttressed by spiral cords. Spiral sculpture of prominent, moderately wide, well elevated primary cords, 6 and a weaker subsutural one on last whorl, passing onto terminal varix; 2 and a weak subsutural one on spire whorls, with upper edge of third major one visible on some specimens; each interspace equal in width to one primary cord; each cord weakly subdivided by a narrow median groove over last 2 whorls, groove prominent on terminal varix; cords very elevated over abapertural face of varix, but low on variceal crest, not forming nodules; one or, in a few interspaces on some specimens, 2 narrow, raised secondary cords in each spiral interspace; 6-8 further narrow, raised, closely spaced cords on canal. Axial sculpture of narrow-crested, widely spaced costae with lightly concave interspaces, *i.e.*, angulating outline of shell in apical view, extending entire height of shell apart from canal, becoming further apart over last whorl, 13-15 on penultimate whorl, 9 on last whorl of all available specimens; not forming nodules at the intersections with spiral cords over most of the shell, but forming low, rounded nodules at intersections where costae are sparser and coarser, on dorsum of last whorl. Entire teleoconch surface crossed by low, very narrow, irregularly placed axial ridges, 5-7 in most axial interspaces. Aperture broadly oval, with narrow, weakly reflected, strongly armed lips; interior of outer lip bearing 7 high, moderately narrow nodules, all except lowest 2 subdivided into two low, narrow, short transverse ridges; inner lip complexly sculptured, bearing one prominent parietal cord on uppermost spiral cord of previous whorl and 7-9 wide, prominent, widely spaced, slightly irregular transverse ridges on inner mid-columellar area, base of columella and left edge of canal; outer mid-columellar area bearing two irregular rows of small rounded nodules, 4-7 nodules in each row. Protoconch not seen.

Dimensions.—Holotype: H 40.7, D 25.8 mm; largest paratype, NMB H 17933: H 33.1, D 23.2 mm.

Types.—Holotype NMB H 17932 (Pl. 37, Figs 6, 8), from lower shellbed, Cantaure Fm (late Early Miocene), near Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela, coll. and pres. Bernard Landau; NMB 17516, same locality as holotype, collected by J. & W. Gibson-Smith (2 paratypes and 2 frags, NMB H 17933-17936; Pl. 37, Figs 7, 9).

Other material examined.—**Fossils: Venezuela: Late Early**

Miocene: NMB 12842, same locality as holotype, old collection (1); NMB 17520, upper shellbed at same locality as holotype, coll. J. & W. Gibson-Smith (1); lower shellbed, Cantaure Fm, near Casa Cantaure, collection of Bernard Landau (7). **Pliocene:** NMB 17606, Caiguire Fm (middle? Pliocene), S flank of Cerro de Caiguire, Cumaná, coll. J. & W. Gibson-Smith (4 specimens referred; incomplete and difficult to compare, but with the prominent spiral cords and large terminal varix of *M. jackwinorum* n. sp.).

Remarks.—*Monoplex jackwinorum* n. sp. is immediately recognizable because of the very prominent, wide terminal varix, the only varix developed on all the specimens seen. Other characters that distinguish it from the other taxa with only a terminal varix, such as *M. cercadicus* (which occurs in smaller numbers at the type locality of *M. jackwinorum* n. sp.), *M. parthenopeus*, and *M. wiegmanni*, are its much smaller maximum size, its low spire with weakly convex outlines, and its strongly thickened inner lip bearing small, rounded nodules in one or two irregular rows near the outer margin, as well as transverse ridges further inside the aperture. With its 6 weakly but clearly bifid, well-raised main spiral cords on the last whorl and 2 or 3 on the spire whorls, the one main secondary cord in the center of each spiral interspace, and its narrow, angling axial costae on early whorls that translate into larger, nodulose costae on the last whorl, *M. jackwinorum* n. sp. is similar to both *M. parthenopeus* and *M. vestitus*, but the small size, the very heavy terminal varix, and the short, oval shape give it a different appearance from any closely similar species.

Distribution.—*Monoplex jackwinorum* n. sp. is recorded so far only from the Cantaure Fm (late Early Miocene) of Paraguaná Peninsula, Venezuela, apart from poor specimens, referred here with some hesitation, from the Caiguire Fm (middle? Pliocene) at Cerro de Caiguire, Cumaná, Venezuela.

Etymology.—It is a great pleasure to name this new species in honor of Win and Jack Gibson-Smith, who collected most of the type material of the new species, and whose large and extensive Venezuelan collections of both fossil and Recent mollusks, as well as published papers in this field, have all been extremely helpful to all working on mollusks of the Caribbean area.

***Monoplex keenae* Beu, 1970**
Pl. 41, Figs 3, 6-7

- Cymatium costatum*. Dall, 1909b: 226; Hertlein & Strong, 1955a: 134, pl. A, fig. 17 (not *Murex costatus* Born, 1778).
Cymatium wiegmanni. Hertlein & Strong, 1939: 370 (not *Triton wiegmanni* Anton, 1838, *fide* Hertlein & Strong, 1955a: 134).
Cymatium (Monoplex) parthenopeum. Keen, 1958: 346, fig. 322; Emerson & Old, 1963b: 24; Piech, 1995: 8 (in part not *Murex parthenopeus* von Salis Marschlin, 1793).

- Septa (Monoplex) parthenopea keenae* Beu, 1970c: 233, pl. 1, figs 4-5, pl. 2, figs 6-11, pl. 3, fig. 17; Kaiser, 1997: 32.
Cymatium (Monoplex) parthenopeum keenae. Keen, 1971: 505, fig. 956; Beu, 1985: 58; Beu & Kay, 1988: 213, figs 8, 81-82; Henning & Hemmen, 1993: 60, pl. 13, fig. 2.
Cymatium parthenopeum. Finet, 1991: 270.
Cymatium parthenopeum keenae. Hickman & Finet, 1999: 70, fig. 61.
Cymatium vestitum. Hickman & Finet, 1999: 72, fig. 65 (not *Triton vestitus* Hinds, 1844).
Cymatium (Monoplex) keenae. Ashton *et al.*, 2008: 107, fig. 2.

Remarks.—I distinguished (Beu, 1970c) *Monoplex keenae* from *M. parthenopeus* (see below) by having 7 major spiral cords on the last whorl, rather than the 5 (with a narrow sixth in some specimens) of *M. parthenopeus*, and by having about one and a half times as many prominent, narrow axial costae per whorl as *M. parthenopeus* (ca. 30 in *M. keenae*, compared with ca. 20 in *M. parthenopeus*). Consequently, the conspicuous, high, fringed axial blades of the periostracum, which in this species coincide with the axial costae of the teleoconch, are about one and a half times as numerous and densely spaced on *M. keenae* as on *M. parthenopeus*. Most specimens of *M. keenae* also have a taller spire than *M. parthenopeus*, and most specimens of *M. keenae* develop varices at growth pauses on at least the last 2-3 whorls and, on some specimens, down the entire shell, whereas few specimens of *M. parthenopeus* develop more than the terminal varix. Finally, the exterior of the teleoconch of *M. keenae* consistently is uniformly pale in color, cream to pale creamy brown with darker varices, whereas *M. parthenopeus* is much more variable in color, and includes markedly darker brown specimens than any specimens of *M. keenae* that I have seen. The color difference also provides the most obvious difference from *M. vestitus*, which is sympatric with *M. keenae* in the eastern Pacific. Specimens are illustrated excellently in color on a webpage (<http://www.femorale.com.br/shellphotos>, last accessed 28 April 2006).

These differences are slight, although after seeing a lot more material in the nearly 40 years since I named *Monoplex keenae* they still appear to be consistent. The difficulty is to decide what status should be allotted to this taxon. It is not surprising that Abbott (1974: 165) and others have regarded the name *M. keenae* as a synonym of *M. parthenopeus*, but to follow that lead would be to mask a significant difference between a taxon in the eastern Pacific fauna and that in the western Atlantic, where typical *M. parthenopeus* occurs. Because one of the aims of this report is to reveal all possible differences between eastern Pacific and western Atlantic taxa that might have arisen as a result of the uplift of the CAI, suppression of the separate taxon status for *M. keenae* is undesirable. Also, there is no question that *M. keenae* is unable to exchange larvae at present with Caribbean specimens of *M. parthenopeus*.

The distinction between the two forms on the two coasts of tropical America is recognized by treating *M. keenae* as a separate species, although investigation of the genetic distinction (or otherwise) of *M. keenae* obviously is very desirable. This provides one of the few tonnoidean cases of a geminate species pair that apparently resulted from subdivision of an originally single species as a result of uplift of the CAI.

Another eastern Pacific species resembling *Monoplex keenae* is *M. vestitus*. Apart from its significantly smaller maximum size (most specimens to 70 mm, rarely to 95 mm H), *M. vestitus* differs from *M. keenae* in (a) its markedly narrower, more oval shape, and shorter spire, (b) in its consistent, uniform medium to dark brown exterior with a pale peribasal band, rather than the cream to pale brown with dark brown varices of *M. keenae*, (c) in its lower, narrower, more closely spaced and more numerous spiral cords, (d) in its narrower, more numerous, and more closely spaced axial costae, (e) in most specimens developing at least a penultimate varix and several having all varices present down the teleoconch, and (f) in its less prominent, narrower transverse ridges on the dark brown columella. The similarity is close enough, though, to suggest the possibility that *M. vestitus* and *M. keenae* resulted from separate migrations into and genetic segregation of stocks of *M. parthenopeus* in the eastern Pacific.

Dimensions.—*Septa (Monoplex) parthenopeum keenae*, holotype: H 92.2, D 52.1 mm; LACM 74-6, Isla Lobos de Afuera, Peru (largest in lot of 5): H 127.8, D 73.8 mm; LACM 45185, Gulf of California: H 160, D 85 mm; GNS WM13362, Playas, Guayas, Ecuador: H 135.5, D 68.7 mm; H 133.9, D 71.4 mm. The maximum recorded height is 162 mm (Skoglund, 1992).

Types.—*Septa (Monoplex) parthenopeum keenae*, holotype CAS 23198, from "Albermarle and Indefatigable Islands," Galápagos Islands.

Other material examined.—**Recent:** I have previously (Beu, 1970c) listed material of this species in American museums, but have recorded little further material; 5 lots at GNS. The northernmost record is from La Paz, Baja California Sur, Mexico (Keen, 1971: 507) and the southernmost ones previously known to me are from Peru (NW and NE of isthmus, Isla Lobos de Afuera, 6°57.1'S, 80°42.3'W, LACM 74-6, 5; 0-2 m, N side of main pier, Paíta, 5°06'S, LACM 72-87, 1; beach between Cabo Blanco and Lobitos, 4°14'-27'S, coll. A. Zilch, 17 October 1950, SMF 141115/1, 1). Ashton *et al.* (2008) recently added a record of several living specimens of *M. keenae* from Antofagasta Bay, northern Chile (23°28'18"S), where it is now common enough for the local fishermen to have given it a Spanish vernacular name, and pointed out that Diaz & Ortlieb (1993) had recorded specimens previously from between Pucusana (12°28'S) and Paracas (13°50'S) in Peru. *Monoplex keenae* clearly occurs further south than has

been thought previously.

Fossils: Galápagos Islands: Pleistocene: Hertlein & Strong (1955a: 135) reported that the specimen that they (Hertlein & Strong, 1938: 1) had identified previously as *M. wiegmanni* (Anton, 1838) from James Island actually is *M. keenae* [identified as *Cymatium costatum* (Born) by Hertlein & Strong, 1955a]. **Pacific Panama: Pleistocene:** NMB 17439, Armuelles Fm, Burica Peninsula (1).

Distribution.—*Monoplex keenae* was reported by Keen (1971: 507) to range from La Paz, Baja California Sur, Mexico, to the Galápagos Islands, but Dall (1909b: 226) had previously reported it (as the synonym *Cymatium costatum*) from Paíta, Peru. Poorman & Poorman (1988) recorded a specimen from a depth of 100 m, off of Bahia de San Carlos, Sonora, western Mexico. The material listed above makes it clear that *M. keenae* ranges from the Gulf of California (where, however, it is rare) at least to Isla Lobos de Afuera, northern Peru (6°57'S) and to the Galápagos Islands. Pleistocene fossils are known from the Galápagos Islands and the Burica Peninsula, Pacific Panama.

***Monoplex krebsii* (Mörch, 1877)**

Pl. 38, Figs 1-5, 8-12; Pl. 47, Fig. 15

Triton (Lampusia) krebsii Mörch, 1877: 30; Küster & Kobelt, 1878: 265, pl. 70, figs 3-4.

Triton domingensis. Guppy, 1876: 522, pl. 29, fig. 2 (not *Triton domingensis* Gabb, 1873).

Triton (Simpulum) corrugatum var. *krebsii*. Tryon, 1880: 13, pl. 8, fig. 50.

?*Tritonium (Lampusia) lineatum*. Gabb, 1873: 211; 1881: 352 (not *Cymatium lineatum* Broderip, 1833).

Tritonium pileare. Dall, 1890: 161 (not *Murex pilearis* Linnaeus, 1758).

Cymatium (Monoplex) corrugatum krebsii. M. Smith, 1948: 10; Piech, 1995: 10.

Cymatium (Septa) krebsii. Clench & Turner, 1957: 220, pl. 112, figs 3-4, pl. 124, figs 1-2 only (in part not *T. krebsii* Mörch, 1877); Weisbord, 1962: 260, pl. 25, figs 1-4; Abbott, 1974: 464, pl. 7, fig. 1757; van Regteren Altena, 1975: 36; H. Vokes & E. Vokes, 1983: 22, pl. 11, fig. 2; Petuch, 1994: pl. 39, figs G-H.

Cymatium (Septa) pileare henicum Woodring, 1959: 204, pl. 36, figs 1, 4.

Cymatium (Septa) krebsi (sic). Warmke & Abbott, 1962: 101; Diaz & Puyana, 1994: 172, fig. 643.

Cymatium (Septa) corrugatum krebsii. Kiliyas, 1973: 167, fig. 122; Beu, 1985: 58; Beu & Kay, 1988: 217; Rios, 1985: 76, pl. 27, fig. 330; 1994: 89, pl. 29, fig. 346.

Cymatium krebsii. Princz & Pacheco, 1981: table; Garcia-Talavera, 1983: 107, pl. 4, fig. 1; de Jong & Coomans, 1988: 69; Lipe & Abbott, 1991: 12, illus.; Vega-Luz & Vega-Luz, 1995: 7; Gofas & Beu, 2002: 97, fig. 5B; Ardovini & Cossignani, 2004: 128, upper right fig.

Cymatium (Monoplex) krebsii. Garcia-Talavera, 1987: 249, pl. 1, fig.

9; Henning & Hemmen, 1993: 63, pl. 12, fig. 2.

Cymatium tranquebaricum. Kalafut, 1988: 17, illus. (not *Triton tranquebaricum* Lamarck, 1816).

Cymatium (Monoplex) corrugatum amictus. Beu & Kay, 1988: 216, figs 85-86 (holotype of *C. pileare henicum* Woodring only; not *Triton amictus* Reeve, 1844).

Cymatium (Septa) henicum. Petuch, 1992: 109, fig. 3F; 1994: pl. 39, figs A-B; 1997: 275, fig. 114L.

Cymatium cfr. *ficoides*. Ardovini & Cossignani, 2004: 128, upper left fig.

Remarks.—*Monoplex krebsii* is distinguished from *M. amictus* and *M. corrugatus* under *M. amictus* (above). *M. krebsii* is easily recognized among western Atlantic species by its rather tall spire and long anterior canal, its very prominent, thin varices, the prominent nodules at the periphery on the intervariceal intervals of most specimens, and its elongate aperture with very prominent, narrow transverse ridges ("teeth") inside the outer lip, and two particularly prominent transverse ridges on the base of the columella, protruding strongly into the aperture. Many Recent specimens have much brighter, narrow, red-brown spiral color bands than either of the similar species *M. amictus* and *M. corrugatus*.

Clench & Turner (1957: 220) commented that *Monoplex krebsii* was a "very rare" species, but subsequent sampling has revealed it to be the most common *Monoplex* species in shallow offshore environments, in *ca.* 20-100 m, throughout the western Atlantic. It is not surprising, then, to find that it is also the best-represented fossil species of *Monoplex*, reflecting the shallow offshore depositional environments of most rocks containing Neogene fossils in the tropical American region, and the poor representation of near-shore faunas in the fossil record.

The specimen illustrated by Kalafut (1988), identified as a living specimen of *Monoplex tranquebaricus* (Lamarck, 1816) in Florida, has very prominent ridges inside the outer lip and an elevated ridge on the base of the columella, and seems to be an extremely short, wide specimen of *M. krebsii* rather than *M. tranquebaricus*. However, an authentic Florida specimen of *M. tranquebaricus* is recorded below. The specimen from Haiti recorded by Guppy (1876) as *Triton domingensis* has been examined at the BMNH Palaeontology Department (GG20269) and is a good specimen of *M. krebsii*. One other specimen of *M. krebsii* (GG20524) accompanies it. The specimen (RMNH 3759) from Santa Marta, Colombia, from which Bandel (1984: 99, text-fig. 154, pl. 9, fig. 5) extracted the illustrated radula attributed to *M. krebsii* is actually a specimen of *M. aquatilis* (Reeve, 1844), and Bandel's usage of the name is not included in the synonymy above. The species recorded by Gabb (1881: 352) from Limón, Costa Rica (latest Pliocene/Early Pleistocene), and the Dominican Republic as *Tritonium lineatum* seems most likely to be *M. krebsii*, because

this is the most common *Monoplex* species in both areas.

Dimensions.—*Triton krebsii*, syntypes: H 55.0, D 31.8 mm; H 54.0, D 30.2 mm; *Cymatium (Septa) pileare henicum*, holotype: H 53.7, D 28.0 mm; Recent, off of Dry Tortugas, Florida, AMNH 103959: H 62.3, D 29.6 mm; Recent, shrimp boat off of Key West, Florida, AMNH 161111: H 75.3, D 34.2 mm; Recent, 50 m, N of Loggerhead Light, Tortugas, Florida, ANSP 341040: H 75.6, D 30.8 mm; Recent, Cabo de la Vela, Colombia, SMF 306647/1: H 71.2, D 34.0 mm; Recent, off of E Honduras, GNS WM17507: H 76.4, D 33.4 mm; figured specimens, NMB 19008 (TU 1240), Limón, Costa Rica, NMB H 17938: H 58.8, D 29.6 mm; NMB H 17939: H 49.8, D 24.3 mm; figured specimen, NMB H 17937, from NMB 19006 (TU 1231), Dominican Republic: H 59.4, D 30.7 mm; NMB 17597 (TU 951), Chipola Fm, Florida, figured specimen, NMB H 17940: H 22.5, D 13.5 mm.

Types.—Clench & Turner (1957: 220) stated that the holotype of *Monoplex krebsii* was probably at ZMC, but virtually none of the type material of taxa named by Mörch (1877) is present in that museum – nor, indeed, is virtually any of Mörch's other type material, other than that of Vermetidae. However, Clench & Turner (1957) also pointed out that two "paratypes" from the Swift collection are present in ANSP 42605, from St. Thomas, West Indies. Because Mörch (1877) did not designate any one specimen as a holotype for any of his taxa, these specimens and any that might originally have been at ZMC are all syntypes. The two specimens at ANSP therefore seem to be the only remaining syntypes of *M. krebsii*. The type locality is St. Thomas, Virgin Islands, Caribbean (Clench & Turner, 1957). *Cymatium (Septa) pileare henicum*, holotype USNM 562584 (Pl. 38, Figs 10, 12), from Stanford University loc. 2611, Gatun Fm (Pliocene), Transisthmian Highway, Panama; Beu & Kay (1988: 216, figs 85-86) illustrated the holotype and regarded it as a specimen of *M. amictus*, but the relatively coarse sculpture and the two prominent ridges on the base of the columella show that it is an incomplete, moderately large specimen of *M. krebsii*.

Other material examined.—**Recent: W Atlantic:** 94 lots examined (plus 127 lots at RMNH from Guiana shelf), at AMNH, ANSP, GNS, LACM, MCZ, NMB, SMF, USNM, ZMA, from North Carolina (1.8 km off Drum Inlet, 1971, *ex* Hal Lewis collection, ANSP 340972, 25), Florida, Texas, Honduras, Antillean islands (Trinidad, Tobago, St. Vincent, St. Barthelemy, St. Thomas, Antigua, Barbados), Aruba, Colombia, Venezuela, Guiana [127 lots (301 specimens) examined at RMNH from *Luymes* and *Snellius* cruises, from the Guiana shelf, in *ca.* 30-85 m], and Brazil (shrimp boats, off of NE Brazil, AMNH 178659, 3; scuba off of Alcobaça, Bahia State, 1 brightly colored, collection of Coltro brothers, São Paulo). **E Atlantic: W Africa:** dredged, 40-60 m, off of S Spanish Sahara, J. H. Otero, *ex* A. R. Arthur collection (GNS

WM17508, 1). **Azores Islands:** W end of Praia beach, Santa Maria Island, coll. A. G. Beu & B. Landau, February 1998 (GNS WM15967, 2 frags). **Canary Islands:** TFMC 324, Dásena sur (port of Santa Cruz de Tenerife), dredged 9-12 m, 1982 (2 good, small, proportions and sculpture agree with *M. krebssii* rather than *M. corrugatus*, although the TFMC collection includes a few small *M. corrugatus* from the Canary Islands also); TFMC 1440, El Socorro, Tenerife sur, 180 m (2 small); TFMC 1437, La Palma (1 good); TFMC 1458, Gan Canaria (1 excellent, brightly colored); TFMC 1435, Punta de Santa Cruz de Tenerife (1 good, small); TFMC 1436, Tazacorte, La Palma (1 small); dredged off of La Palma (GNS WM17511, 1).

Fossils: **Florida: Late Early Miocene,** Chipola Fm: TU 951 = NMB 17594 (NMB H 17940, 1, small, assigned here because of prominent spiral sculpture, high varices, and prominent apertural ridges; Pl. 38, Fig. 8). **Pliocene/Pleistocene?:** Caloosahatchee River, coll. W. H. Dall, "from the Caloosahatchie marls" [USNM 112199, 1; the specimen identified by Dall (1890: 161) as *Cymatium pileare*]; other Florida specimens were illustrated by Petuch (1994: pl. 39) from the Kissimmee River at Okeetantie, Okeechobee, and from Capeletti Brothers pit at Miami; **Pleistocene:** Bermont Fm, Capelletti Brothers pit no. 1, 8 km W of turnpike opposite NW 47th Avenue Metro, Miami, Dade Co, collection of Bernard Landau (1). **Jamaica: late Pliocene:** Bowden: UCMP S-2 (1). **Atlantic Costa Rica: Latest Pliocene-Early Pleistocene:** Moín: NMB 17792 (3); 18079 (2); 18113 (4); 18272 (2); 18273 (5); 18274 (1); 18275 (6); 18277 (1); 18278 (8); TU 953 (GNS WM18875, 2); 954 (GNS WM18876, 6); 1240 = NMB 19008 (45; 2 illustrated, NMB H 17938, H 17939; Pl. 38, Figs 1-3; GNS WM16954, 15; WM18877, 21); 1307 (GNS WM18878, 6); USGS 20468 (6); 21051 (3); Moín Fm, Puerto Limón, coll. T. Kemperman (ZMA, 2); TU 1240, Moín Fm, Los Corales, Limón, collection of Bernard Landau (18); Lomas del Mar reef member, Moín Fm (Late Pliocene-Early Pleistocene), Lomas del Mar West, Puerto Limón, coll. P. D. Taylor & J. A. Todd, February 1998 (BMNH Palaeontology Department, 1); basal Moín Fm mudstone member (Late Pliocene), Rte. 32, 3 km W of Puerto Limón, coll. J. A. Todd, February 1988 (BMNH Palaeontology Department, 8). Robinson (1991) also recorded 21 specimens from the Moín Fm at Limón in four Tulane University collections that I have not examined (TU 954, 9; 1239, 1; 1240, 3; 1489, 8). **Atlantic Panama: Middle Miocene:** lower Gatun Fm: BMNH Palaeontology Department, bed 4 of Gale & Todd, "Sand Dollar Hill," Sabanita, Colon Province (BMNH Palaeontology Department, GG22582, 1, illustrated; Pl. 47, Fig. 15). **Pliocene:** Escudo de Veraguas Fm: NMB 18681 (1); NMB 18682 (1); Shark Hole Point Fm: NMB 18724 (1); apparently Fish Hole Reef Member of Shark Hole Point Fm (see

Appendix 3): USGS 8307, Minnitimbi Creek, Colon Island (1). **Pleistocene:** NMB 18372, Swan Cay (2); NMB 18743, Swan Cay (1). **Colombia: Pliocene:** Plato, Departamento de Magdalena (UCMP, 2). **Dominican Republic: Late Early Miocene:** Baitoa Fm: NMB 17265 (1). **Late Miocene/Early Pliocene:** Gurabo Fm: TU 1225 (1); 1231 = NMB 19006 (8; 1 illustrated, NMB H 17937; Pl. 38, Fig. 4); 1412 (GNS WM18883, 1); BMNH Palaeontology Department, GG20524, "Miocene," Río Yaque, Santo Domingo, coll. Col. T. S. Heneken, ca. 1848 (1). **Early Pliocene:** Gurabo Fm: NMB 15803 (1); 15813 (1); 15817 (1); TU 1210 (GNS WM16906, 5; WM18879, 3); 1211 (GNS WM16911, 4); 1212 (5); 1213 (GNS WM16905, 2; WM18880, 2); 1214 (GNS WM18881, 2); 1278 (GNS WM18882, 4); 1210, Gurabo Fm, Río Gurabo, collection of Bernard Landau (6); 1219, Río Amina, collection of Bernard Landau (1). **Trinidad: Holocene:** NMB 10186 (4); 10187 (1). **Venezuela: Late Early Miocene:** Cantaure Fm, S of Casa Cantaure, Paraguaná Peninsula, Falcón, collection of Bernard Landau (2). **Pliocene:** NMB 12045 (1); 12892 (3); 13338 (1); 17512 (29); 17513 (2); 17531 (5); 17561 (1); 17606 (5); 18169 (3); USGS 24548 (1); Cerro Negro Member, Cubagua Fm, house at Las Calderas, Cubagua Island, Nueva Esparta (UCMP S-155, 3) (possibly actually from Tortuga Fm, Pleistocene); 6 km E of Castillo of Cumaná, Sucre (UCMP S-112, 4); Mare Fm, Quebrada Maria Abajo (PRI 26190, 1; specimen illustrated by Weisbord, 1962: pl. 25, figs 1, 3); same as last (PRI 29191, 1; specimen illustrated by Weisbord, 1962: pl. 25, figs 2, 4). **Pleistocene:** NMB 12884 (1); 17542 (3); USGS 18410 (1).

Distribution.—*Monoplex krebssii* lives at present throughout the western Atlantic, from Cape Hatteras, North Carolina (Porter, 1970), USA, south to Amapa, northern Brazil (Rios, 1994: 89). Two large, colorful frags were collected by Bernard Landau and AGB on the beach at Praia, Santa Maria Island, Azores, in February 1998, and a fragmentary specimen at MNHN from Vila Franco do Campo, São Miguel, Azores, was illustrated by Gofas & Beu (2002: fig. 5B). The only other record from the eastern Atlantic is that by Garcia-Talavera (1983: 107; 1987: 249) from the Canary Islands, amplified by the records above. Ardevini & Cossignani (2004: 128) also illustrated two Canary Islands specimens in color. Fossils are newly recorded here from the Early Miocene Chipola Fm of Florida and from the Early Miocene Cantaure Fm of the Paraguaná Peninsula, Venezuela, and occur widely throughout the Atlantic part of the tropical American region in Miocene to Pleistocene deposits. They are moderately common in the Dominican Republic, occur at many localities in the Atlantic coastal area of Venezuela, and are particularly common and beautifully preserved in the Late Pliocene-Early Pleistocene Moín Fm near Limón, Costa Rica. There are no records from the eastern Pacific, which in itself provides a comment on the

degree to which these supposedly wide-ranging planktotrophs were transported through the Central American seaway; it was evidently a filter barrier already by late Miocene time.

Monoplex lignarius (Broderip, 1833)

Pl. 37, Figs 10, 12-14, 18

Triton lignarius Broderip, 1833: 5; Reeve, 1844a: pl. 13, fig. 40;

Hinds, 1844b: 12, pl. 4, figs 15-16; C. B. Adams, 1852: 117.

Tritonium lignarium. Menke, 1850: 190.

Triton (Simpulum) lignarius. Tryon, 1880: 15, pl. 9, fig. 63.

Cymatium lignarium. Dall, 1909b: 226; Olsson, 1924: 124 (list); Abbott, 1974: 165.

Cymatium (Ranularia) kugleri Rutsch, 1942: 143, pl. 9, fig. 5.

Cymatium (?Monoplex) lignarium. Keen, 1971: 507, fig. 957.

Cymatium (Septa) lignarium. Kilias, 1973: 172, fig. 126.

Cymatium (Turritriton) lignarium. Beu, 1985: 60; Henning & Hemmen, 1993: 103, pl. 21, fig. 6; Piech, 1995: 14.

Cymatium (Monoplex) lignarium. Beu, 2001: 712, fig. 1.7; López de la Fuente & Ramos, 2004: 85.

Remarks.—*Monoplex lignarius* is an unusual, small (most specimens are not more than 25 mm H), short and wide, strongly inflated shell with only the very prominent, wide terminal varix developed on most specimens. C. B. Adams (1852: 117) commented on the terminal varix being “enormously developed.” Some specimens develop also a penultimate varix; Hinds (1844b: 12) long ago noted that “it seems liable to considerable variation in the number and relation of its varices.” The sculpture is of numerous, narrow, well-raised spiral cords, crossed by a few widely spaced, narrow axial costae, and by many low, narrow axial costellae that give the cords a finely granulose appearance. The most distinctive character is the armor of the aperture, which has low, closely spaced ridges inside the outer lip, several low transverse ridges on the inner lip, and a row of small, sharply rounded nodules scattered irregularly along the outer margin of the inner lip. Recent specimens have a rich orange-brown coloration with the spiral cords darker than the rest, and the teeth and nodules inside the aperture are pale, white on many specimens, on a dark brown background. One of the largest specimens seen, from Panama (Mrs. de Burgh collection, BMNH) has a bright orange aperture, so it resembles a short specimen of the West African species *M. trigonus*. It is conceivable, then, that *M. lignarius* evolved as a sister species to *M. trigonus*.

The holotype of *Cymatium kugleri*, NMB H 6169 (Pl. 37, Fig. 12), from the Springvale Fm (Early Pliocene; Donovan, 1994) at Springvale Quarry, Trinidad, agrees in every respect with Recent specimens of *Monoplex lignarius*. This therefore turns out to be another of the paciphile species that, like *Bursa rugosa*, occurred in the Caribbean region during Neogene time, but now live only in the eastern Pacific. Specimens also occur in the Cujarao Fm of northern Venezuela, but I have

not seen fossils from the eastern Pacific.

Dimensions.—*Triton lignarius*, lectotype: H 32.1, D 21.8 mm; paralectotypes: H 31.4, D 21.4 mm, and H 29.1, D 18.9 mm; *Cymatium (Ranularia) kugleri*, holotype: H 21.7, D 15.8 mm; NMB H 17948, from NMB 13112, Carrizal, Venezuela: H 24.3, D 17.0 mm; Recent, LACM 69-13, Banderas Bay, Nayarit, W Mexico: H 27.0, D 17.7 mm; Recent, LACM 68-194, Sayulita, Nayarit, W Mexico: H 27.1, D 18.3 mm; Recent, LACM-A.9334.73, Palo Seco, W Panama: H 26.0, D 18.5 mm; GNS WM9316, Recent, Mazatlan, Mexico: H 23.7, D 17.6 mm.

Types.—*Triton lignarius*, lectotype and 2 paralectotypes BMNH 1968528a-c, from “Puerto Potrero and Panama.” The largest specimen (H 32.1 mm; Pl. 37, Fig. 18) is the one illustrated by Reeve (1844a: pl. 13, fig. 40), and is here designated the lectotype. The type locality is here designated as Panama Bay. *Cymatium (Ranularia) kugleri*, holotype NMB H 6169 (Pl. 37, Fig. 12), from Springvale Fm (Early Pliocene; Donovan, 1994), Springvale Quarry, Trinidad. I claimed (Beu, 2001: fig. 7) that the specimen that I illustrated (NMB H 17948), one of three from the Mataruca Member of Cujarao Fm (Late Miocene), loc. NMB 13112, Carrizal, E of La Vela, Falcón, Venezuela, was a paratype of *C. kugleri*, but this is incorrect; Rutsch (1942) designated only the holotype.

Other material examined.—**Recent:** 30 lots examined, nearly all at LACM, 4 at GNS, from W Mexico (northernmost: La Paz, Baja California Sur, LACM-A.3991, 1), W Costa Rica, W Panama, and Ecuador (southernmost: Punta Malposa, Manta, MCZ 206330, 2). Two specimens at the National Museum of Wales (NMW a4.23; Pl. 37, Figs 10, 13) are labeled “St Helena,” but this is incorrect; they must actually be from either Cabo Santa Elena, Costa Rica, or, more probably, Bahia Santa Elena, S of Manta, Ecuador.

Fossils: **Trinidad:** **Early Pliocene:** USGS 21809, Springvale Quarry (1). **Venezuela:** **Late Miocene:** NMB 13112, Mataruca Member of Cujarao Fm, Carrizal, E of La Vela, Falcón, Venezuela (3; 1 illustrated, NMB H 17948; Pl. 37, Fig. 14); NMB 17530, Mataruca Member of Cujarao Fm, Cementario de Carrizal, Falcón, coll. J. & W. Gibson-Smith (4).

Distribution.—Keen (1971: 507) recorded *Monoplex lignarius* as ranging from the Gulf of California to Negritos, Peru. The records by Olsson (1924) did not extend the range any further south. The material listed above ranges from La Paz, Baja California Sur, to Manta, Ecuador, but *M. lignarius* evidently is uncommon in the Gulf of California and to the south of Panama. Fossils are recorded here only from the Caribbean part of the study area, from only two localities: Springvale Quarry, Trinidad, Early Pliocene, and Cujarao Fm, Late Miocene or Early Pliocene, at Carrizal, Falcón, Venezuela. This is a paciphile species, then, which has changed

its distribution from the Caribbean to the eastern Pacific after Early Pliocene time.

***Monoplex longispira* n. sp.**

Pl. 36, Figs 3, 5

Description.—Shell large for genus, with unusually tall spire in relation to aperture height, short last whorl, strongly and evenly inflated whorls sculptured much as in *Monoplex aquatilis*, and numerous varices down entire teleoconch; 7 varices present on holotype, slightly irregularly placed on early spire whorls, with more than one varix per whorl on early whorls of holotype, but regularly placed at each two-thirds of a whorl (each 240° around the spiral) on last three whorls. Teleoconch of 7 whorls; protoconch not seen. Spiral sculpture of 7 primary cords on last whorl (crossing varices), uppermost closely submarginating suture, deeply subdivided in half by median groove; other 6 cords wide and strap-like with few grooves on their weakly convex crests over most of whorl surface, subdivided over varices by deep grooves, forming a fasciculate pattern (one wide, prominent central cord margined on each side by a subsidiary cord); cords forming only low ridges where they cross varices; second cord from posterior (uppermost undivided one) protruding to define narrow, steeply inclined, weakly concave sutural ramp; 3 or 4 primary cords visible on spire whorls; 10 lower, more closely spaced cords on base and anterior siphonal canal; 1-3 low, wide secondary cords of varying width filling all primary spiral interspaces. Entire surface crossed by obvious but low, narrow axial ridges, with interspaces each about equal in width to one ridge, grouped in places to form low, rounded, widely spaced, axially aligned nodules on primary spiral cords, 7-8 on each cord in each of last 2-3 intervariceal intervals on holotype. Aperture short and wide for a large *Monoplex* species, with much more deeply excavated columella and more strongly out-curved, evenly curved outer lip than in *M. aquatilis*; terminal varix a little narrower than in *M. aquatilis* of comparable size; entire aperture a little more coarsely and widely callused and armed than in *M. aquatilis*, with inner lip extending a little further to left of aperture and with much more clearly, sharply defined left margin than in *M. aquatilis*; closely sculptured with numerous prominent, long, transverse ridges over whole height of lip and down left edge of anterior siphonal canal, apart from short, wide, smooth posterior anal notch margined by low parietal swelling, swelling bearing two prominent transverse ridges; interior of outer lip bearing 7 prominent rounded swellings and a weak anterior eighth (much as in *M. parthenopeus*), corresponding to interspaces of exterior spiral cords; each swelling bearing a moderately long, very prominent

transverse ridge, each ridge subdividing in half at outer margin; uppermost (posteriormost) swelling bearing two transverse ridges, subdividing into four parts at margin. Anterior siphonal canal short, straight, directed a little to left, probably slightly incomplete.

Dimensions.—Holotype, NMB H 71929: H 92.9, D 49.6 mm.

Type material.—Holotype, NMB H 17929 (Pl. 36, Figs 3, 5), Gurabo Fm, Late Miocene, from locality TU 1250 (= NMB 18558), Río Verde, 10 km N of La Vega, Dominican Republic.

Other material examined.—**Fossils: Dominican Republic: Late Early Miocene:** TU 1363, Baitoa Fm, Boca de los Rios, below waterfall in Arroyo Hondo (GNS WM18890, 1 outer lip frag, agreeing with holotype); 1364 = NMB 18560, Baitoa Fm, Boca de los Rios, above waterfall in Arroyo Hondo (1 small, not certainly identified).

Distribution.—*Monoplex longispira* n. sp. is recorded only from Miocene rocks of the Dominican Republic, although it was presumably more widespread than this in the Caribbean area during Miocene time.

Remarks.—At first, I assumed that the holotype of *Monoplex longispira* n. sp. was a specimen of *M. aquatilis*, but the much shorter aperture, the much more deeply excavated columella, the more widely and prominently callused aperture, and the relatively tall spire demonstrate that it is distinct. The other possibility seemed to be that it is a very large, tall-spined specimen of *M. cercadicus*, but not only is the spire very much taller than in *M. cercadicus*, it also has numerous varices down the entire teleoconch, whereas all other material assigned to *M. cercadicus* has one or at most two varices, and a more strongly out-turned, strongly lirate interior of the outer lip. *Monoplex cercadicus* also has much narrower, more widely spaced spiral cords. The only remaining possibility is that the holotype represents a rare, distinct species, of which I have seen only the one good adult specimen and a few small fragments. The type locality, Río Verde, is one from which I have seen little other material, and this possibly explains why only one good specimen has been seen of *M. longispira*. The depositional site of the Gurabo Fm at Río Verde seems likely to have been unusually deep, around 150-350 m, as cited by E. Vokes (in E. & H. Vokes, 1989: 21) for Arroyo Zalaya. It is therefore possible that this was a bathyal species, but the robust holotype appears more like a shallow-water specimen, and it seems more likely that the holotype was transported down-slope from shallower water.

Etymology.—The species name refers to the most distinctive character of the new species – its tall spire and correspondingly short last whorl; a noun in apposition.

Monoplex macrodon (Valenciennes, 1832)

Pl. 38, Figs 13-16

Triton macrodon Valenciennes, 1832: 305.*Triton (Lampusia) vestitum*. Stearns, 1894: 188, 203 (in part not *Triton vestitus* Hinds, 1844).*Cymatium pileare*. Dall, 1909b: 226; Strong & Hanna, 1930: 18; Finet, 1991: 270 (not *Murex pilearis* Linnaeus, 1758).*Cymatium vestitum*. Hertlein & Emerson, 1953: 351, pl. 27, fig. 12 only (in part not *Triton vestitus* Hinds, 1844); Hertlein & Allison, 1960: 15.*Cymatium (Septa) pileare*. Emerson & Old, 1963b: 20, fig. 18 (in part not *Murex pilearis* Linnaeus, 1758); Keen, 1971: 507, fig. 959.*Cymatium (Monoplex) macrodon*. Beu, 1985: 58; Beu & Kay, 1988: 210, figs 63-73; Henning & Hemmen, 1993: 64, pl. 14, fig. 3; Piech, 1995: 10; Kaiser, 1997: 32; 2007: 38, pl. 26, figs 3a-b.*Cymatium pileare macrodon*. Emerson, 1991: 68 (list); Hickman & Finet, 1999: 71, fig. 62.

Remarks.—*Monoplex macrodon* is one of the species of the “*Monoplex pilearis* complex,” distinguished above from *M. aquatilis*. The characters, types, range and comparisons were reviewed in detail by Beu & Kay (1988) and need only be summarized here. The differences from the similar western Atlantic specimens of *M. pilearis* are the slightly finer exterior sculpture, the more nearly scarlet red (rather than deep, dull red-brown) of the exterior of most specimens, the significantly taller spire of almost all specimens of *M. macrodon* than of *M. pilearis*, and the brighter red color of the interior of the outer lip, which is a pale, dull red in Atlantic specimens of *M. pilearis* and a brighter, salmon red in *M. macrodon*. Specimens are illustrated excellently in color on a webpage (<http://www.femorale.com.br/shellphotos>, last accessed 28 April 2006). I am the first to agree that *M. pilearis* and *M. macrodon* are very similar, and they undoubtedly are very closely related in a phylogenetic sense, probably forming a pair of sister species, one of the better tonnoidean examples of an Atlantic and Pacific geminate species pair. The subspecies relationship between them preferred by some authors (e.g., Emerson, 1991) is a matter of personal choice. The important point to note is that these two taxa, one living on each side of the Isthmus of Panama, are *different*, rather than identical.

Before Beu & Kay's (1988) work, 20th-century taxonomists all had identified this species as either *Monoplex vestitus* or *M. pilearis*. Kay and I (Beu & Kay, 1988) proposed a neotype for Valenciennes' (1832) otherwise unrecognizable name, to make it available for the eastern Pacific species. The existence of the two species *M. vestitus* and *M. “pilearis”* in the eastern Pacific was first pointed out by Strong & Hanna (1930) and was clarified by Emerson & Hertlein (1963).

Dimensions.—Neotype of *Triton macrodon*: H 81.3, D 41.7 mm. Most specimens do not exceed ca. 60 mm H.

Types.—*Triton macrodon* Valenciennes, neotype AMNH 74263, designated by Beu & Kay (1988), from Puritan Expedition sta. 35, 1-6 m, Isla San Juanito, Islas Tres Marias, Nayarit, W Mexico.

Other material examined.—**Recent:** 31 lots examined, at AMNH, GNS, LACM, SMF, USNM, ZMA, from W Mexico (northernmost: 8-30 m, Cape San Lucas, LACM 66-12, 1), W Costa Rica, W Panama, W Colombia, Cocos Island, Clipperton Island, and the Galápagos Islands (11 m, Isla Marchena, Galápagos, USNM 780586, 1; unusually tall and narrow).

Distribution.—A total of only 52 specimens of this evidently rare species has been examined at the main American museums, GNS, and ZMA. I am aware of authentic modern records of *Monoplex macrodon* from the Gulf of California to western Colombia, and from Clipperton and Cocos islands, and possibly the Galápagos Islands (the one Galápagos specimen that I have seen is taller and narrower than all others, and possibly represents a distinct species (Beu & Kay, 1988); but the Galápagos Islands specimen illustrated by Hickman & Finet (1999: fig. 62) closely resembles specimens from the mainland). Kaiser (2007: 38-39) recorded specimens collected alive at Clipperton Island. Emerson (1991) added a record from the Revillagigedo Islands. The material from Gorgona Island, Colombia, recorded as *M. pilearis* by Cantera *et al.* (1979) presumably refers to *M. macrodon*, and that recorded by Cosel (1984) certainly does (examined at SMF). It seems very likely that *M. macrodon* extends south at least to Ecuador, and Dall's (1909b) record of *M. pilearis* from Peru presumably refers to this species. There are no records of fossils. It seems likely that *M. macrodon* is a sister species of *M. pilearis*, that is, that they form a true geminate species pair, in the sense of a speciation event resulting from uplift of the CAI.

Monoplex mundus (Gould, 1849)

Pl. 39, Figs 14, 16-17; Pl. 40, Figs 4, 6; Pl. 41, Figs 1, 5

Triton gemmatus var. B Reeve, 1844a: pl. 15, fig. 60c only (not *Triton gemmatus* Reeve, 1844).*Triton mundum* Gould, 1849: 143; 1856: 506, pl. 17, figs 297-297b; 1862: 66; Johnson, 1964: 112.*Tritonium mauritianum* Tapparone-Canefri, 1876b: 243.*Triton (Simpulum) gemmatus*. Tryon, 1880: 13, pl. 7, figs 43-44 (in part not *Triton gemmatus* Reeve, 1844).*Tritonium mundum*. Tapparone-Canefri, 1881: 26.*Septa gemmata*. Rippingale & McMichael, 1961: 67, pl. 7, fig. 10; Hinton, 1972: 12, pl. 6, fig. 16 (not *Triton gemmatus* Reeve, 1844).*Cymatium gemmatum*. Barnard, 1963: 28; Salvat & Rives, 1975: 305, fig. 173; Hinton, 1978: 30, figs 8-8a; Salvat *et al.*, 1988: 102, pl. 13, fig. 7; Finet, 1991: 270 (not *Triton gemmatus* Reeve, 1844).*Cymatium (Septa) gemmatum*. Kilias, 1973: 168, fig. 124; 1981: 707

(not *Triton gemmatus* Reeve, 1844); Kay, 1979: 222, fig. 79C.

Cymatium (Monoplex) mundum. Beu, 1985: 58; 1998b: 105, figs 32a-j; 1999: 26, figs 50-51; Lai, 1989: 125, fig. 45; Emerson, 1991: 65, figs 11-25; 1993: 70, figs 3-4; Piech, 1993: 88, figs 1-2; 1995: 10; Henning & Hemmen, 1993: 65, pl. 12, fig. 5; Wilson, 1993: 245, pl. 42, fig. 11; Kaiser, 1997: 32; Okutani, 2000: 289, pl. 143, fig. 20; Zhang & Ma, 2004: 149, text-fig. 92; Mogollon, 2004: 1, fig. 1; Beu & Segers in Poppe, 2008: 644, pl. 267, fig. 9.

Cymatium (Septa) mundum. Kilburn, 1984: 2; Springsteen & Leobrera, 1986: 116, pl. 31, fig. 13.

Cymatium (Monoplex) gemmatum. Finet, 1985: 19 (not *Triton gemmatus* Reeve, 1844).

Cymatium mundum. Kubo in Kubo & Kurozumi, 1995: 75, fig. 7; Lee & Chao, 2003: 41, pl. 4, fig. 98.

Remarks.—Emerson (1991) clarified the application of this name, and he and I (Beu, 1998b) each provided data on the types and a range of material examined. Again, this need only be summarized here. *Monoplex mundus* is the small, usually white or cream species that is moderately common in the Indo-West Pacific, but has usually been known as *M. gemmatus*. This name actually applies to a much less common, smaller, narrower, pale orange-brown species with more dominant spiral sculpture. The real *M. gemmatus* is limited to the western Pacific, where it is recorded from southern Japan to Queensland and New Caledonia (Beu, 1998b) and to eastern Polynesia (Austral Islands; Emerson, 1991). *Monoplex mundus* is a slightly wider, more coarsely sculptured shell with several nodules around the shoulder angle in each intervariceal space on most specimens, and with much wider and thicker varices than *M. gemmatus*. *Monoplex mundus* resembles small specimens of *M. pilearis* in some characters, but can be distinguished by the much smaller maximum size (to ca. 47 mm H, but rarely exceeding 40 mm), the much paler color of Recent material, the more elongate shape, and the much heavier varices.

The first to realize the distinction between *Monoplex mundus* and *M. gemmatus* was Tapparone-Canefri (1881: 26), who listed the two as distinct species, included in the synonymy of *Tritonium gemmatum* “excl. fig. 60c,” listed Reeve’s figure (1844a, pl. 15, fig. 60c) in the synonymy of *T. mundus*, and listed his name *Tritonium mauritianum* as a synonym of *T. mundus*. The two species also were distinguished and illustrated by Springsteen & Leobrera (1986) and Emerson (1991).

Dimensions.—*Triton mundum*, lectotype: H 29.2, D 16.7 mm; largest seen, GNS WM 15552, Tryon Island, southern Great Barrier Reef, Australia: H 47.3, D 25.0 mm.

Types.—*Triton mundum*, lectotype USNM 5695, designated by Johnson (1964: 112), illustrated by Emerson (1991: figs 12-13); from Tutuila, American Samoa; paralectotypes USNM 612311 and MCZ 169249. *Tritonium mauritianum*, types not seen, from Mauritius, presumably in Museo Civico

di Storia Naturale “Giacomo Doria,” in Genoa.

Other material examined.—**Recent:** **W Atlantic:** **Florida:** S end of Lake Worth, Palm Beach Co, Florida, coll. Vera Lyman, ex A. D’Attilio collection and ex Abbey Specimen Shells (GNS WM 15228, 1; illustrated, Pl. 41, Fig. 1); Gulf Stream, off of Palm Beach Co, Florida, coll. F. Lyman, 1940 (LACM 115537, 1). Piech (1993) recorded three additional specimens: dredged, 149 m, off of Palm Beach Co, Florida, Lyman family, 1940 (AMNH 181298, 1); from shrimp boats, 185 m, off of Key West, Florida, 1978 (Sunderland collection, 2; Piech, 1993: figs 1-2). **E Pacific:** **Galápagos Islands:** Emerson (1991: 65) recorded the first specimens from the Galápagos Islands: Academy Bay, Isla Santa Cruz, fresh beach specimen, June 1966 (AMNH 139553, 1); locality same as last, with hermit crab, at low tide, December 1965 (AMNH 232145, 1; Emerson, 1991: figs 21-22); with hermit crab, South Channel, between Isla Baltra and Isla Santa Cruz, collected ca. 1975 (1, collection of C. Angermayer). **Pacific Panama:** Emerson (1993) recorded a single specimen from the low tide mark at Punta Itaco, Golfo de Montijo. **Peru:** Mogollon (2004) recorded and illustrated a single specimen taken alive by a shrimp trawler in 20 m off of Puerto Pizarro, Departamento de Tumbes (03°30.0’S, 80°23.0’W).

Fossils: **Cuba:** **Pleistocene:** USGS 12103B, Naval Station, Guantanamo Bay (1). **Barbados:** **Pleistocene:** USGS 18381, Pine, terrace fauna near airport (1, illustrated, Pl. 40, Fig. 4).

Distribution.—*Monoplex mundus* lives now throughout the Indo-West Pacific province from Durban, South Africa, to the northern Indian Ocean and from Yamaguchi Prefecture, western Honshu, Japan (Beu, 1999), south to southern Queensland, Australia (Capricorn Group, southern Great Barrier Reef) and New Caledonia (Beu, 1998b) eastward throughout Polynesia to Hawaii (Kay, 1979) and the Austral Islands (Emerson, 1991; although this is not among species collected recently at the Austral Islands in a detailed MNHN survey). The only records in the eastern Pacific are the three specimens recorded by Finet (1985) and Emerson (1991) from the Galápagos Islands, the specimen recorded by Emerson (1993) from western Panama, and the specimen recorded by Mogollon (2004) from Peru. In the western Atlantic, the only records are five specimens from off of southeastern Florida, USA, but it probably occurs much more widely, but uncommonly. Within the study area, the only fossil record is one Pleistocene specimen each from Cuba and Barbados.

Monoplex nicobaricus (Röding, 1798)

Pl. 13, Fig. 1

Tritonium nicobaricum Röding, 1798: 126; Iredale, 1929a: 345.

Triton chlorostomum Lamarck, 1822: 185; Kiener, 1842: 19, pl. 12, fig. 2; Deshayes, 1843: 636; Krebs, 1867: 398.

Triton chlorostomus. Reeve, 1844a: pl. 8, fig. 25.

- Triton pulchellus* C. B. Adams, 1850a: 60; Krebs, 1867: 398.
Triton (Simpulum) chlorostomum. Chenu, 1859: 151, fig. 688.
Triton (Lampusia) chlorostomum and var. *pumilio* Mörch, 1877: 29.
Triton (Simpulum) chlorostomus. Tryon, 1880: 13, pl. 7, figs 47-48.
Triton chlorostoma. E. A. Smith, 1891: 413.
Lampusia chlorostoma. Dall & Simpson, 1901: 417; Dall, 1903b: 132.
Cymatium chlorostomum. Maury, 1922: 116; Lebour, 1945: 478, fig. 24 (larva).
Cymatium chlorostoma. Piele, 1926: 80.
Triton (Lampresia [sic]) chlorostomus. Coulon, 1933: 126.
Cymatium (Lampusia) chlorostoma. Morretes, 1949: 92.
Cymatium (Cymatriton) nicobaricum. Clench & Turner, 1957: 210, pl. 111, figs 5-6, pl. 113, fig. 4, pl. 120, figs 1-3; Andrews, 1971: 104, illus.; 1977: 131, illus.; Abbott, 1974: 164 (not pl. 7, fig. 1760 = *C. aquatile*); Coelho *et al.*, 1981: 120, fig. 6; H. & E. Vokes, 1983: 22, pl. 11, fig. 5; Kilburn, 1984: 2, pl. Bg; Diaz & Puyana, 1994: 172, fig. 641.
Cymatriton nicobaricum. Hertlein & Allison, 1960: 15; Habe, 1961: 45, pl. 22, fig. 6; 1964: 71, pl. 45, fig. 6.
Cymatium (Ranularia) nicobaricum. Warmke & Abbott, 1962: 100, pl. 18, fig. g.
Cymatium nicobaricum. Work, 1969: 662; Kaufmann & Götting, 1970: 370, fig. 83; Hinton, 1972: 12, pl. 6, fig. 3; 1978: 29, fig. 11; Salvat & Rives, 1975: 305, fig. 172; Kay, 1979: 216, fig. 77D; Garcia-Talavera, 1983: 102; Cosel, 1982b: 54; Jensen & Harasewych, 1986: 428, fig.; Drivas & Jay, 1988: 64, pl. 17, fig. 5; Diaz & Götting, 1988: 156; Lipe & Abbott, 1991: 12, illus.; Vega-Luz & Vega-Luz, 1995: 7; Kubo in Kubo & Kurozumi, 1995: 76, fig. 5; Guerreiro & Reiner, 2000: 112-113; Lee & Chao, 2003: 41, pl. 4, fig. 99; Arduvini & Cossignani, 2004: 128, lower right fig.
Cymatium (Septa) nicobaricum. Kiliyas, 1973: 174, fig. 128; 1981: 707; Nordsieck & Garcia-Talavera, 1979: 115, pl. 24, fig. 3; Rios, 1985: 76, pl. 27, fig. 332; 1994: 89, pl. 29, fig. 348; Springsteen & Leobreria, 1986: 112, pl. 30, fig. 13; Petuch, 1994: pl. 39, fig. C; 1997: 303, fig. 114, fig. K.
Cymatium vespacium. Bandel, 1984: 99, pl. 9, fig. 4 (not *Triton vespacium* Lamarck, 1816).
Cymatium (Monoplex) nicobaricum. Beu, 1985: 58; 1998b: 107, figs 23a, 29i; Garcia-Talavera, 1987: 253, pl. 1, fig. 8; Lai, 1989: 123, fig. 37; Henning & Hemmen, 1993: 66, pl. 12, fig. 7; Wilson, 1993: 245, pl. 41, fig. 9; Piech, 1995: 10; Bosch *et al.*, 1995: 98, fig. 354; Kaiser, 1997: 32; 2007: 39, pl. 26, figs 4a-b; Okutani, 2000: 287, pl. 142, fig. 17; Redfern, 2001: 61, pl. 31, figs 260A-B; Zhang & Ma, 2004: 139, text-figs 85a-c; Beu & Segers in Poppe, 2008: 644, pl. 267, fig. 2.

Remarks.—*Monoplex nicobaricus* is easily recognized by (a) its moderately tall, strongly stepped spire and short to moderately long, strongly twisted anterior canal, (b) its very strongly angled, coarsely nodulose whorls and coarse sculpture of prominent, wide spiral cords with the interspaces filled by 2 or 3 secondary and tertiary cords, all forming low nodules on the varices, and crossed by numerous low, heavy, irregular axial costae that form many small nodules at the sculptural

intersections, (c) its thickly callused, smooth aperture with 7 prominent, smoothly rounded ridges inside the out-turned outer lip, and several low transverse ridges over the whole height of the inner lip, and (d) its distinctive, large, narrowly and sharply conical protoconch with weakly impressed sutures. Recent specimens are very distinctive because of the bright orange-red aperture with paler transverse ridges, and the dark gray-brown grooves between nodules on the exterior surface, giving the exterior an overall pale gray coloration.

Dimensions.—Tenerife, Canary Islands, Recent (MNHN): H 58.3, D 33.1 mm; La Palma, Canary Islands, GNS WM15188: H 53.2, D 26.5 mm; illustrated specimen, GNS WM16367, Pelican Shoals, Florida: H 52.1, D 30.7 mm; H 52.5, D 29.4 mm; Guadeloupe, GNS WM17007: H 53.7, D 28.2 mm; Bonaire, GNS WM16366: H 46.4, D 29.0 mm; Taiwan, GNS WM16337: H 75.5, D 38.3 mm; Rarotonga, Cook Islands, GNS WM13938: H 74.8, D 39.8 mm.

Types.—*Triton chlorostomum*, lectotype MHNG 1100/6/3, designated by me (Beu, 1998b: 108), with 3 paralectotypes, MHNG 1100/6/1, 2, 4, without locality; Clench & Turner (1957: 211) designated the type locality as Jamaica. The lectotype is the specimen illustrated by Kiener (1842: pl. 12, fig. 2), and was also designated by me (Beu, 1998b) as the neotype of *Tritonium nicobaricum*. *Triton pulchellus*, holotype MCZ 186135, from Jamaica. No type material is known for Mörch's *Triton chlorostomum* var. *pumilio*.

Other material examined.—**Recent:** **W Atlantic:** Western Atlantic lots of this abundant species have not been listed; 11 lots at GNS, from Bahamas, Florida Keys, Cuba, Puerto Rico, Guadeloupe (4 lots), St. Lucia, and Bonaire. Bandel's (1984: 99, pl. 9, fig. 4) voucher specimens from Santa Marta, Colombia, from which radulae supposedly of *Monoplex vespacius* were prepared are actually *M. nicobaricus* (RMNH, 2 specimens). **E Atlantic:** **Canary Islands:** El Medano, Tenerife, intertidal (MNHN, 1); Santa Cruz de la Palma, dived in 3-6 m (MNHN, 2); Tenerife (MNHN, 1); Candelaria, Tenerife (TFMC 1459, 1 large); dredged 25-30 m, Radazul, Tenerife (TFMC 1463, 1 small); La Teresitas, Tenerife (TFMC 1465, 1 large); Tenerife (TFMC 1460, 3; TFMC 34, 9); between Candelaria and Güimar, Tenerife (TFMC 1462, 2 small); Puerto Cruz (TFMC 1464, 1 small); Playa de Alcalá, Tenerife (TFMC 1554, 3); low tide, Punta de la Rasca, S Tenerife (GNS WM17405, 7); 10 m, La Palma (GNS WM15188, 1); 3-15 m, Bahia de la Puerta, La Palma (GNS WM14954, 2); 10-15 m, Sardina, NW Gran Canaria (GNS WM16043, 1; WM18361, 1). **Cape Verde Islands:** beach W of Mindelo, Baio Porto Grande, São Vicente Island (MNHN, 1).

Fossils: **Bermuda: Pleistocene:** "south shore of Bermuda" (USNM, 1). **Dominican Republic: Pleistocene:** La Isabella Fm, El Castillo, La Isabella, collection of Bernard Landau (1, good). **Atlantic Panama: Pleistocene?:** USGS 22391,

dredged, Payardi Island (1). **Colombia: Pleistocene:** terrace 10 m above high tide, La Cieba, Departamento de Atlantico (UCMP S-46, 2). **Bonaire: Pleistocene:** Kralendijk, collection of Bernard Landau (1). **Venezuela: Pleistocene:** NMB 17568, Catia Member of Playa Grande Fm, Cabo Blanco (1).

Distribution.—*Monoplex nicobaricus* is a common shallow-water species throughout the Indo-West Pacific province, from Durban, South Africa, and the Red Sea eastward to Hawaii (Kay, 1979) and to eastern French Polynesia (*e.g.*, it is the most abundant tonnoidean in MNHN collections from the Marquesas Islands). It also occurs rarely at Clipperton and Cocos islands and at the Galápagos Islands in the eastern Pacific (Hertlein & Allison, 1960: 15; Emerson, 1991; Skoglund, 1992; Kaiser, 2007: 39), and commonly from Kii Peninsula, Honshu, Japan (Habe, 1964), south to the western end of Rottnest Island, southern Western Australia (Wilson, 1993; Beu, 1998b), and to Sydney Harbor, New South Wales (Iredale, 1929a). In the western Atlantic, it is less common, but occurs from the Bahamas and southern Florida (Clench & Turner, 1957), USA, south to Bahia, Brazil (Rios, 1994). *Monoplex nicobaricus* is one of the few common species in Florida to northern Brazil that has *not* been recorded in small numbers from further north on the eastern coast of the USA by Porter (1974). It is recorded from Ascension and St. Helena islands, is recorded from Madeira in the eastern Atlantic, is moderately common at the Canary Islands (Nordsieck & Garcia-Talavera, 1979: 115; Garcia-Talavera, 1987: 253; Ardovini & Cossignani, 2004: 128, lower right fig., illustrated in color), and specimens are recorded above from the Canary and Cape Verde islands. Petuch (1994: pl. 39C) illustrated a Holocene fossil specimen from Capeletti Brothers pit no. 11, Miami, Florida. In the study area, fossils are recorded only from a few Pleistocene localities, so this is evidently another of the tonnoideans that entered the Atlantic only during Pleistocene time.

***Monoplex panamensis* n. sp.**

Pl. 40, Figs 1, 3, 5, 7

Description.—Shell of moderate size for genus (to 65 mm H), relatively low and wide, with moderately tall spire with weakly stepped outline, moderately wide, moderately steeply sloping sutural ramp developing over last two whorls, becoming prominent and weakly concave on last whorl of large specimens, and rather short, wide, open siphonal canal inclined slightly toward dorsum. Varices wide and rounded, thinner over sutural ramp than below; only terminal one present on some specimens, two on others; one specimen has other, irregular varices developed on spire. Spiral sculpture commencing as three narrow cords with interspaces each equal in width

to one cord, one at center of sutural ramp and two on whorl sides; one on sutural ramp weakening down spire and two on whorl sides strengthening down spire; on last whorl, six major spiral cords passing onto varix, all low and broadly rounded, crests undivided except for very faint, narrow median groove over last quarter whorl of largest specimen; sutural ramp with low, wide, flat to weakly convex subsutural band and 2-4 wide to narrow, low, closely spaced secondary cords, with interspaces below ramp filled with one low, flat secondary cord and one tertiary cord of same height as secondary cord situated on each side of secondary one, all cords on whorl sides separated only by narrow grooves; with 6-7 further low, rounded, closely spaced cords on canal. Axial sculpture commencing as low, faint, closely spaced costae on early spire whorls, 20-25 on early whorls, forming faintly elevated nodules on two major spiral cords below sutural ramp; axial costae increasing in size and decreasing in number down shell to form 8-10 prominent folds on last whorl, commencing abruptly at sutural ramp and fading out over base, forming prominent, anteroposteriorly compressed (spirally elongate) nodules where they cross uppermost major spiral cord, and progressively smaller nodules on 3-4 cords below that. Entire teleoconch surface crossed by numerous low, faint, narrow, rather widely spaced, highly irregularly positioned axial ridges, forming weak, ill-defined gemmae on spiral sculpture of spire whorls but only low, ill-defined transverse ridges on main spiral cords on last whorl. Aperture large, broadly oval, with unusually deep excurrent (posterior) notch; lips narrow, well armed; interior of outer lip flared moderately widely over terminal varix, bearing a group of 3-4 closely spaced, prominent transverse ridges interior to sutural ramp and 6 groups each of 2 prominent transverse ridges below that; inner lip without distinct parietal ridge, coarsely ridged for entire height, transverse ridges wide, prominent, closely spaced, weakly anastomosing, ceasing abruptly at lower margin of excurrent notch to define notch. Protoconch not seen.

Dimensions.—Holotype: H 65.0, D 42.3 mm; figured paratype, NMB H 17945: H 44.8, D 29.6 mm; paratype, NMB H 17946: H 54.3, D (incomplete) 30.4 mm.

Types.—Holotype NMB H 17944 (Pl. 40, Figs 1, 3), from NMB 18503, Tuira Fm (Late Miocene), 1 km downstream from NMB 18501 (NMB 18501 is Tuira Fm (late Miocene), downstream from Boca de Tigre, 1 km below confluence with Río Cubilele, Río Chico, Darien, Atlantic coast of Panama); figured paratype NMB H 17945 (Pl. 40, Figs 5, 7), from NMB 18502, Tuira Fm (Late Miocene), Río Chico, 50 m downstream from and *ca.* 5 m stratigraphically above NMB 18501; one paratype NMB H 17946, from NMB 18525, Tuira Fm (Late Miocene), Río Tupisa, left bank, a few bends above Boca de Chiatí, upstream from Punta Grande, and *ca.* 700 m downstream from NMB 18522; one paratype NMB

H 17947, from NMB 18532, Tuira Fm (Late Miocene), Río Tupisa, Darien, upper landing place at Punta Grande (formation names and ages follow Coates *et al.*, 2004).

Other material examined.—**Fossils: Panama, Darien: Late Miocene:** NMB 18493, Tuira Fm, village of Punta Grande, Río Tupisa (= NMB 18531) (2 poor); NMB 18508, lower Chucunaque Fm, Río Chico, 200 m upstream from Comun village, first pueblo above Yaviza (1); NMB 18516, Tuira Fm, Río Tuquesa, left bank, 3 km below Marraganti (1); NMB 18535, Tuira Fm, Río Tuquesa, between Charco Chivo and village of Marraganti (1). **Atlantic Panama: Late Miocene:** Gatun Fm: NMB 18258, Cativa, Colon (1). **Pliocene:** Cayo Agua Fm: NMB 17633, Cayo Agua (1); 18719, as last (1 frag). **Ecuador: Late Miocene:** NMB 19122, Angostura Fm, shellbed 2.5 km below oyster bed, Punta Verde, 30 km ENE of Esmeraldas, Esmeraldas Province (2 small, incomplete).

Remarks.—*Monoplex panamensis* n. sp. resembles both *M. parthenopeus* and *M. tranquebaricus* in many characters, but differs from both in having smooth, undivided major spiral cords, without the median groove present on the major cords of all specimens of both living species. The new species more closely resembles *M. wiegmanni* and *Linatella caudata* in spiral sculpture, but still here it differs in detail. *Monoplex panamensis* n. sp. consistently has 6 moderately elevated, convex major spiral cords on the last whorl, with each interspace filled by a wide, low, central secondary cord with a low, very narrow tertiary thread filling each space between the primary and secondary cords. The regular pattern of low, wide, undivided cords alternating with flat, weakly grooved interspaces is not present on any other species of *Monoplex* of which I am aware, although a few extreme, weakly sculptured specimens of *M. wiegmanni* can be similar. *Monoplex panamensis* n. sp. also differs from both *M. wiegmanni* and *L. caudata* in having a more steeply inclined sutural ramp, producing a markedly taller and less stepped spire and a narrower, more fusiform shell shape than in either *M. wiegmanni* or *L. caudata*, although the holotype has a penultimate varix placed well to the right side on the last whorl that has affected the usual slightly narrower shape. The apertural armature of *M. panamensis* n. sp. is particularly similar to that of short, wide specimens of *M. wiegmanni*, although the transverse ridges on the inner lip are a little coarser and more prominent in most specimens of *M. panamensis* n. sp. than in any of the similar species. Also, *M. panamensis* n. sp. is unique in not having a true parietal ridge, distinguished from the other inner lip ridges by its larger size and by its distinct angle to the other ridges, as in all other species of *Monoplex*, including *M. wiegmanni*; the parietal side of the posterior apertural notch is merely demarcated by the absence of the closely spaced, parallel transverse ridges present down the rest of the columella.

Distribution.—*Monoplex panamensis* n. sp. is recorded only

from the Late Miocene and, much less commonly, Early Pliocene rocks of the Panama Isthmus, in Atlantic Panama and, in particular, in Darien, and from the Late Miocene Angostura Fm at one locality in Ecuador. It occurs on both coasts of the Central American Isthmus, clearly indicating that the Panama seaway was still open at the time when the rocks containing it were deposited.

Etymology.—The specific name, “from Panama,” reflects the provenance of the type material.

Monoplex parthenopeus (von Salis Marschlin, 1793)

Pl. 40, Figs 2, 8-9; Pl. 41, Figs 2, 4; Pl. 42, Figs 1, 5, 7

Murex costatus Born, 1778: 295; 1780: 297, illus. (junior primary homonym of *Murex costatus* Pennant, 1777).

Murex parthenopeus von Salis Marschlin, 1793: 370, pl. 7, fig. 4; Aufrere, 1795: 462, frontispiece; Dillwyn, 1817: 696; Wood, 1825: 127, pl. 25, fig. 30.

Monoplex australasiae Perry, 1811: pl. 3, fig. 3.

Murex doliare Brocchi, 1814: 398; Pinna & Spezia, 1978: pl. 32, figs 2-2a.

Murex intermedius Brocchi, 1814: 400, pl. 7, fig. 10; Pinna & Spezia, 1978: 150, pl. 35, figs 3-3a.

Triton succinctum Lamarck, 1816: pl. 416, fig. 2, “Liste des objets”: 5; 1822: 181; Kiener, 1842: 33, pl. 6, fig. 1; Deshayes, 1843: 628.

Murex costulatus Risso, 1826b: 197; Arnaud, 1978: 113, pl. 10, fig. 152.

Triton olearium. Reeve, 1844a: pl. 19, fig. 32 (not *Murex olearium* Linnaeus, 1758).

Triton americanum d'Orbigny, 1841a: 163, pl. 23, fig. 22.

Triton brasiliense Gould, 1849: 142.

?*Triton fossatum* Gould, 1860: 329 (unidentifiable).

Tritonium americanus. Krebs, 1864: 22.

Tritonium costatum. Krebs, 1864: 23.

Triton abbreviatus Bellardi, 1873: 216, pl. 14, figs 6a-b.

Triton (Simpulum) acclivis Hutton, 1873: 13, fig. 8.

Triton (Lampusia) costatum. Mörch, 1877: 27.

Triton (Simpulum) olearium. Tryon, 1880: 11, pl. 3, fig. 19, pl. 4, fig. 24, pl. 5, figs 27-29, pl. 6, fig. 37 (not *Murex olearium* Linnaeus, 1758).

Triton olearium var. *escoffierae* Fontannes, 1879: 26, pl. 3, figs 4a-b.

Triton parthenopeum vars. *milum* and *peribrantum* Gregorio, 1884: 95-96.

Triton parthenopeum vars. *stimum*, *sbilpum*, and *antupum* Gregorio, 1885: 39-40.

Triton (Simpulum) costatus. Watson, 1886: 390.

Lampusia olearium?. Dall, 1889: 132.

Triton succinctus. Kobelt, 1890: 21, pl. 38, figs 1-2, pl. 39, fig. 1.

Lampusia olearium. Dall, 1903b: 132.

Tritonium hirsutum “Fab. Colon.” Franseschini, 1906: 45 (adoption of a pre-Linnean name).

Lotorium costatum. Ihering, 1907: 427.

Cymatium olearium. Maury, 1922: 116 (not *Murex olearium* Linnaeus, 1758).

- Dissentoma prima* Pilsbry, 1945a: 59, text-fig. 1 (larval shell); Pilsbry, 1945b: 142; Jaume & Borro, 1946: 20, figs 1-4.
- Cymatium (Cabestana) costatum*. Morretes, 1949: 92.
- Cymatium echo* Kuroda & Habe, 1950: 30 (*nomen nudum*); Kira, 1955: 43, pl. 21, fig. 13 (*nomen nudum*); 1958: 53, pl. 21, fig. 13.
- Cymatium (Monoplex) doliarium* and var. *minor* Segre, 1952: 13-18, pl. 1, figs 1-4, pl. 2, figs 1a-2b (with long synonymy).
- Cymatium (Monoplex) costatum* and var. *minor*. Segre, 1954: 62-64, pl. 3, figs 1a-c.
- Cymatium (Cabestana) parthenopeus (sic)* var. *robusta* Bellatante, 1954: 76.
- Cymatium costatum*. Perry & Schwengel, 1955: 150, pl. 29, fig. 210.
- Cymatium (Monoplex) parthenopeum*. Clench & Turner, 1957: 228, pl. 110, fig. 4, pl. 112, figs 7-8, pl. 113, figs 9, 19, pl. 128, figs 1-3; Warmke & Abbott, 1962: 101, pl. 18, fig. f; Weisbord, 1962: 262, pl. 15, figs 4, 6; Andrews, 1971: 106, illus.; 1977: 133, illus.; Abbott, 1974: 165, fig. 1767; van Regteren Altena, 1975: 37; Coelho *et al.*, 1981: 125, fig. 10; Okutani, 1983: 259, illus.; 2000: 287, pl. 142, fig. 19; H. & E. Vokes, 1983: 23, pl. 11, fig. 10; Wilson, 1993: 246, pl. 41, fig. 5; Diaz & Puyana, 1994: 173, fig. 644; Piech, 1995: 9 (in part); Beu, 1998b: 110, figs 34a-f; 1999: 28, figs 53-60 (with further synonymy); Zhang & Ma, 2004: 141, text-figs 87a-b; Landau *et al.*, 2004: 60, pl. 4, fig. 6, pl. 9, fig. 3; Clavijo *et al.*, 2005: 385; Beu & Segers in Poppe, 2008: 646, pl. 268, fig. 10.
- Cymatium parthenopeum*. Olsson & McGinty, 1958: 15; Kaufmann & Götting, 1970: 371, fig. 85; Burnay & Montiero, 1977: 32, fig. 25; Lipe & Abbott, 1991: 10-11, illus.; Vega-Luz & Vega-Luz, 1995: 7; Kubo in Kubo & Kurozumi, 1995: 76, fig. 3; Wellens & Wils, 1997: 79, fig. 10; Ávila *et al.*, 1998: 499; Guerreiro & Reiner, 2000: 109-110; Ardovini & Cossignani, 2004: 129, upper left fig.; Chirli, 2007: 95, pl. 35, figs 3-8 (with long synonymy).
- Monoplex echo*. Kira, 1962: 56, pl. 22, fig. 13; Kuroda *et al.*, 1971: 126, 192, pl. 30, figs 1-2; Fukuda *et al.*, 1992: 24, 30, 64, pl. 14, fig. 206.
- Cymatium (Linatella) valentinei* Olsson & Petit, 1964: 562, pl. 83, figs 1-1a.
- Cymatium (Monoplex) echo iwakawanum* "Kuroda et Kira" Shikama, 1964: pl. 62, fig. 7 (*nomen nudum*).
- Cymatium (Monoplex) parthenopaeum (sic)* vars. *elongatum*, *evariosus*, *obesum*, *nodosum*, *subnodosum*, *curtum*, *major*, and *minor* Settepassi, 1970: Cymatiidae i-iv, pls 5-9.
- Septa (Monoplex) parthenopea parthenopea*. Beu, 1970c: 229, text-fig. 1a, pl. 1, figs 2-3, pl. 3, figs 18-19, pl. 4, figs 20-28, pl. 5, figs 29-34.
- Cymatium (Monoplex) parthenopeum parthenopeum*. Kilburn, 1984: 2, pl. B, fig. e; Beu, 1985: 58.
- Cymatium (Septa) parthenopeus (sic)*. Kiliass, 1973: 178, fig. 130.
- Cymatium (Septa) parthenopeum*. Kiliass, 1981: 707; Macsotay & Campos Villarroel, 2001: 67.
- Cymatium (Monoplex) parthenopeum echo*. Beu, 1985: 58.
- Cymatium (Septa) parthenopeum parthenopeum*. Rios, 1985: 76, pl. 27, fig. 334; 1994: 89, pl. 30, fig. 350; Calvo, 1987: fig. 80 (radula).
- Monoplex parthenopeum echo*. Okutani, 1986: 112-113, 2 lower left figs.
- Cymatium parthenopaeum (sic)*. Barash & Danin, 1992: 116.
- Cymatium (Monoplex) valentinei*. Petuch, 1994: pl. 39, fig. 1; 1997: 303, fig. 114j].
- Remarks.**—*Monoplex parthenopeus* is one of the most widespread of shallow-water benthic mollusks, probably exceeded only by *Turritriton labiosus*, but it is not common at any one locality within the study area, and it is not surprising to find that fossils are not common in the region. When recording a specimen from New Caledonia, I listed (Beu, 1998b) the synonyms of this species and reviewed its type material, range, and taxonomy, so this need only be summarized here. The synonymy above merely includes actual synonyms and recent references to western Atlantic specimens. Useful, extensive lists of further mentions in the European literature were provided by Priolo (1964: 526), Malatesta (1974: 266), Landau *et al.* (2004), and Chirli (2007: 95). The distinctions are pointed out above from the Pleistocene and Recent eastern Pacific species *M. keenae*.
- Among the western Atlantic species of *Monoplex*, *M. parthenopeus* stands out because of its large size (commonly 100-140 mm H, and reaching *ca.* 190 mm) and its unusually wide shape. The wide shape results from the strongly inflated whorls, and from the presence of a rather wide, very gently sloping, lightly concave sutural ramp, so that the spire is prominently stepped in outline. Another important character is the lack of varices before the terminal one on most specimens, perhaps 80% of most populations, but a few specimens are found in most localities with a penultimate varix, and a very few (< 5%) are found with all varices present and prominent down the entire teleoconch. The sculpture also is distinctive, because it is dominated by relatively few, wide, prominent spiral cords, with a narrow median groove around the center of each cord, and with interspaces about equal in width to one cord; a narrow secondary cord lies in the center of each interspace on the whorl sides, and strengthens to rival the major cords over the canal. Specimens from most of the species' range have 6 major spiral cords on the last whorl above the neck, *i.e.*, passing onto the terminal varix, the lowest one or two being lower and narrower than those above, but most specimens from Japan and some from the northern Indian Ocean have only 5 equally strong spiral cords on the last whorl above the neck. This prominent, widely spaced spiral sculpture results in most specimens having only 2 very prominent spiral cords on spire whorls. The spiral sculpture is crossed by low, narrow axial costae, expressed more as slight angulations of the spiral outline than as continuous ribs between the spiral cords, and over the last whorl or two some of these strengthen to form true costae and to form low nodules on the spiral cords of many specimens. The aperture also is distinctive, because in

Recent specimens both lips are a polished dark brown, crossed by very prominent white transverse ridges; narrow ridges are closely spaced over the full height of the inner lip, and 6 pairs or groups of ridges inside the out-turned outer lip correspond to the interspaces between the spiral cords on the exterior. The exterior of most specimens is a fairly uniform cream to pale brown, apart from much darker varices with white spots on most of the spiral cords on the varices, but some specimens have additional bars or wide zones of lighter and darker brown. As noted earlier (Beu, 1998b), greater experience of the geographical range and range of variation of this species since my earlier paper (Beu, 1970c) has shown that the Japanese "subspecies" *M. parthenopeus echo* intergrades with the rest of the world population, and I now think it likely that this is one taxon, although the eastern Pacific form seems best treated as the separate species *M. keenae*.

Dimensions.—*Murex costatus*, holotype: H 106.5, D 59.3 mm; *Cymatium (Linatella) valentinei*, holotype: H 119.8, D 74.9 mm; large New Zealand specimen, GNS RM 5527, Mill Bay, Manukau Harbor, Auckland: H 131.6, D 76.0 mm; *Triton succinctum*, lectotype: H 82.5, D 53.2 mm; *T. americanum*, lectotype: H 95.0, D 47.7 mm; R. von Cosel's material at SMF, 40-60 m, between Don Diego and La Mesa, off of Goajira Peninsula: H 153, D 81 mm; Guadeloupe, collection of D. Lamy: H 173.2, D 84.8 mm; Venezuela, SMF 306457: H 147.4, D 84.3 mm. Bernard (1984: pl. 22, fig. 97) recorded a specimen from Gabon of 192 mm H.

Types.—*Murex costatus* Born, 1778 (junior primary homonym of *M. costatus* Pennant, 1777), holotype in NHMV (Beu, 1998b: fig. 34e); this specimen was designated by me (Beu, 1998b) as the neotype of *M. parthenopeus*. The type locality is the Bay of Naples. *Murex doliare*, lectotype designated and illustrated by Pinna & Spezia (1978: 147, pl. 32, figs 2-2a), from the Piacenzian (Pliocene) of Collini Pisane, Piacenza, Italy, at the Museo di Storia Naturale di Milano, no. i5191. *Murex intermedius*, holotype illustrated by Pinna & Spezia (1978: 150, pl. 35, figs 3-3a), from the Piacenzian (Pliocene) of Valle Andona, Piacenza, Italy, at the Museo di Storia Naturale di Milano, no. i5171. *Triton succinctum*, lectotype MHNG 1099/85, designated by me (Beu, 1998b: 111), the specimen illustrated by Kiener (1842: pl. 6, fig. 1), with one paralectotype, MHNG 1099/86. According to Arnaud (1978), the type material of *M. costulatus* and *M. daubuissonius* of Risso (1826b) is lost. *Triton americanum*, lectotype BMNH 1854.12.4.525a (Pl. 41, Fig. 4), designated by me (Beu, 1998b), with 2 paralectotypes, from Río de Janeiro, Brazil. *Triton brasilianum*, holotype USNM 5694 (Johnson, 1964: 78), from Río de Janeiro, Brazil. *Triton abbreviatum*, one unfigured syntype remaining at Museo Regionale di Scienze Naturale, Torino, no. BS.010.01.011, from the Piacenzian (Pliocene) of R. Torsero, Italy (Ferrero

Mortara *et al.*, 1981). *Triton (Simpulum) acclivis*, holotype NMNZ, M.117; type locality designated by me (Beu, 1998b) as Manukau Harbor, Auckland; this specimen was designated by me (Beu, 1998b: 111) as the neotype of *Monoplex australasiae*. *Tritonium hirsutum* consists merely of the validation of a pre-Linnean name, and has no separate type material; Franeschini (1906: 45) stated that *T. parthenopeus* is a synonym. *Dissentoma prima*, holotype ANSP 181369, dredged off of Singer Island, Lake Worth, Florida; identified by Pilsbry (1945b) as a larval shell of *C. martinianum*, i.e., *M. pilearis*, and by Beu & Kay (1988: 209) as a larval shell of *M. parthenopeus*. *Cymatium (Cabestana) parthenopus* var. *robusta*, lectotype BMNH 1967693, designated by me (Beu, 1970c: 230), the specimen illustrated by Reeve (1844a: pl. 20, fig. 32); 3 paralectotypes at MNHN. *Cymatium (Linatella) valentinei*, holotype USNM 644661 (Pl. 41, Fig. 2), from Pinecrest beds (middle Pliocene) at Brighton, Highlands Co, Florida. I am not aware of the location of any further type material.

Other material examined.—**Recent:** **W Atlantic:** Again, most western Atlantic lots at American museums of this common species are not listed; 12 lots at GNS, from Florida (3 lots), Colombia, Guadeloupe (Pl. 40, Fig. 9), French Guiana, and Brazil (6 lots, mostly from Rio de Janeiro area). The northernmost record is Cape Hatteras, North Carolina (Porter, 1974: 200), and the southernmost specimens seen are from Uruguay (Cabo Santa Maria, Rocha, MACN 23573, 2, with 2 *Cabestana felipponei*; Cabo Santa Maria, SMF 306456, 1).

Fossils: **Florida: Pliocene:** E bank of Slough Ditch, N of Highway 10, Brighton, Florida, Pinecrest beds (USNM 644661, 1, holotype of *Cymatium (Linatella) valentinei*; illustrated, Pl. 41, Fig. 2); TU 770, Pinecrest Fm, 2-5 km W of Rte. 70, W side Kissimmee River, S. Hoerle collection (USNM, 2 large); 729, Pinecrest Fm, 0.1-0.5 miles S of S-65D, Florida, S. Hoerle collection (USNM, 1, large); another Florida specimen, of Holocene age, was illustrated by Petuch (1994: pl. 39, fig. 1) from Capaletti Brothers pit no. 11, Miami. **Mexico: Pliocene:** TU 638 (1 frag). **Jamaica: Late Pliocene,** Bowden: NMB 10635 (2; 1 illustrated, NMB H 17949; Pl. 40, Fig. 8); USGS 2580 [USNM 135297, 1 juvenile; the specimen mentioned by Woodring, 1928: 297, as *Cymatium (Lampusia)* sp. A]. **Dominican Republic: Late Early Miocene:** Baitoa Fm: TU 1364, Arroyo Hondo, Baitoa, Río Yaque del Norte, collected by M. Taviani (Institute of Zoology, University of Bologna, 2). **Late Miocene:** Cercado Fm: NMB 16839 (1, small). **Late Miocene/Early Pliocene:** Gurabo Fm: TU 1225 (GNS WM18887, 1 juvenile). **Early Pliocene:** Mao Adentro Limestone: TU 1281 = NMB 19012 (1 small; illustrated, NMB H 17950; Pl. 40, Fig. 2). **Atlantic Panama: Late Miocene:** Gatun Fm: NMB 17649 (1); TU 757 = NMB 19025 (1 small); USGS 8408 (1 small); TU 961, Gatun Fm, Cativa, Colon, collection of Bernard Landau (1

small). **Venezuela: Pliocene:** NMB 17512 (6); NMB 17531 (1); Mare Fm, 115 m SSW of crossing of Quebrada Mare Abajo and coast road (PRI 26192, 1, specimen illustrated by Weisbord, 1962: pl. 25, figs 5-6). **Pleistocene:** NMB 17542 (3); USGS 6825, Margarita Island, Pleistocene/Holocene? (1). **Holocene:** NMB 17565, Punta Tonel, Margarita Island (2); Tortuga Fm, Las Calderas Canyon, Cubagua Island, collection of Bernard Landau (2 large). **Uruguay: Holocene:** Punta Carretas, Montevideo, "Platense" (MLP 1403, 1 small). Material was also reported from this locality by Ihering (1907: 427), and his record is repeated in Clavijo *et al.*'s (2005: 385) catalog of Uruguayan Quaternary mollusks.

Distribution.—*Monoplex parthenopeus* lives now throughout the Mediterranean Sea, although it is rare in the east (recently recorded from the eastern Mediterranean coast of Turkey, by Kabasakal & Karhan, 2006), from southern Spain and Portugal (common in fishermen's nets along the Algarve coast; pers. obs.) south to Angola in the eastern Atlantic (Bernard, 1984: 62, pl. 22, fig. 97, Gabon; Gofas *et al.*, 1984: 68, figs 26b-c); at most or all of the Atlantic islands, including the Canary and Cape Verde islands (material at GNS); from Cape Hatteras, North Carolina (Porter, 1970; 1974: 200), USA, south to Cabo Santa Maria, Rocha, Uruguay (recorded above), in the western Atlantic, including Bahia de Portete, Caribbean coast of Colombia (Diaz, 1990); from False Bay, Capetown, to Mozambique (Kilburn & Rippey, 1982; 48 lots examined at NMP) in southern Africa, and possibly throughout eastern Africa; one specimen from Tuléar, Madagascar, collection of M. J. C. Martin, Nice (pers. comm., Aug. 1999); common in the northern Indian Ocean and Gulf of Arabia (Bosch *et al.*, 1995; 15 specimens at GNS, WM13282); in the Red Sea (Wellens & Wils, 1997: 79, fig. 10, "only found at Port Sudan and Sharm-el-Sheik"; Na'Ama Bay, Sharm el Sheikh, E. Wils, GNS WM16807, 1; Halaib, Red Sea, GNS WM16408, 1); around southern Australia from Lancelin in Western Australia (Wilson, 1993: 246) to as far north as Moreton Bay, southern Queensland, and the Swain Reefs off of easternmost central Queensland (material at GNS), and rarely to Cape Flattery, northern Queensland (Beu, 1970c); throughout New Zealand, where it is moderately common at the northeastern North Island, and sporadic in the south (material from Fiordland, southeastern South Island, at NMNZ and GNS); at the Kermadec, Lord Howe, and Norfolk Islands; rarely in New Caledonia; rarely in Hawaii (scuba, 25 m, off of Maui, GNS WM16414, 2); common in southern Japan, from Kyushu to Boso Peninsula, Honshu, in Yamaguchi Prefecture, Japan Sea coast of Honshu, and in the Seto Inland Sea (Beu, 1999); uncommon as far south as Taiwan (Lai, 1989: fig. 33; material at GNS). It is therefore more ubiquitous in the Mediterranean, Atlantic, and South Africa than in the western Pacific, where it is strictly a "Pacific

fringe" species, with a similar range to those of *Charonia lam-pas* and *Monoplex exaratus*; there are very few reliable records from the tropical western Pacific (apart from Hawaii, and the one specimen from New Caledonia; one specimen from the Philippine Islands illustrated by Beu & Segers in Poppe, 2008: 646, pl. 268, fig. 10).

Fossils are well known in the Miocene and Pliocene of southern Europe and the Mediterranean area, were reported from the Pleistocene of Porto Santo, Madeira Archipelago, by Gerber *et al.* (1989), are reported here rather rarely from the late Early Miocene to Pleistocene of the tropical American region (all in the Atlantic part of the study area), and were reported from the late Middle Pleistocene of New Zealand (oxygen isotope stage 7, at Te Piki, near East Cape; Beu, 1976a). Richards (1962: 79, pl. 17, fig. 16) also recorded Pleistocene fossil specimens from Cape Hatteras, North Carolina. Most of the pre-Pleistocene records from outside of Europe and the Mediterranean area are based on small (*ca.* 40-50 mm H) specimens that do not display the diagnostic characters well, and only the European Miocene-Pliocene, Florida Plio-Pleistocene, and Pleistocene specimens from elsewhere within the present study area are identified with certainty. A single specimen is present in a recent collection from the Kere River (Middle Pleistocene, oxygen isotope stage 7), Espiritu Santo, Vanuatu. A specimen from the Chipola Fm (late Early Miocene) in Florida seems to represent a possible direct ancestor of *M. parthenopeus* (see below, under *Monoplex* n. sp. A) but this might also be an early, very coarsely sculptured specimen of *M. parthenopeus*.

Monoplex pilearis (Linnaeus, 1758)

Pl. 39, Figs 1-15, 18

Murex pileare Linnaeus, 1758: 749; 1767: 1217; Gmelin, 1791: 3534.

Tritonium olearium. Röding, 1798: 126 (not *Murex olearium* Linnaeus, 1758).

Triton pileare. Lamarck, 1816: pl. 415, figs 4a-b, "Liste des objets": 4; 1822: 182; Quoy & Gaimard, 1833: 539, Atlas (1835): pl. 40, fig. 13; Kiener, 1842: 15, pl. 7, fig. 1.

Lampusia pilearis. Schumacher, 1817: 250; Dall & Simpson, 1901: 417; Skwarko & Sufiati, 1994: m18.

Triton haemastoma Valenciennes, 1832: 304.

Triton martinianum d'Orbigny, 1841a: 162 (in part, = *Triton aquatilis* Reeve, 1844).

Triton pilearis. Reeve, 1844a: pl. 7, fig. 23; Küster & Kobelt, 1872: 196, pl. 42, figs 3-4, pl. 56, fig. 4; E. A. Smith, 1891: 413.

Litiopa effusa C. B. Adams, 1850a: 71; Turner, 1956: 136, pl. 21, fig. 3 (larval shell).

Tritonium martinianum. Krebs, 1864: 24.

Tritonium pileare. Krebs, 1864: 24; Tapparone-Canefri, 1881: 24; Coomans, 1963: 65.

?*Tritonium vestitum*. Krebs, 1864: 24 (not *Triton vestitus* Hinds,

- 1844).
- Tritonium (Simpulum) beccarii* Tapparone-Canefri, 1875: 587, pl. 19, fig. 7; Mienis, 1990: 10, illus. (holotype); Singer, 1990: 21, fig. 6a (holotype).
- Triton (Lampusia) martinianum*. Mörch, 1877: 28; Coomans, 1963: 80.
- Triton martinianum latior* Mörch, 1877: 29 (*nomen nudum*).
- Triton veliei* Calkins, 1878: 235, pl. 18, figs 1-2.
- Triton (Simpulum) pilearis*. Kobelt, 1878a: 245; Tryon, 1880: 12, pl. 6, fig. 36 (in part not *Murex pilearis* Linnaeus, 1758); Tesch, 1915: 66, pl. 82, figs 146a-b.
- Tritonium (Simpulum) pilearis* var. Martin, 1899: 141, pl. 22, figs 323-323a, 324.
- Lampusia pileare*. Dall, 1903b: 132.
- Aquillus pilearis*. Schepman, 1907: 180.
- Simpulum pileare*. Maury, 1917a: 269.
- Eutritonium pileare*. Martin, 1919: 87, 126, 128, 130-131, 137; 1926: 10; 1928: 8; van der Vlerk, 1931: 239.
- Cymatium vestitum insulare* Pilsbry, 1921: 320.
- Cymatium pileare*. Pilsbry, 1922: 356; Oostingh, 1935: 226; Hirase, 1936: 66, pl. 95, fig. 5; Cox, 1948: 39; Nowell-Usticke, 1959: 60; Weaver, 1966: 104, pl. 26, 2 upper right figs; Work, 1969: 662; Matthews & Kempf, 1970: 27; Hinton, 1972: 12, pl. 6, fig. 4; 1978: 29, fig. 1; Rios, 1975: 79, pl. 22, fig. 321; Princz & Pacheco, 1981: table; Calvo, 1987: fig. 79 (radula); Drivas & Jay, 1988: 64, pl. 17, fig. 8; Salvat *et al.*, 1988: 100, pl. 12, fig. 8; de Jong & Coomans, 1988: 69, fig. 380; Diaz & Götting, 1988: 156; Leal, 1991: 117 (in part); Lipe & Abbott, 1991: 12, illus. (in part); Oliveira & Trinchao, 1993: figs 1, 4; Guerreiro & Reiner, 2000: 107.
- Cymatium (Lampusia) pileare*. Woodring, 1928: 297; Beets, 1941: 90 (with further synonymy); 1986: 26; van Regteren Altena, 1942: 101 (with further synonymy).
- Saginafusus pricei perficus* Iredale, 1931: 227, pl. 23, fig. 1.
- Cymatium (Lampusia) pileare* var. *martiniana*. Bayer, 1933: 46; Bellatante, 1954: 82.
- Triton (Lampresia) (sic) pileare*. Coulon, 1933: 125.
- ?*Lampusia pilearis* var. Trechmann, 1933: 30.
- Cymatium andoi* Nomura, 1935: 167, pl. 8, fig. 21.
- Cymatium aquatile*. M. Smith, 1937: 112, pl. 42, fig. 4; Morris, 1960: 177, pl. 14, fig. 5 (not *Triton aquatilis* Reeve, 1844).
- Cymatium martinianum*. Abbott, 1954: 195, pl. 9, fig. 1; Olsson & McGinty, 1958: 15; Vega-Luz & Vega-Luz, 1995: 7; Ardovini & Cossignani, 2004: 128, lower left fig.
- Cymatium (Septa) pileare*. Clench & Turner, 1957: 216, pl. 112, figs 1-2, pl. 122, figs 1, 3 only; pl. 123 (in part only); Woodring, 1959: 204; Kira, 1961: 54, pl. 21, fig. 14; Warmke & Abbott, 1962: 100, pl. 2, fig. a; Kaufmann & Götting, 1970: 371, fig. 84; Kilias, 1973: 182; Abbott, 1974: 163, col. pl. 7, fig. 1753 (in part); van Regteren Altena, 1975: 36; Andrews, 1977: 132, illus.; Kay, 1979: 221, figs 76D, 77A (labeled as *C. aquatile*), 77B; Saunders, 1980: 10 (in part); Bernard, 1981: 17, right fig.; Coelho *et al.*, 1981: 122, fig. 8; Rios, 1985: 76, pl. 27, fig. 335; 1994: 89, pl. 30, fig. 351; H. & E. Vokes, 1983: 22, pl. 11, fig. 4; Springsteen & Leobrera, 1986: 112, pl. 30, fig. 14; Diaz & Puyana, 1994: 172, fig. 642; Macsotay & Campos Villarroel, 2001: 67, pl. 12, fig. 31.
- Cymatium (Lampusia) pileare martinianum*. Abbott, 1958: 52.
- Septa pilearis*. Kira, 1962: 56, pl. 22, fig. 14.
- Cymatium (Septa) pileare martinianum*. Weisbord, 1962: 257, pl. 24, figs 9-12; Andrews, 1971: 105, illus.; Humfrey, 1975: 122, pl. 13, fig. 2 only; Bernard, 1984: 62, pl. 22, figs 98a-b.
- Cymatium (Septa) martinianum*. Shikama & Horikoshi, 1963: pl. 47, fig. 6; Petuch, 1994: pl. 39, fig. F.
- Cymatium pileare martinianum*. Rios, 1970: 72, pl. 18, upper left fig.
- Lampusia pileare*. Wilson & Gillett, 1971: 78, pl. 53, figs 12-12a; Short & Potter, 1987: 46, pl. 22, fig. 2.
- Septa (Septa) pilearis*. Rosewater, 1975: 17, fig. 6.
- Cymatium parthenopeum*. Bandel, 1984: 100, pl. 9, fig. 6 (not *Murex parthenopeum* von Salis Marschlins, 1793).
- Cymatium pileare*. Bandel, 1984: 98, pl. 9, fig. 3 (in part, = *Triton aquatilis* Reeve, 1844).
- Cymatium (Monoplex) pileare*. Beu, 1985: 58; 1998b: 114, figs 33d-e, 34c; 1999: 32, figs 62-63 (with further synonymy); 2005: 83, figs 211-221; Beu & Kay, 1988: 203, figs 3, 17-20, 42-48; Lai, 1989: 123, fig. 35; Singer, 1990: 30, pl. 27, fig. 6; Henning & Hemmen, 1993: 67, pl. 14, fig. 1; Wilson, 1993: 246, pl. 41, fig. 4; Bosch *et al.* 1995: 99, fig. 356; Okutani, 2000: 287, pl. 142, fig. 13; Beu & Segers in Poppe, 2008: 646, pl. 268, figs 6, 8-9, 11.
- Cymatium (Monoplex) martinianum*. Beu, 1985: 58; Beu & Kay, 1988: 206, figs 49-62; Henning & Hemmen, 1993: 65, pl. 14, fig. 2; Piech, 1995: 10; Redfern, 2001: 61, pl. 31, figs 259A-C.
- Cymatium (Septa) pileare pileare*. Garcia-Talavera, 1987: 253, fig. 3 (center), pl. 1, fig. 3.
- Cymatium (Septa) pileare orientalis* Garcia-Talavera, 1987: 254, pl. 1, fig. 2.
- Cymatium* cfr. *martinianum*. Ardovini & Cossignani, 2004: 128, bottom central fig.

Remarks.—Since *Monoplex martinianus* was separated from *M. pilearis*, its types clarified, and its range discussed by Beu & Kay (1988), confusion has continued to reign over the characters and status of *M. aquatilis*, *M. pilearis*, and *M. martinianus*. Both a large specimen of *M. aquatilis* and three specimens of the other, smaller Atlantic species that has usually been known as *M. pilearis* are present among d'Orbigny's type material at BMNH, and Beu & Kay (1988: figs 49-50) selected a specimen of the "*pilearis* form" as the lectotype of *M. martinianus* (Pl. 39, Figs 5, 10). We regarded *M. martinianus* as a smaller, shorter and wider, more weakly sculptured, and paler-colored species than *M. pilearis*, with shorter ridges inside the outer lip and a paler red aperture, limited to the western Atlantic and, rarely, the eastern Atlantic. However, continued examination of collections of this species "complex" from around the world in museums has demonstrated (as noted above, under *M. aquatilis*) that the distinction between specimens resembling *M. pilearis* and *M. martinianus* is not clear-cut and not supportable. Some live-collected Florida specimens examined (TFMC 292, 295, 298) have a bright black inner lip, with

very clearly visible, almost white transverse ridges. Also as noted above, specimens of *M. pilearis* from the western Indian Ocean (Mozambique and Madagascar) are neatly intermediate in all characters between western Pacific specimens of *M. pilearis* and the Atlantic shells that we (Beu & Kay, 1988) identified as *M. martinianus*. I conclude that *M. pilearis* varies clinally in a regular way, the largest, tallest, narrowest, and most brightly colored specimens occurring in the main western Pacific arcs from southern Japan to eastern Australia and New Caledonia, the smallest, shortest, and least brightly colored specimens occurring in the Atlantic, and intermediate specimens intergrading across the Indian Ocean. This therefore is regarded as a single species here, because in my opinion, a cline should not be subdivided arbitrarily into subspecies. Garcia-Talavera (1987) tried to restrict the application of the name *M. pilearis* to Atlantic specimens, and provided the name *Cymatium pileare orientale* for Indo-West Pacific specimens, but there is no doubt that the lectotype of *Murex pileare* is an Indo-West Pacific shell (Gualtieri's specimen most likely came from the Red Sea) and this action is not supportable.

Monoplex aquatilis occurs in both the Indo-West Pacific and the Atlantic, is a paler, yellow to orange shell with a uniform pale orange aperture (although the dorsum bears large red to dark brown blotches on many specimens), and has larger nodules and much higher varices than in *M. pilearis*. In my opinion, these species are not particularly closely related, at least in the sense of not being recently segregated sister taxa. However, Atlantic specimens of *M. pilearis* are closely similar to the eastern Pacific species *M. macrodon*, and differences between them are pointed out under *M. macrodon*.

Miocene and early Pliocene fossils identified as *Monoplex pilearis* from the Dominican Republic (Pl. 39, Figs 1-4) are similar in shape to Recent Atlantic specimens, but the illustrated specimens are more finely sculptured than Recent ones. Examination of three complete specimens in the collection of Bernard Landau (listed below) demonstrated that some Dominican Republic fossils are identical to Recent specimens in all characters, and I am in no doubt that they are conspecific with Recent material. I have seen Recent Pacific material of *M. pilearis* from offshore localities (living in ca. 20-50 m, rather than intertidally) with weaker sculpture than usual, resembling the Dominican Republic fossils, and it seems possible that the weakly sculptured Dominican Republic specimens lived a little further offshore than most other specimens. It is important for biogeography to note that *M. pilearis* has been present in the Atlantic since at least late Early Miocene time, as it has in the central western Pacific (Java; Beu, 2005: 83).

Dimensions.—Large Recent specimen, NMB 17685, Laguna de Buche, Estado Miranda, J. & W. Gibson-Smith collection (one of 46 in sample): H 88.4, D 41.4 mm; TFM 248, Boca

Raton, Florida: H 89.8, D 44.7 mm; *Triton martinianum*, lectotype: H 36.0, D 20.7 mm (Beu & Kay, 1988: table 1); figured specimen, NMB H 17942, from NMB 19004 (TU 1212), Río Gurabo, Dominican Republic: H 37.2, D 19.2 mm; figured specimen, NMB H 17943, from NMB 15844, Dominican Republic: H 42.9, D 22.1 mm; figured specimen, shrimp boat, 33-37 m, NW of Manaure, off of Goajira Peninsula, Colombia, in R. von Cosel's material in SMF: H 87.6, D 45.3 mm; H 74.3, D 38.7 mm; Exmouth, Western Australia, GNS WM18406: H 115.4, D 52.3 mm; trawled off of Bundaberg, Queensland, GNS WM18405: H 112.6, D 51.4 mm.

Types.—Beu & Kay (1988) and I (Beu, 1998b: 114) each discussed the type material of *Monoplex pilearis* and most of its synonyms. The lectotype (designated by Beu & Kay, 1988) of *Murex pilearis* (Beu, 1998b: figs 33d-e), the specimen illustrated by Gualtieri (1742: pl. 49, fig. G) [designated because the specimen bearing this name in Linnaeus' collection in London is the Mediterranean species *Monoplex corrugatus* (Lamarck, 1816)], is in the collection of the Department of Zoology, University of Pisa, Museo di Storia Naturale a del Territorio, Certosa di Calci, in the countryside outside Pisa; the type locality was designated by me (Beu, 1998b) as Amboina, Indonesia. *Triton haemastoma*, holotype at MNHN, from "Acapulco" (spurious). *Tritonium beccarii*, holotype at Museo Civico di Storia Naturale "Giacomo Doria," in Genoa, not seen, illustrated by Mienis (1990) and Singer (1990), from Massawa, Ethiopia, Red Sea. *Triton martinianum*, lectotype (Pl. 39, Figs 5, 10) designated by Beu & Kay (1988: 208-209, figs 49-50), BMNH 1854.10.4.409, with 2 paralectotypes, from St. Lucia, Caribbean (the 2 paralectotypes are *M. pilearis*; one further paralectotype, BMNH 1854.10.4.408, is *M. aquatilis*; Pl. 35, Figs 8, 10). *Litiopa effusa* (a larval shell of *M. pilearis*), lectotype designated by Turner (1956: 136, pl. 21, fig. 3) MCZ 186589, from Jamaica. *Triton veliei*, 5 "idiotypes" (syntypes?) MCZ 150085, from "Key West, Florida, ex Grand Rapids Public Museum." *Cymatium vestitum insulare*, lectotype (designated by Emerson & Old, 1963a: 22) ANSP 35279, "Sandwich Islands," with 1 paralectotype, ANSP 139220, from Honolulu Harbor, Oahu, Hawaii. *Cymatium andoi*, holotype at Institute of Geology & Paleontology, Tohoku University, Sendai, Japan, IGPS 53973, from the Pliocene Byoritsu Fm, Taiwan. *Saginafus pricei perficus*, holotype AMS C.57800, from Sydney Harbor *Triton* dredgings, New South Wales, Australia. *Cymatium pileare orientale*, holotype TFM C.M.T24, from Mactan Island, Philippine Islands (Garcia-Talavera, 1987: 249, fig. 2 left).

Other material examined.—**Recent:** The abundant Indo-West Pacific fossil and Recent material need not be listed here. I listed (Beu, 2005: 84) Indonesian fossils. **W Atlantic:** Beu & Kay (1988) listed extensive western Atlantic ma-

terial that we had examined, and this is not repeated here. The listed lots, 13 further lots examined since, and 17 lots at GNS are from Bermuda, Bahamas, Florida Keys, Cuba, Cayman Islands, Jamaica, Haiti, Dominican Republic, Puerto Rico, Lesser Antilles (St. Thomas, St. John, Tortula, Antigua, Dominica, Guadeloupe, St. Lucia, St. Martin, Grenada, Antigua, Barbados, Trinidad, Tobago), E Mexico, E Costa Rica, Honduras, E Panama, E Colombia, Aruba, Bonaire, Curaçao, Venezuela, and Bahia, NE Brazil (Ponta de Serrambi, Pernambuco, GNS WM13357, 2); 25 lots from Venezuela examined at NMB, J. & W. Gibson-Smith collection; 29 lots from Caribbean coast of Colombia examined in R. von Cosel's material at SMF. Bandel's (1984: 100, pl. 9, fig. 6) 2 voucher specimens for radular mounts of *Monoplex parthenopeus* from Santa Marta, Colombia, are actually *M. pilearis*, as are 2 of his (Bandel, 1984: 98, pl. 9, fig. 3) 3 voucher specimens of *M. pilearis*; the third is *M. aquatilis* (RMNH, 5). **Central Atlantic islands: Ascension Island:** Ascension Island, 1970-1971 (USNM 735705, 2). **E Atlantic: Canary Islands:** Dársena comercial (*i.e.*, commercial port), Santa Cruz de Tenerife (TFMC 265, 1); Dársena sur, Santa Cruz de Tenerife, dredged in 9-12 m (TFMC 284, 1); El Médano, Tenerife (TFMC 264, 1); Tenerife (TFMC 263, 1; TFMC 262, 1); Adeje, Tenerife (TFMC 285, 2); Playa de las Teresitas, San Andrés, Tenerife (TFMC 270, 2); Sardina del Norte, Gran Canaria (TFMC 268, 1); La Palma (TFMC 269, 2; TFMC 277, 1; TFMC 279, 1; TFMC 436, 4 good); intertidal, Caleta de Adeje, Tenerife (TFMC 278, 1); Gran Canaria (TFMC 271, 2); San Cristobal, Gran Canaria (TFMC 266, 1; TFMC 272, 2); Tazacorte, La Palma (TFMC 288, 3); Candelaria, Tenerife (TFMC 273, 1, unusual specimen with wide, prominent cords, resembling *M. parthenopeus*, but with aperture as in *M. pilearis*); 5 m, Playa las Americas, Tenerife (GNS WM15197, 1); 10 m, Tenerife (GNS WM15196, 1); off of Sardina, NW Gran Canaria (GNS WM18362, 3); San Cristobal, Gran Canaria (GNS WM16330, 2). **Liberia:** Freeport area, Monrovia (USNM 767929, 1; illustrated, Pl. 39, Fig. 8). **Gabon:** Port Gentil, piles of a semisubmersible platform, 0°40.7'S, 8°49.6'E, coll. C. Chevalier, 1980-1989 (MNHN, 2).

Fossils: Cuba: Pleistocene: USGS 12103a (1). **Barbados: Pleistocene:** NMB 10121 (5); Coral Rock, collection of Bernard Landau (2). **Dominican Republic: Late Early Miocene:** Baitoa Fm: TU 1364 (GNS WM18884, 1 small, good). **Late Miocene:** Cercado Fm: NMB 16982, Río Cana, collection of Bernard Landau (2); Cerros de Sal Fm, Barahona, S Dominican Republic, USGS 8591 (1). **Early Pliocene:** Gurabo Fm: NMB 15844 (NMB H 17943, 1, illustrated; Pl. 39, Figs 1-2); TU 1212 = NMB 19004 (NMB H 17942, 1, illustrated; Pl. 39, Figs 3-4); 1215, Gurabo Fm, Río Gurabo, collection of Bernard Landau (1). **Pleistocene:** La Isabella

Fm, El Castillo, La Isabella, collection of Bernard Landau (3). **Trinidad: Holocene:** NMB 10186 (4); 10663 (NMB H 18044, 1, illustrated; Pl. 39, Fig. 18). **Atlantic Costa Rica: Late Pliocene:** basal Moín Fm mudstone member, Rte. 32, 3 km W of Puerto Limón, coll. J. A. Todd, February 1998 (BMNH Palaeontology Department, 1). Robinson (1991) also recorded a single frag from the Moín Fm at Limón in TU 1239, a collection that I have not examined. **Atlantic Panama: Pleistocene:** USGS 5211 (1; labelled by Woodring "not listed"). **Colombia: Pleistocene:** UCMP S-46, terrace 10 m above high tide, La Cieba, Departamento de Atlantico (17); CAS locality 295, Playa of Tierra Bomba, Departamento de Bolivar, near Cartagena (1). **Venezuela: Pleistocene:** NMB 13346 (1); USGS 6288 (1). **Holocene:** NMB 17565 (1); Tortuga Fm, Las Calderas Canyon, Cubagua Island, collection of Bernard Landau (1).

Distribution.—In the Atlantic, *Monoplex pilearis* ranges now from Cape Hatteras, North Carolina [assuming that Porter's (1970) record refers to this species], USA, south throughout the western Atlantic to São Paulo State, southern Brazil, and to Fernando de Noronha and Trindade islands (Rios, 1994: 89). Matthews (1968) recorded specimens (as "*Cymatium pileari*") found uncommonly in the gut of the toadfish or "pacomon," *Amphychthus cryptocentrus*, caught off of Fortaleza, Ceará, Brazil. In the eastern Atlantic, it was recorded from the Canary Islands by Garcia-Talavera (1987) and the Cape Verde Islands (Beu & Kay, 1988), and widely but sparsely along the West African coast from near Freeport, Liberia, to Gabon. Ardovini & Cossignani (2004: 128, 2 lowest left figs) illustrated specimens in color from Sierra Leone and the Canary Islands. In the study area, fossils are known only from the Caribbean, where they are uncommon, and range in age from late Early Miocene to Pleistocene. Indo-West Pacific Recent records were summarized by me (Beu, 1998b, 1999) and fossil ones by me (Beu, 2005). *Monoplex pilearis* occurs throughout the Indian Ocean as far south as Natal, eastern South Africa, and in the western Pacific, ranges from southern Honshu, Japan, to Sydney Harbor, Australia, and as far east as the Marquesas and Austral Islands in eastern French Polynesia (Richard, 1987; material examined at MNHN). Fossils are known mainly from Miocene and Pliocene rocks of Indonesia and the Dominican Republic, but also occur in the Pliocene of Taiwan and Okinawa, and in the late Middle Pleistocene (oxygen isotope stage 7) Kere River fauna of Espiritu Santo Island, Vanuatu (one specimen in GNS).

Monoplex ritteri Schmelz, 1989
Pl. 43, Figs 2-4

Cymatium (Guttarium) ritteri Schmelz, 1989: 137, figs 1a-b, 2a-b; Vokes, 1997: 212.
Cymatium ritteri. Petuch, 1997: 101, fig. 33J.

Remarks.—*Monoplex ritteri* is a small (30–45 mm H), rather generalized species of *Monoplex* with a moderately short to moderately tall spire, and the last whorl tapering unusually gradually into the moderately long, open, straight anterior canal. The sculpture consists of 6 quite prominent, narrow major spiral cords on the last whorl (passing onto the terminal varix) with 2 or 3 narrow secondary cords in each interspace, all crossed by many low, narrow, irregular axial ridgelets and a few large, angling axial folds forming small to quite large, sharp nodules at the periphery, with 2 or 3 nodules in each intervariceal interval on the last whorl. The major spiral cords are each subdivided by a very narrow groove where they cross each varix. Most large specimens have only two varices, although a few have three; varices are quite low and narrow. The aperture has lightly flared, well-thickened lips, with 7 large, prominent ridges inside of the outer lip, each ridge subdividing into two over the outer part of the lip, and with numerous thin to thick, irregular transverse ridges on the inner lip; in most specimens, two ridges on the base of the columella are more prominent than the others. Some specimens (from the Chipola Fm) have the uppermost nodule inside the outer lip subdivided into three narrow ridges.

The presence of a pair of slightly more prominent transverse ridges on the base of the columella than those higher up suggests that *Monoplex ritteri* possibly has a phylogenetic relationship to *M. krebsii*, in which this character is more strongly developed. The much less prominent varices, finer spiral sculpture, and unusual, tapering last whorl clearly distinguish *M. ritteri* from *M. krebsii*, and suggest that the relationship is not very close. Also, a single small Chipola Fm specimen is referred above (with some hesitation) to *M. krebsii*, so *M. ritteri* obviously was not directly ancestral to *M. krebsii*, and any phylogenetic link evidently was earlier than during Early Miocene time.

Dimensions.—*Monoplex ritteri*, holotype: H 30.0, D 16.5 mm; paratype USNM 445742: H 39.0, D 20.0 mm (Schmelz, 1989: 137); TU 830, Chipola Fm, Tenmile Creek, GNS WM16504: H 53.3, D 29.5 mm; TU 547, Chipola River, GNS WM16503: H 47.4, D 26.0 mm; TU 546, Tenmile Creek, GNS WM16502: H 44.4, D 24.4 mm; figured specimens, from NMB 17516, Cantaure, Venezuela: NMB H 17951, H 39.4, D 22.2 mm; NMB H 17952, H 36.6, D 22.4 mm.

Types.—*Cymatium (Gutturnium) ritteri*, holotype USNM 445741, from TU 951, Chipola Fm (late Early Miocene), Tenmile Creek, ca. 2 km W of Chipola River, Calhoun Co, Florida; with 1 paratype, USNM 445742, from TU 546, same formation, Tenmile Creek, Chipola River (none seen).

Other material examined.—**Fossils: Florida: Late Early Miocene:** Chipola Fm, TU 546, basal bed, Tenmile Creek, Calhoun Co, collection of Bernard Landau (5); same local-

ity, TU 546 (GNS WM16502, 8); TU 547, W bank Chipola River, 600 m upstream from Fourmile Creek, Calhoun Co (GNS WM16503, 1); TU 830, Tenmile Creek, Chipola River, Calhoun Co (GNS WM16504, 11); TU 826, Farley Creek, Calhoun Co, collection of Bernard Landau (1); frags also seen in Chipola collections TU 458, 459, 820B, and 999. **Venezuela: Late Early Miocene,** Cantaure: NMB 17516 (10; 2 specimens illustrated, NMB H 17951, H 17952; Pl. 43, Figs 2–4); locality same as last, collection of Bernard Landau (7).

Distribution.—*Monoplex ritteri* is recorded only from the Chipola Fm in Florida, USA, and the Cantaure Fm on the Paraguaná Peninsula, Venezuela, both late Early Miocene in age. This is an intriguing addition to a growing list of tonnoidean taxa in common to the two formations; others include *Eudolium subfasciatum* Sacco, 1890 (Vokes, 1986; Gibson-Smith, 1988), *Bursa rhodostoma*, *Semicassis aldrichi* (Dall, 1890), *Monoplex cercadicus*, and probably *Distorsio jungi* n. sp., all recorded in the present work. The wide variety of these taxa suggests that similarity of depositional environment is as much responsible for the taxa in common as is the similarity in age. Species in some other tonnoidean genera are distinct in these two faunas, e.g., *Sconsia laevigata* (G. B. Sowerby I, 1850) at Cantaure, *S. paralaevigata* Gardner, 1947, in the Chipola Fm, *Cypraecassis cantaurana* n. sp. at Cantaure, *C. chipolana* Duerr, 2001, in the Chipola, and several other species are recorded from only one or the other of these localities.

Monoplex tranquebaricus (Lamarck, 1816)

Pl. 43, Figs 5–7, 9–14

Triton tranquebaricum Lamarck, 1816: pl. 422, fig. 6, “Liste des objets”: 5; 1822: 642; Kiener, 1842: 42, pl. 7, fig. 2; Deshayes, 1843: 642.

Triton chemnitzii Gray, 1839: 110.

Triton tranquebaricus. Reeve, 1844a: pl. 14, fig. 55; H. & A. Adams, 1853: 102.

Triton balteatus “Beck MS” Reeve, 1844a: expl. to pl. 14, fig. 20 (in synonymy).

Tritonium adansonii Dunker, 1853: 26, 65.

Triton (Simpulum) tranquebaricum. Chenu, 1859: 151, fig. 687.

?*Triton (Linatella?) tranquebaricum* var. a. Mörch, 1877: 32.

Triton (Linatella) tranquebaricus. Kobelt, 1878: 247.

Triton (Simpulum) tranquebaricus. Tryon, 1880: 14, pl. 8, figs 52–53.

Sympulum (sic) tranquebaricum. Rochebrune, 1881: 304.

Eutriton (Simpulum) problematicum Dautzenberg & Fischer, 1906: 33, pl. 3, figs 2–5.

Triton (Lampresia) (sic) tranquebaricus. Coulon, 1933: 126.

Cymatium tranquebaricum. Marche-Marchad, 1958: 23; Burnay & Monteiro, 1977: 32, fig. 24; Garcia-Talavera, 1983: 101; Bernard, 1984: 60, figs 95a–b; Vega-Luz & Vega-Luz, 1995:

- 7; Guerreiro & Reiner, 2000: 108; Ardovini & Cossignani, 2004: 129, in part, central left fig. only (not upper right fig., = *Monoplex exaratus*).
- Cymatium problematicum*. Marche-Marchad, 1958: 23; Warén & Bouchet, 1990: 79, fig. 101.
- Cymatium (Linatella) tranquebaricum*. Kilius, 1973: 128, fig. 94; 1981: 705.
- Cymatium (Septa) tranquebaricum*. Nordsieck & Garcia-Talavera, 1979: 115, pl. 24, fig. 4.
- Cymatium (Monoplex) tranquebaricum* and var. *linatelloides* Garcia-Talavera, 1987: 249, 253, pl. 1, fig. 4.
- Cymatium (Monoplex) tranquebaricum*. Beu, 1985: 58; Henning & Hemmen, 1993: 68, pl. 12, fig. 8; Piech, 1995: 11.
- Cymatium tranquebaricum* forma *problematicum*. Ardovini & Cossignani, 2004: 129, 2 center right figs.

Remarks.—*Monoplex tranquebaricus* has a rather stout shell with a prominent, gently sloping, slightly concave sutural ramp that produces a strongly stepped spire. The spire is rather short, and the last whorl is wide and strongly inflated, tapering rapidly into a straight, open anterior canal that is moderately long on most specimens, but very short on some. The sculpture is dominated by six moderately wide, prominent spiral cords on the last whorl and two on spire whorls, all clearly subdivided by a narrow median groove, and all crossed by numerous (8-15 on the last whorl) narrow, prominent axial folds, producing moderately to very prominent nodules on the peripheral spiral cord and decreasing rows on the cord or two below. The whole surface is crossed by axial costellae that vary from very fine and close to rather coarse and sparse. The aperture has narrow, moderately thickened lips, the outer a little flared over the inner part of the terminal varix, bearing 7 pairs of prominent, narrow transverse ridges; the outer part of the inner lip bears several prominent ridges, especially on the base of the columella. An important character is that most specimens develop only the rather low terminal varix, and only a few specimens develop more than two. Recent specimens have dark purplish brown spiral cords on a paler brown background.

The form named *Eutriton problematicum* by Dautzenberg & Fischer (1906: 33) is common in most samples of *Monoplex tranquebaricus*, and is based on small, short, strongly nodulose specimens, most of which have more than one varix. These specimens have a much shorter and wider appearance than the "typical" large, relatively elongate specimens with smaller nodules and only one varix. However, the specimen illustrated by Lamarck (1816: pl. 422, fig. 6) and here regarded as the holotype of *Triton tranquebaricum* (Pl. 43, Figs 11-12) is a small, short, strongly nodulose shell with two varices that would be classified as the "*problematicum* form." These two forms intergrade completely, and in my opinion the *problematicum* form is merely part of the variation of *M. tranquebaricus*.

Dimensions.—*Triton tranquebaricum*, holotype: H 39.8,

D 26.7 mm; GNS WM14951, off of Conakry, Guinea: H 59.7, D 39.8 mm; H 64.1, D 38.0 mm; GNS WM13562, off Casamance River: H 71.2, D 37.5 mm; 3 figured specimens, NMB H 18046-18048, from NMB 12884, Pleistocene, Quebrada Araya, Araya Peninsula, Venezuela: H 50.2, D 33.8 mm; H 47.5, D 32.8 mm; H 44.8, D 29.6 mm; Recent, Tortugas, Florida, ANSP 352530: H 52.1, D 31.2 mm; Recent, Mariguitar, Venezuela, NMB 17690: H 20.0, D 12.4 mm.

Types.—No type material of *Triton tranquebaricum* had been identified when I examined Lamarck's collection in 1979. According to Rosalie de Lamarck's annotations on Lamarck's personal copy of Lamarck (1822) (at MHNG), Lamarck originally owned one specimen. One lot was recognized in the reference collection at MHNG, from the collection of Baron Delessert, containing two specimens of *Monoplex tranquebaricus* similar to Lamarck's (1816) illustration, labeled "Oc. Indien." The larger of the two (H 39.8 mm) matches Lamarck's (1816: pl. 422, fig. 6) and Kiener's (1842: pl. 7, fig. 2) figures very closely in all details, and is unusual (and resembles the figures) in having prominent col-labral folds, raised into prominent nodules where they cross the spiral cords, all over the dorsum of the last whorl. This specimen (Pl. 43, Figs 11-12) appears to be that illustrated by both Lamarck and Kiener, and is assumed to be the holotype of *Triton tranquebaricum*. It also appears to be the specimen illustrated by Chenu (1859: 151, fig. 687). The type locality is here designated as Île Gorée, Sénégal, West Africa. I do not know the location of the other type material of names listed above; that of *Eutriton problematicum* is presumably in the Musée Océanographique, Monaco.

Other material examined.—**Recent: W Atlantic: Florida:** shrimp net in 48 m, NW of Loggerhead Light, Dry Tortugas, Florida, May 1970, D. & R. Black on *M/V Donna L* (ANSP 352530, 1, ex Hal Lewis collection; illustrated, Pl. 43, Figs 6, 9). **Venezuela:** Puerto de la Cruz, Estado de Anzoátegui, Venezuela, dredged in shallow water, February 1976, F. Fernández (TFMC, 1); NMB 17690, Mariguitar, Golfo de Cariaco, J. & W. Gibson-Smith collection (2 small, with 1 *Linatella caudata*). **E Atlantic:** 31 lots examined, in GNS (9 lots), IRSNB, MNHN, and SMF, from the Cape Verde Islands, Mauretania, Sénégal, Guinée, Gambia, Ghana, Gabon, and Angola; 14 lots from the Canary Islands examined at TFMC; including: dredged in 9 m, Dársena comercial, Santa Cruz de Tenerife (TFMC 587, 3 live-collected; TFMC 586, 2 live-collected; GNS WM15186, 1). **Fossils: Colombia: Miocene/Pliocene:** USGS 11520 (1; illustrated, Pl. 43, Figs 13-14). **Venezuela: Pliocene:** 2.5 km NE of "Castillo," Cumaná, foot of Cumaná Hills, Sucre Province (UCMP S-110, 1). **Pleistocene:** NMB 12884, Araya Peninsula (5; 3 specimens illustrated, NMB H 18046-18048; Pl. 43, Figs 5, 7, 10);

12892 (2); USGS 18410 (1); 24573 (1 large).

Distribution.—*Monoplex tranquebaricus* is a poorly known species that has been mentioned very little in the modern literature, and its range also is poorly known. I have seen Recent material from off of the West African coast from the Canary Islands (recorded also by Garcia-Talavera, 1983: 33, 101, 216) and Cape Verde Islands and from Mauretania to Angola. Bernard (1984) illustrated typical specimens from Gabon, and it is probably largely limited to tropical West Africa. Ardovini & Cossignani (2004: 129) illustrated four West African and Cape Verde Islands specimens in color. A single undoubted specimen at ANSP was collected off of Florida, USA [the record by Kalafut (1988) apparently being based on a short, wide specimen of *M. krebsii*], another specimen from Venezuela is present at TFMF, and two small Recent specimens from Venezuela are present at NMB. Therefore it is not surprising to find several records of fossil specimens from the Atlantic coasts of Colombia and Venezuela, apparently almost all Pliocene or Pleistocene in age (the age of the Tubará Fm of Colombia is poorly known, and the assigned “Miocene” age is probably wrong; this and the other anomalous-looking records in the present monograph suggest that it is actually Pliocene or Pleistocene). This is another West African species that, like *Cabestana cutacea* and *Monoplex trigonus* (Gmelin, 1791), has no pre-Pleistocene fossil record whatsoever in the Mediterranean region, and apparently never has lived there. Pleistocene fossils have also been recorded from Tenerife, Canary Islands (Garcia-Talavera *et al.*, 1978).

***Monoplex trigonus* (Gmelin, 1791)**

Pl. 44, Figs 1-2

Murex trigonus Gmelin, 1791: 3549.

Triton caudatus. Kiener, 1842: 16, pl. 9, fig. 2 (not *Ranella caudata* Say, 1822).

Triton ficoides Reeve, 1844a: pl. 13, fig. 51; 1844c: 116; Tryon, 1880: 13, pl. 7, fig. 46.

Triton samier Petit de la Saussaye, 1852a: 46, pl. 8, fig. 51.

Triton (Simpulum) ficoides. Tryon, 1880: 13, pl. 7, fig. 46.

Sympulum (sic) ficoides. Rochebrune, 1881: 304.

Tritonium ficoides. Locard, 1897: 301.

Cymatium ficoides. Dautzenberg, 1910: 68; 1912: 40; Tomlin, 1923: 90.

Cymatium trigonum. Fischer-Piette, 1942: 217; Nicklès, 1950: 86; Marche-Marchad, 1958: 23; J., W. & F. Gibson-Smith, 1971: 263, pl. 1; Burnay & Monteiro, 1977: 33, fig. 26; Finlay & Vink, 1982: 133; Bernard, 1984: 62, fig. 99; Garcia-Talavera, 1987: 249; Vega-Luz & Vega-Luz, 1995: 7; Guerreiro & Reiner, 2000: 111; Ardovini & Cossignani, 2004: 129, 2 lower left figs.

Cymatium (Septa) trigonum. Kilius, 1973: 191, fig. 137; 1981: 709.

Cymatium (Monoplex) trigonum. Beu, 1985: 58, fig. 16; Henning & Hemmen, 1983: 69, pl. 12, fig. 6; Piech, 1995: 11.

Remarks.—*Monoplex trigonus* is included here because of a single Recent specimen collected in Venezuela. It resembles *M. krebsii* most closely of the western Atlantic species, and has a very similar long, straight canal, similar prominent varices, and a similarly strongly armored aperture. *Monoplex trigonus* differs from *M. krebsii* mainly in having a very much shorter spire, so that the canal looks disproportionately long compared with that of *M. krebsii*, and in having a bright scarlet-orange aperture with paler transverse ridges, rather than the plain white aperture of *M. krebsii*. Also, although the apertures are similar, the inner lip of *M. trigonus* spreads more widely over the previous whorl in the parietal area than in *M. krebsii*; the transverse ridges on the inner lip are fewer and coarser and lack the protruding basal columellar pair of *M. krebsii*, and those inside the outer lip consist of two rows of short ridges, with a narrow smooth area between them, where only one row of longer nodules is present in *M. krebsii*.

Dimensions.—*Triton ficoides*, holotype: H 55, D 28 mm (Bishop & Way, 1976); holotype of *Murex trigonus*, MNHN: H 47, D 48 mm (Fischer-Piette, 1942: 218); Recent Venezuelan specimen, BMNH 1983099: H 42, D 23 mm (J., W. & F. Gibson-Smith, 1971: 264).

Types.—The type material of *Murex trigonus* consists of the specimen illustrated in the reference cited by Gmelin (1791: 3549), “le Samier” of Adanson (1757: 122, pl. 8, fig. 14). Gmelin (1791) cited the locality as “Habitat in Senegalia.” As pointed out by Fischer-Piette (1842: 217-218), a single specimen of *Monoplex trigonus* identified as “le Samier” remains in Adanson’s collection at MNHN; Fisher-Piette (1942: 218) noted that “le denomination donnée par Gmelin, *Murex trigonus*, ... est fondée entièrement sur le Samier” [the name given by Gmelin ... is founded entirely on le Samier]. The specimen in Adanson’s collection is therefore regarded as the holotype of *Murex trigonus*. Fischer-Piette (1942: 218) noted that the specimen is “rolled”, *i.e.*, apparently abraded on a beach. *Triton ficoides*, holotype in Jane Saul collection, Cambridge University Zoological Museum (Bishop & Way, 1976: 44), from “Africa” (not seen). The type locality is here designated as Gorée, Sénégal.

Other material examined.—**Recent: W Atlantic: Venezuela:** beach, Camuri Grande, Distrito Federal, Venezuela, coll. F. Gibson-Smith, 1967 (BMNH 1983099, 1; specimen recorded by J., W. & F. Gibson-Smith, 1971; Pl. 44, Figs 1-2). **E Atlantic:** 62 lots examined at BMNH, GNS, IRSNB, MCZ, MNHN, RMNH, NMP, SMF, and TFMF, from the Cape Verde Islands, Mauretania, Sénégal, Liberia, Ghana, République Congo, Gabon, and Angola. **Canary Islands:** dredged in Dársena comercial (port) of Santa Cruz de Tenerife (TFMC 1442, 3 dd); TFMF, Santa Cruz de La Palma (1); off mouth of Barranco La Cometa, Gran Canaria Island (TFMC 1441, 1). **St. Helena:** dived in la Bahía, *ca.* 10 m, F. Garcia-

Talavera (TFMC 328, 1).

Fossils: Mediterranean: Piacenzian, Pliocene: Pecoraro, Laureana di Borretto, Reggio Calabria, SW Italy, coll. and pres. Paolo Crovato, Naples (GNS WM17056, 1). **Tyrrhenian, Pleistocene:** conglomerate, Reggio Arangea, opposite Messina, SW Italy, in collection Paolo Crovato, Naples (6; + GNS WM17061, 5); Tyrrhenian, fine sand, Saracinello, a few km S of Reggio Arangea, in collection Paolo Crovato, Naples (1).

Distribution.—Apart from the single Venezuelan specimen listed above, *Monoplex trigonus* is limited at present to West Africa, where it ranges at least from the Canary and Cape Verde Islands and Mauretania to Gabon (Bernard, 1984) and Angola (material at MNHN). This is another West African species that has almost no record, fossil or living, in the Mediterranean Sea. There is also no fossil record of *M. trigonus* in the tropical American region. However, sparse specimens (listed above, but apparently not recorded previously) occur as Pliocene and Pleistocene fossils in southern Italy and along the Mediterranean coast of France, and Leonardi (1935: 15, pl. 3, figs 1-3) illustrated two Pleistocene fossil specimens from Barma Grande, Monaco. Pleistocene fossils also have been recorded from Tenerife, Canary Islands (Garcia-Talavera *et al.*, 1978) and from the Cape Verde Islands (Garcia-Talavera, 1999: 17). Like *Bursa corrugata*, *Monoplex trigonus* apparently entered the Mediterranean briefly during Pleistocene interglacial periods, but rapidly became extinct again, probably after each incursion. I am not aware of fossil specimens of *M. trigonus* from the tropical American region.

Monoplex turtoni (E. A. Smith, 1890)
Pl. 42, Figs 2-4, 6, 8

Triton turtoni E. A. Smith, 1890b: 268, pl. 21, figs 13-13a.

Cymatium (Septa) turtoni. Kilias, 1973: 192, fig. 138.

Cymatium (Monoplex) turtoni. Beu, 1985: 58; Henning & Hemmen, 1993: 70, pl. 13, fig. 5; Piech, 1995: 11.

Cymatium (Monoplex) parthenopeum. Garcia-Talavera, 1987: 250 (in part not *Murex parthenopeum* von Salis Marschlins, 1793).

Remarks.—Although *Monoplex turtoni* has been recorded only from St. Helena, the opportunity is taken here to refigure the available material for comparison with other Atlantic taxa. The type material of *Triton turtoni* and the single specimen presented to the USNM by Turton (the only material that I have seen) indicate that this is indeed probably an endemic species restricted to St. Helena. It is most similar to *M. parthenopeus*, with the same dark brown inner lip with white transverse ridges, and dark brown areas surrounding the white ridges inside the outer lip. However, it differs from *M. parthenopeus* in its much smaller maximum size (the lectotype, 47 mm H, is the largest recorded specimen, compared with at

least 190 mm for *M. parthenopeus*), its much taller and narrower shape, and its much larger protoconch. The protoconch (Pl. 42, Figs 4, 6) is tall and narrowly conical, with weakly impressed sutures, but nevertheless is considerably wider than and approximately three times the size of that of an average specimen of *M. parthenopeus* (Pl. 42, Figs 1, 5, 7). Although protoconchs of ranellids vary somewhat in size, and that of *M. vespacius*, in particular, seems to vary clinally in size across the Indian Ocean, that of *M. parthenopeus* remains the same size worldwide, and it seems unlikely that its normally small protoconch could vary enough to encompass the type material of *M. turtoni*. This is therefore probably an endemic St. Helena species.

Garcia-Talavera (1987: 250) recorded normal specimens of *Monoplex parthenopeus* from St. Helena. He pointed out that it seems unlikely that such an exceedingly widespread species as *M. parthenopeus* could develop an endemic daughter species at St. Helena. However, scenarios can be envisaged in which (*e.g.*) Pleistocene range restriction as a result of lowered sea temperatures during a glacial period could isolate a small population of *M. parthenopeus* at St. Helena long enough for a daughter species to evolve. *Monoplex turtoni* and *M. parthenopeus* are regarded as separate species until they can undergo molecular analysis.

Dimensions.—Lectotype of *Triton turtoni*: H 47.0, D 22.2 mm; largest paralectotype: H 28.9, D 16.0 mm; USNM 123966: H 28.7, D 15.0 mm.

Types.—*Triton turtoni*, 11 syntypes BMNH 1889.10.1.2435-2445, from St. Helena Island, South Atlantic; the largest syntype (BMNH 1889.10.1.2435; Pl. 42, Figs 2-3) is the specimen illustrated by E. A. Smith (1890b: pl. 21, figs 13-13a), and is here designated the lectotype. The paralectotypes are either much smaller, or are mere juveniles, some little more than a protoconch (Pl. 42, Figs 4, 6, 8).

Other material examined.—St. Helena, pres. Turton (USNM 123966, 1; presumably a paralectotype); MCZ unreg., 9 tubes of small specimens in ethanol, collected by T. Mortensen, St. Helena.

Distribution.—The present information indicates that *Monoplex turtoni* is limited to St. Helena Island. There is no fossil record.

Monoplex vespacius (Lamarck, 1822)
Pl. 44, Fig. 5

Triton vespacium Lamarck, 1822: 185; Kiener, 1842: 18, pl. 3, fig. 2; Deshayes, 1843: 636; Reeve, 1844a: pl. 15, figs 61a-b; Küster & Kobelt, 1871: 179, pl. 52, fig. 3.

Triton elongatus Reeve, 1844a: pl. 15, fig. 59, 1844c: 117; Küster & Kobelt, 1876: 208, pl. 58, fig. 9.

Triton (Guttarium) vespacium. Tryon, 1880: 22, pl. 12, figs 94-96 (in part); E. A. Smith, 1891: 413.

- Tritonium (Ranularia) vespacum*. Tapparone-Canefri, 1881: 36.
Tritonium (Ranularia) elongatum. Tapparone-Canefri, 1881: 35.
Triton (Guttarium) vespacum. Coulon, 1933: 129.
Cymatium (Lampusia) pileare var. *borneana* Cox, 1948: 39, pl. 4, figs 1a-b.
Turritriton vespacum. Habe & Kosuge, 1966a: 43, pl. 15, fig. 12.
Cymatium (Septa) vespacum. Kiliyas, 1973: 193 (in part); 1981: 709 (in part); Springsteen & Leobrer, 1986: 113, pl. 31, fig. 2.
Cymatium (Lampusia) bayeri. Kanno *et al.*, 1982: 106, pl. 19, figs 2a-b (not *Cymatium bayeri* van Regteren Altena, 1942).
Cymatium (Turritriton) vespacum. Beu, 1985: 60; Lai, 1989: 125, fig. 46; Piech, 1983: 90, figs 3-6; 1995: 15; Henning & Hemmen, 1983: 105, pl. 21, fig. 4.
Cymatium comptus. Drivas & Jay, 1988: 64, pl. 17, fig. 11 (not *Triton comptus* A. Adams, 1855).
Cymatium occidentale. Oliveira & Tostes, 1993: fig. 2 (in part, lower fig. only; not *Triton rubecula occidentale* Mörch, 1877).
Cymatium (Monoplex) vespacum. Wilson, 1993: 246 (in part; not pl. 42, figs 3a-b, = *C. thersites* Reeve, 1844); Beu, 1998b: 97, figs 23k, 29a-i, 30a-k; 2005: 86, figs 227-230; Okutani, 2000: 287, pl. 142, fig. 16; Beu & Segers in Poppe, 2008: 646, pl. 268, figs 1-5, 7.
Cymatium vespacum. Kubo in Kubo & Kurozumi, 1995: 75, fig. 8.
Cymatium (Turritriton) indomelanicum Garcia-Talavera, 1997: 27, figs 1, 2 (right), 3 (left), 4 (2 left specimens), 5 (right), 6, 7 (right), 8 (left).
Cymatium (Monoplex) thersites. Okutani, 2000: 287, pl. 142, fig. 12 (not *Triton thersites* Reeve, 1844).

Remarks.—*Monoplex vespacum* is distinguished above from the more common western Atlantic species *M. comptus*. *M. vespacum* is identifiable by its markedly larger size than *M. comptus*, by its upper two major spiral cords being weakly subdivided where they cross the varices, rather than undivided as in *M. comptus*, by the ridges on the inner and outer lips not being as prominent as in *M. comptus*, and by the banded lighter and darker gray-brown color pattern with varices banded white and red-brown, rather than nearly uniform cream to dark brown with uniform brown varices as in *M. comptus*. There are very few reliable records of *M. vespacum* in the western Atlantic (the only ones of which I am aware are by Piech, 1993, and Oliveira & Tostes, 1993: fig. 2, lower shell), whereas most of the records of *M. gemmatus* and *M. vespacum* from the Atlantic by previous authors refer to *M. comptus*. In contrast, *M. vespacum* is more common than *M. comptus* in the Indo-West Pacific.

Previously (Beu, 1998b), I identified the holotype of *Cymatium pileare* var. *borneana* Cox (1948: 39) as *Monoplex comptus*, but I now have had another opportunity to examine the holotype, and conclude that the median grooving of the spiral cords (weak but definite over the varices, absent elsewhere) demonstrate that it is a specimen of *M. vespacum* that has not completed secreting the final varix.

After carefully comparing specimens in the GNS col-

lection (57 lots of Indo-West Pacific *Monoplex vespacum*), I conclude that the dark form named *Cymatium indomelanicum* by Garcia-Talavera (1997) intergrades with *M. vespacum*. All characters such as the coloration of the varices (pale or dark where they cross the sutural ramp), subdivision of the spiral cords, and size of the protoconch are moderately variable in this species. Indian Ocean specimens tend to be darker in color than others, and many also have an unusually large protoconch, but all forms intergrade and in my opinion this is part of the variation of one species. The protoconch seems to vary clinally in size across the Indo-West Pacific, reaching a maximum size in the western Indian Ocean.

Dimensions.—MNHN, New Caledonia, Lagon sta. 965: H 60.0, D 24.7 mm; holotype of *Cymatium indomelanicum*: H 34, D 17 mm (Garcia-Talavera, 1997: 29); paratype GNS WM17457: H 31.0, D 17.1 mm; Piech (1993) recorded Atlantic specimens with H 41 mm (Roatan Island, Honduras, Piech collection) and H 22 mm (Key Largo, Florida, Sunderland collection).

Type material.—*Triton vespacum*, lectotype designated by me (Beu, 1998b), MHNG 1100/5/4, the lower of the two specimens figured by Kiener (1842: pl. 3, fig. 2), with four paralectotypes; I also designated (Beu, 1998b) the type locality as Bohol Island, Philippine Islands. *Triton elongatus*, holotype BMNH 1967635, from the Philippine Islands, a specimen of *Monoplex vespacum* with a moderately long anterior canal. *Cymatium pileare* var. *borneana*, holotype NMB H 14421, with 5 paratypes, from Togopi Fm (Pleistocene), Dent Peninsula, North Borneo. *Cymatium (Turritriton) indomelanicum*, holotype at TFMC, from Pemba, northern Mozambique, with paratypes 2, 3, 5, and 6 from Mozambique, Kenya (paratypes 3, 5) and Natal, South Africa; paratype 1, Pemba, Mozambique, at BMNH; paratype 4, dredged off of Pemba, Mozambique, GNS WM17457.

Other material examined.—**Recent: W Atlantic:** Reliable illustrated records have been published by Piech (1993: figs 3-6): 4.5 m, Pickle's Reef, off of Key Largo, Florida (Sunderland collection, 1); Roatan Island, Honduras (Piech collection, 1; illustrated, Pl. 44, Fig. 5); and by Oliveira & Tostes (1993: lower shell in fig. 2), presumably (like the other specimens in their illustrations) from Itaparica, Bahia, Brazil.

Distribution.—*Monoplex vespacum* lives throughout the Indo-West Pacific province, from eastern South Africa, East Africa, and the Red Sea eastward to eastern Polynesia (although it is not reported from Hawaii; Kay, 1979), and from at least as far north as Taiwan, south to Woodman's Point, Fremantle, Western Australia, and to Moreton Bay in southern Queensland (Beu, 1998b). It is abundant in New Caledonia (Beu, 1998b). The records from the western Atlantic (above) indicate a sporadic occurrence from southern Florida, USA, to northern Brazil. Although fossils are reported from Miocene

and younger rocks in the Philippine Islands and Indonesia, there is no fossil record in the Atlantic, implying that the rare Atlantic records result from larval transport around southern Africa from the Indian Ocean.

Monoplex vestitus (Hinds, 1844)

Pl. 44, Figs 3-4, 6-12

Triton vestitus Hinds, 1844a: 21 [July]; 1844b: 11, pl. 4, figs 1-2 [October]; 1844c: 436 [December]; Reeve, 1844a: pl. 20, fig. 101 [August]; C. B. Adams, 1852: 118; Tryon, 1880: 12, pl. 7, figs 38-39; Keen, 1966: 269.

Triton vestitus ? var. *senior* C. B. Adams, 1852: 118; Turner, 1956: 85.

Triton (Simpulinus [sic]) haemastoma. Mörch, 1860: 82 (not *Triton haemastoma* Valenciennes, 1832).

Cymatium vestitum. Dall, 1909b: 171, 226; Jordan, 1926: 241; M. Smith, 1944: 22, fig. 264; Hertlein & Emerson, 1953: 351, 362, pl. 27, fig. 12; Hertlein & Strong, 1955a: 135; 1955b: 363; Finet, 1991: 270.

Cymatium (Lampusia) vestitum. M. Smith, 1948: 3, pl. 5, fig. 6.

Cymatium (Septa) vestitum. Emerson & Old, 1963b: 22, figs 21-23; Keen, 1971: 507, fig. 960; Abbott, 1974: 163.

Cymatium (Monoplex) vestitum. Beu, 1985: 58; Beu & Kay, 1988: 212, figs 74-80; Henning & Hemmen, 1993: 70, pl. 13, fig. 4; Piech, 1995: 11; Kaiser, 1997: 32; López de la Fuente & Ramos, 2004: 86.

Remarks.—*Monoplex vestitus* is a distinctive, endemic eastern Pacific species, which is compared with *M. keenae* above. It is recognizable by its relatively short spire, by its wide, rather oval shape, by most specimens having at least two varices rather than the one that is usual in *M. keenae*, by having narrower and more numerous spiral cords and narrower and more numerous axial folds, by having narrower and more widely spaced transverse ridges on the dark brown inner lip, and by having an almost uniform medium to dark brown exterior, apart from a conspicuous paler peribasal band, compared with the uniform cream to pale brown with dark brown varices of *M. keenae*. The large Pleistocene specimen recorded here from the Burica Peninsula, western Panama, at first was identified as *M. aquatilis*, and throws light on the distinction between these two species. The specimen of *M. vestitus*, although faded, retains the dark brown inner lip characteristic of *M. vestitus* (pale orange in *M. aquatilis*) and its whorl surface has a distinctive shape, with a unique axially aligned contraction immediately after and parallel to each varix. The spiral cords also are a little narrower and more clearly subdivided by a median groove than in *M. aquatilis*.

C. B. Adams (1852: 118) stated that “*Triton vestitus* ? var. *senior*” differed from *Monoplex vestitus* in being “not so deeply colored” and one whorl larger. This suggests the possibility that he was describing *M. keenae*. Turner (1956: 85),

in her revision of the eastern Pacific mollusks named by C. B. Adams, noted that the type material of *Triton vestitus* ? var. *senior* is lost. To prevent the possibility of this name affecting the validity of the name *M. keenae*, the neotype proposed below is a specimen of *M. vestitus*.

Dimensions.—NMB H 17928, Burica Peninsula, W Panama, Pleistocene: H 95.5, D 47.2 mm; GNS WM 13828, Pedro Gonzales Island, Panama Bay: H 85.1, D 44.8 mm; USNM 36631, W Panama: H 75.9, D 39.3 mm; GNS WM 13365, Isla Gubanador, Panama Bay: H 59.1, D 31.4 mm. The maximum recorded height is 117.9 mm (Skoglund, 1992; although this is so large as to suggest that it was based on the very similar *Monoplex keenae*).

Types.—*Triton vestitus*, from “Realejo, Gulf of Nicoya, and Bay of Honda, on the west coast of America, among the rocks of the shore”; location of type material unknown, as is that of the specimen illustrated by Reeve (1844a: pl. 20, fig. 101). Probably, like that of much of the *Sulphur* material, the type material was sold by Captain Sir Edward Belcher (Keen, 1966). Neotype of *T. vestitus* designated here, USNM 32329 (Pl. 44, Figs 3-4), Recent, Islas Tres Marias, Nayarit, Mexico, ex Stearns collection. *Triton vestitus* var. *senior*, “type lost” (Turner, 1956: 85), collected by C. B. Adams “near Panama”; the neotype of *T. vestitus*, designated here, also is here designated the neotype of *T. vestitus* var. *senior*.

Other material examined.—**Recent: E Pacific:** The LACM collection includes 27 lots, and GNS 5 lots, not listed in full; northernmost: shrimp boats, Guaymas, Sonora, Mexico (LACM.R-46, 1), the only lot from Sonora; S Mexico 1 lot; W Nicaragua 1 lot; W Costa Rica 15 lots (29 specimens); W Panama 3 lots LACM + 5 lots GNS; W Colombia 2 lots; intertidal on rocks, Punta Brava, Bahia Santa Elena, Ecuador, 2°12'23"S, 81°00'05"W (LACM-AHF 19-33, 1 small); southernmost, Peru: 20 m, on rock, off of Lorenzo Island, near Callao, 12°06'25"S, 77°11'07"W (LACM-AHF 365-35, 1 juvenile with good protoconch).

Fossils: Pacific Costa Rica: Pliocene: Charco Azul Group, Penita Fm, Quebrada la Penita, Burica Peninsula, collection of Bernard Landau (1). **Pacific Panama: Pleistocene:** NMB 17441 (NMB H 17928, 1; largest seen: Pl. 44, Figs 10, 12). **Ecuador: Early Pliocene:** NMB 19124 (1 outer lip frag).

Distribution.—*Monoplex vestitus* lives now from the Gulf of California to at least as far south as Callao, Peru (listed above), the Chincha Islands, Peru (Dall, 1909b: 171), and to Paita, Peru (Peña, 1970), the Galápagos Islands (Keen, 1971; Finet, 1991), and at Cocos Island, Costa Rica (Montoya, 1983), and Gorgona Island, Colombia (Cantera *et al.*, 1979; Cosel, 1984; Skoglund, 1992). Most material in collections is from western Costa Rica and Panama. The only fossil records are the Pliocene and Pleistocene specimens from the Burica Peninsula of Pacific Costa Rica and Panama and one fragment

from Ecuador, all recorded here.

Monoplex wiegmanni (Anton, 1838)

Pl. 45, Figs 1-3, 7

Murex argus var. β Gmelin, 1791: 3547.

Fusus wiegmanni Anton, 1838: 77; Anton in Philippi, 1845: 19,

Fusus pl. 2, figs 2, 4; Schniebs, 2000: 85, figs 8a-b.

Triton chemnitzii. Reeve, 1844a: pl. 11, fig. 37; C. B. Adams, 1852: 115; Küster & Kobelt, 1871: 164, pl. 43, fig. 6 (not *Triton chemnitzii* Gray, 1839).

Cassidaria setosa "Hinds" Reeve, 1844a: expl. to pl. 11, fig. 37 (in synonymy of *Triton chemnitzii*).

Triton perforatus Conrad, 1849b: 156; 1849c: 280, pl. 39, fig. 6.

Tritonium nodosum "Martini" Menke, 1850: 189 (adoption of a non-binominal name).

Ranularia (Lagena) wiegmanni. Mörch, 1853: 110.

Triton (Linatella) wiegmanni. Mörch, 1860: 82, Tryon, 1880: 15, pl. 9, fig. 57.

Cymatium wiegmanni. Dall, 1909b: 226; Pilsbry & Olsson, 1941: 39, pl. 7, fig. 1; M. Smith, 1944: 22, fig. 269.

Triton cf. *barthelemyi*. Li, 1930: 268, pl. 7, figs 53-53a (not *Triton barthelemyi* Bernardi, 1857, = *Septa spengleri* Perry, 1811).

Triton (Lagena) wiegmanni. Coulon, 1933: 131.

Cymatium (Linatella) wiegmanni. Schwengel, 1938: 1; M. Smith, 1948: 12, pl. 4, fig. 13; Keen, 1958: 344, fig. 321; 1971: 505, fig. 955; Abbott, 1974: 164.

Cymatium (Linatella) cynocephalum. Clench & Turner, 1957: 242, pl. 135, fig. 1; Kilius, 1973: 126, fig. 93 (not *Triton cynocephalum* Lamarck, 1816).

Linatella (Linatella) wiegmanni. Beu, 1985: 60, fig. 25; Beu & Cernohorsky, 1986: 253, figs 23-27, 34-35; Henning & Hemmen, 1993: 108, pl. 20, fig. 4; Piech, 1995: 17.

Cymatium (Monoplex) wiegmanni. Beu, 2001: 712; López de la Fuente & Ramos, 2004: 86.

Remarks.—I pointed out (Beu, 1998b: 83) that the operculum of *Monoplex wiegmanni*, with an anterior terminal nucleus, differs markedly from that of *Linatella caudata*, which has a subcentral nucleus near the center of the columellar margin and, because *M. wiegmanni* in many characters resembles *M. parthenopeus*, I transferred *M. wiegmanni* to *Monoplex*. As noted above, *M. cercadicus* resembles *M. wiegmanni* even more closely than does *M. parthenopeus*, and appears to be a feasible ancestor for *M. wiegmanni*. It now seems reasonable to include *M. wiegmanni* in *Monoplex* alongside such similar species as *M. cercadicus*, *M. panamensis* n. sp., *M. parthenopeus*, and *M. tranquebaricus*. It is clear that having only a terminal varix is no guide to phylogenetic relationships in Cymatiinae, as it is obviously easy for this character to develop readily and independently through ceasing to develop varices on the spire, in several genera of Cymatiinae and in several groups of *Monoplex* species.

Monoplex wiegmanni is easily recognized by (a) its wide

shape, (b) its wide, gently sloping sutural ramp bordered by a moderately to very prominent angulating keel, (c) its strongly stepped spire, (d) its sculpture of low, wide, closely spaced spiral cords not unlike those of *Linatella caudata*, lacking virtually all axial sculpture, (e) its moderately long anterior canal, relatively short and straight in many shallow-water specimens but longer and strongly twisted in some taller specimens collected offshore, (f) in most specimens developing only the terminal varix, which is a relatively thin, flared margin in many specimens rather than a marked thickening, and (g) having low but obvious ridges inside the outer lip, more prominent inside the sutural ramp than lower down, and many large, moderately prominent to very obvious pale transverse ridges on the inner lip, situated on a dark brown background in many well-callused specimens. Living specimens have a heavy, strongly pilose periostracum not unlike that of *M. parthenopeus*, but with shorter bristles. *Monoplex wiegmanni* differs from *M. parthenopeus* and *M. keenae* in its wider shape, its much lower and wider spiral cords and virtually complete lack of axial sculpture, its much more prominent shoulder angle and sutural ramp, producing a more strongly stepped spire, and in having an even weaker tendency to produce varices. It differs from *M. cercadicus* in its larger size, its wider and lower spiral cords, and its more marked shoulder angulation and sutural ramp, forming a more prominently stepped spire than in *M. cercadicus*. *Monoplex panamensis* n. sp. is perhaps the most nearly similar species, but differs from *M. wiegmanni* in having a much less prominent peripheral angulation bordering the sutural ramp (the shoulder angle), in having much thicker and more prominent varices, and in defining its posterior excurrent canal in a unique way, by the transverse ridges on the inner lip merely ceasing rather than by the development of a parietal ridge, which is lacking in *M. panamensis*.

Dimensions.—LACM 23202, Panama: H 94.5, D 58.4 mm; LACM 95768, Changame Island, Panama Bay: H 87.0, D 57.2 mm. The maximum recorded height appears to be 144.8 mm (Beu & Cernohorsky, 1986; Skoglund, 1992).

Types.—Beu & Cernohorsky (1986: 254) designated the specimen from Anton's collection illustrated in color by Philippi (1845 in 1842-1851: *Fusus* pl. 2, fig. 2) as the lectotype of *Fusus wiegmanni*. However, Schniebs (2000: 85, figs 8a-b) illustrated the holotype of *F. wiegmanni* (Staatliches Museum für Tierkunde Dresden, MTD2809). Our lectotype designation (Beu & Cernohorsky, 1986) therefore was unnecessary and has no status. The holotype is unlocalized; the type locality is here designated as Venado Island, Panama Bay. *Triton perforatus*, no type material known, although the excellent drawing published by Conrad (1849c: pl. 39, fig. 6) leaves no doubt of the identity of this name. The holotype of *F. wiegmanni* is here designated the neotype of *Triton perforatus*. A specimen in Menke's collection (SMF 314358/1),

acquired recently by SMF in Bronn's collection, identified by Menke as *Tritonium nodosum*, is a specimen of *Monoplex wiegmanni* from Mazatalan, western Mexico. This is the remaining syntype of *Tritonium nodosum*, because this name is not available from Martini & Chemnitz's (1769-1795) non-binominal work, and was made available by Menke (1850). The other names in the synonymy have been applied incorrectly to this species, and have no separate type material.

Other material examined.—**Recent:** 66 lots examined at GNS, LACM, MCZ, SMF, and USNM, from W Mexico (northernmost: La Paz, Baja California Sur, LACM 95770, 2; MCZ 205217, 1), W Costa Rica, W Panama, W Colombia, Ecuador, and Peru (Paíta, USNM 32323, 1; 9-37 m, off of Tumbes, between Caletto la Cruz and Puerto Pizarro, 3°28'S, 80°36'W, shrimp boat *Maria Elena*, LACM 72-83, 4).

Fossils: **Atlantic Costa Rica: Pliocene:** NMB 17784, Río Banáno (1). **Pacific Costa Rica: Pleistocene:** NMB 17739 (1); 17745 (1). **Pacific Panama: Pleistocene:** NMB 17443 (1); 18074 (1); 18076 (9); 18305 (2); 18435 (2); same locality, collection of Bernard Landau (3; 1 large). **Panama, Darien: Late Miocene:** NMB 18532, Tuira Fm (1); 18534, Tuira Fm (1).

Distribution.—*Monoplex wiegmanni* lives now from the Gulf of California to Peru (Keen, 1971), but does not seem to be recorded from any of the offshore islands in the eastern Pacific. Fossils are reported here from the Pliocene and Pleistocene of the Atlantic and Pacific coasts of Costa Rica and the Pacific coast of Panama, and two specimens are recorded from the Late Miocene Tuira Fm in Darien (throwing doubt on the suggested evolution from *M. cercadicus*, Miocene-Pliocene of the Dominican Republic). Also, an excellent specimen was illustrated from the Pliocene Canoa Fm at Punta Blanca, western Ecuador, by Pilsbry & Olsson (1941: 39, pl. 7, fig. 1). One of the fossils extends the range of *M. wiegmanni* into the Atlantic coastal region of the CAI during mid-Pliocene time, at the Río Banáno, near Limón, Costa Rica.

Monoplex williamsi (Maury, 1924)

Murex williamsi Maury, 1924: 141, pl. 6, fig. 8; Vokes, 1971: 117; 1990a: 6, pl. 12, fig. 5 (holotype), 6 (copy of Maury's fig.); Schmelz, 1989: 137; Simone & Mezzalana, 1994: 38, pl. 10, fig. 274 (copy of Maury's fig.).

Remarks.—This is another species from the late Early Miocene Pirabas Fm of Brazil that, like *Monoplex chlorostomoides* and *M. infelix*, discussed above, does not have enough characters visible to be able to comment on its relationships. However, it is based on a species with low, rounded, non-spinose varices, resembling a short specimen of *M. pilearis*, and certainly does not belong in *Murex*. Vokes (1971: 117) included this spe-

cies in her catalog of the Muricidae, although Schmelz (1989: 137) and (Vokes, 1990a: 6) later pointed out that it is not a muricid. The holotype was illustrated again by Vokes (1990a: pl. 12, figs 5-6).

Types.—Recorded only from the type material, from Pirabas Fm (late Early Miocene) at Bahia Pirabas, Paraná, Brazil (Simone & Mezzalana, 1994; see comments on age under *Monoplex chlorostomoides*).

Monoplex n. sp. A

Pl. 61, Fig. 3

Remarks.—A single incomplete specimen from the Chipola Fm of Florida, with the dorsum of the last whorl missing, evidently represents a further species not otherwise seen in this project — although it is possible that the juvenile specimen from the Chipola Fm mentioned under *Monoplex krebsii* represents the same species. It is very prominently sculptured, and closely resembles *M. parthenopeus* in most characters, although the available specimen is only 49.7 mm H — and so either very immature, or a much smaller species than *M. parthenopeus*. It has six evenly spaced, relatively narrow, primary spiral cords, narrower and a little more evenly spaced than in *M. parthenopeus*, and the varices (four present, on slightly more than the last two whorls), axial ridges, and prominent apertural armature are very similar to those of *M. parthenopeus*. However, this apparently unnamed species differs from *M. parthenopeus* in its wider sutural ramp, markedly fewer, more prominent transverse ridges on the inner lip, with 3-4 particularly prominent ridges on the base of the columella, and in its narrower and more prominent nodules inside the outer lip. Also, although the prominent spiral cords and axial ridges on early spire whorls closely resemble those of *M. parthenopeus*, the axial ridges on the last two whorls become more oblique to the coiling axis on the right side of the shell (in conventional spire-up apertural view) to produce a strongly inclined appearance that decreases across the whorl face to become parallel to the varix at the end of each intervariceal interval, a character that I have not observed in *M. parthenopeus*. It appears feasible that this specimen represents an unnamed species that was directly ancestral to *M. parthenopeus*, perhaps at last helping to explain the mystery of the origins of this now almost ubiquitous species. However, it should also be noted that this specimen is approximately coeval with the earliest records (above) of *M. parthenopeus* from the Baitoa Fm in the Dominican Republic, so it is possible that the Chipola specimen is merely an early, coarsely sculptured specimen of *M. parthenopeus*.

Dimensions.—H 49.7, D 27.4 mm (D incomplete, originally ca. 29 mm).

Material examined.—**Fossils: Florida: Late Early Miocene,** Chipola Fm: TU 826, Farley Creek, Chipola River, Calhoun

Co, Florida, collection of Bernard Landau (1, incomplete).

***Monoplex* n. sp. B**

Pl. 53, Fig. 8

Remarks.—A single incomplete specimen from the Gatun Fm of Atlantic Panama seems to represent a further, unnamed species of *Monoplex*. It resembles *M. pilearis* in general appearance, but is shorter and wider, with a very much shorter spire, more prominent, wider but thinner varices, and more prominent, narrower, more elevated primary spiral cords and more prominent secondary spiral threads than in *M. pilearis*. Further, more complete specimens are needed before this distinctive species can be described.

Dimensions.—H 31.5, D (incomplete) 22.2 mm.

Material examined.—**Fossils: Atlantic Panama: Middle Miocene:** Lower Gatun Fm, *ex situ*, Los Lomos quarry, Cativa, Colon Province, coll. P. Jeffery (BMNH Palaeontology Department, GG22583, 1 incomplete).

Genus ***RANULARIA*** Schumacher, 1817

Ranularia Schumacher, 1817: 77, 253 (as *Ranula* on p. 77). Type species (by subsequent designation, Gray, 1847: 133): *Murex clavator* Chemnitz, 1795 (non-binominal) (= *Ranularia longirostra* Schumacher, 1817; *M. clavator* cited in its synonymy; = *Tudicla gutturnium* Röding, 1798), Miocene to Recent, western Pacific.

Tritonocauda Dall, 1904: 133. Type species (by original designation): *Murex caudatus* Gmelin, 1791, Recent, Indo-West Pacific.

Retusum Jousseaume, 1892: 344. Type species (by monotypy): *Triton retusum* Lamarck, 1822 (= *Monoplex oboesus* Perry, 1811), Recent, northern Indian Ocean.

Remarks.—*Ranularia* is a distinctive genus. Not only do most of the included species have a short to very short spire and a long, narrow anterior canal, but also they all have an operculum with a subcentral nucleus, against or near the center of the columellar margin. The center of diversity of the genus is the central western Pacific, from New Caledonia to the Philippine Islands, but even so, it is surprising to find that there is no fossil record of the genus in the Atlantic before Pleistocene time.

Two rather different groups of species are included in *Ranularia*. The typical group [in the literal sense of resembling the type species, *R. gutturnia* (Röding, 1798)] contains species that are relatively small and narrow, with a small spire and last whorl and a long anterior siphonal canal. The other group consists of larger species such as *R. dunkeri* (Lischke, 1868), *R. pyrum* (Linnaeus, 1758), and the few large specimens that I have seen of *R. rehderi* (A. H. Verrill, 1950) (see below), which have a larger last whorl and a shorter anterior

canal than the smaller species; the spire is also rather tall for *Ranularia* species. Recently there has been a tendency in the popular literature to refer this latter group of larger species to *Lotoria*. Although their teleoconchs resemble those of *Lotoria* species, the critical character is the operculum; it has an anterior terminal nucleus in *Lotoria*, but a subcentral one near the mid-columellar margin in *Ranularia*. The relatively large species *R. dunkeri*, *R. pyrum*, and *R. rehderi* clearly are referable to *Ranularia* by this character. There also exists a range of species that in many respects are intermediate between the smaller and larger ones of *Ranularia* in teleoconch size and shape, such as *R. cynocephalum* (Lamarck, 1816) (see below), *R. testudinaria* (A. Adams & Reeve, 1850) (Indo-West Pacific), and *R. trilineata* (Reeve, 1844) (northern Indian Ocean and the Red Sea). In my opinion, *Ranularia* is a single genus. On the basis of the opercular nucleus position, the highly distinctive species *Cymatium armatum* (G. B. Sowerby III, 1897) should be referred to *Lotoria* (Beu, in prep.).

The first reviser of the generic name was Dall (1904: 133), who listed the spelling “*Ranula* Schumacher, 1817” in the synonymy of *Ranularia* Schumacher, 1817; *i.e.*, he selected the spelling *Ranularia* as the valid one.

Ranularia cynocephalum (Lamarck, 1816)

Pl. 45, Figs 4-6, 8-9

Triton cynocephalum Lamarck, 1816: pl. 422, fig. 3, “Liste des objets”: 5; 1822: 184; Kiener, 1842: 3, pl. 12, fig. 1; Deshayes, 1843: 633.

Triton cynocephalus. Reeve, 1844a: pl. 8, fig. 26.

Triton moritinctus Reeve, 1844a: pl. 13, fig. 49; 1844c: 115.

Tritonium cynocephalum. Krebs, 1864: 23; Coomans, 1963: 64, 72, 80.

Triton (Gutturnium) cynocephalum. Mörch, 1877: 32

Triton (Gutturnium) cynocephalus. Tryon, 1880: 19, pl. 11, figs 80-81, pl. 15, fig. 152; Coulon, 1933: 128.

Lampusia cynocephala. Dall & Simpson, 1901: 417; Dall, 1903b: 132.

Tritonium moritinctum. Locard, 1897: 301.

Cymatium cynocephalum. Maury, 1922: 116; Piele, 1926: 60; Leal, 1991: 118; Calvo, 1987: fig. 78 (radula); Guerreiro & Reiner, 2000: 105-106; Ardovini & Cossignani, 2004: 127, lower right fig.

Cymatium (Ranularia) caribbaeum Clench & Turner, 1957: 204, pl. 111, figs 3-4, pl. 113, fig. 3, pl. 117, figs 1-2; Warmke & Abbott, 1962: 100, pl. 2, fig. b, pl. 18, fig. k; Kilias, 1973: 131, fig. 95; van Regteren Altena, 1975: 36 (in part); Coelho *et al.*, 1981: 119, fig. 5; Bernard, 1982: 16, illus. H. & E. Vokes, 1983: 23, pl. 11, fig. 9; Macsotay & Campos Villarroel, 2001: 67, pl. 13, figs 4, 7.

Cymatium (Ranularia) sarcostomum (*sic*). Clench & Turner, 1957: 206, pl. 118, figs 1-5 (not *Triton sarcostoma* Reeve, 1844).

Cymatium caribbaeum. Matthews & Kempf, 1970: 27; Kaufmann & Götting, 1970: 370, fig. 82; Lipe & Abbott, 1991: 12-13,

- illus.; Diaz & Puyana, 1994: 172, fig. 639.
Cymatium sarcostomum (sic). Matthews & Kempf, 1970: 28.
Cymatium (*Ranularia*) *sarcostoma*. Kiliyas, 1973: 153; 1981: 706 (in part).
Cymatium (*Ranularia*) *moritinctum caribbaeum*. Abbott, 1974: 165, pl. 7, fig. 1765; Okutani, 1983: 257, illus.
Cymatium moritinctum caribbaeum. Shoemaker *et al.*, 1978: 126; Bandel, 1984: 99, pl. 9, fig. 7.
Cymatium moritinctum. Bosch *et al.*, 1982: 77, upper fig.
Ranularia moritincta. Kilburn & Rippey, 1982: 75, pl. 2, fig. 10, pl. 17, fig. 13; Kilburn, 1984: 3, pl. C, fig. j.
Cymatium (*Ranularia*) *cynocephalum*. Beu, 1985: 59; Rios, 1985: 75, pl. 27, fig. 328; 1994: 88, pl. 29, fig. 342; Beu & Cernohorsky, 1986: 260, figs 3-4; Garcia-Talavera, 1987: 257; Singer, 1990: 23, 27; Wilson, 1993: 246, pl. 42, figs 7a-b (not fig. 5, as in caption); Henning & Hemmen, 1993: 75, pl. 18, figs 1-2; Piech, 1995: 11; Bosch *et al.*, 1995: 99, fig. 358; Redfern, 2001: 62, pl. 31, figs 261A-B; Zhang & Ma, 2004: 121, pl. 3, fig. 1.

Remarks.—*Ranularia cynocephalum* is the only moderately common species of *Ranularia* in the Atlantic, and is highly distinctive because of (a) its moderately tall, stepped spire in some specimens (the tallest spire of Atlantic *Ranularia* species), (b) its long, straight or slightly curved siphonal canal, (c) its sculpture of one or several rows of small to quite large nodules, (d) the presence of only one or two varices on all specimens, (e) its well thickened, smooth aperture with seven prominent, rounded ridges inside the outer lip and, in particular, (f) its prominent red-brown color patch on the parietal area. The red-brown color patch is unique to *R. cynocephalum*; *R. rehderi* has a dark brown to almost black-colored area, larger than that of *R. cynocephalum*, occupying most of the columella, and *R. gallinago* (Reeve, 1844) has no distinctively colored area on the inner lip.

This species has had a complicated nomenclatural history. All authors had followed Kiener (1842: pl. 12, fig. 1, an excellent colored lithograph of the species here called *Ranularia cynocephalum*) in the interpretation of this species, until Clench & Turner (1957: 206) pointed out that the original figure in *Tableau Encyclopédique et Méthodique* (Lamarck, 1816: pl. 422, fig. 3) appears to represent a different species. They interpreted Lamarck's figure as representing *Monoplex wiegmanni*, and renamed the Atlantic species *Cymatium caribbaeum*. However, Beu & Cernohorsky (1986) pointed out that both the specimen illustrated by Lamarck and that illustrated by Kiener are among Lamarck's syntypes of *Triton cynocephalum* and, indeed, all of Kiener's (1842) figured specimens apparently are from among Lamarck's type material. The specimen illustrated by Lamarck (1816) is an immature specimen of a *Ranularia* species with a thin, partly broken outer lip (possibly *R. pyrum?*), and Kiener (1842) merely chose a better specimen from Lamarck's material to illustrate. Beu & Cernohorsky (1986) designated the specimen figured by Kiener (1842) as

the lectotype of *Triton cynocephalum*.

Ranularia cynocephalum is quite variable in the height of the spire and the number and prominence of the nodules. Clench & Turner (1957) treated the finely sculptured specimens as one species, *R. caribbaeum*, and the more coarsely sculptured specimens as another, *R. sarcostoma* (Reeve, 1844). They also regarded *Triton moritinctus* as a synonym of *R. sarcostoma*. However, this added more confusion, because (a) there is only one, variable *Ranularia* species in the Atlantic with a red-brown parietal area, (b) *R. sarcostoma* is a distinct western Pacific species lacking a parietal color patch (Beu, 1998b: fig. 33i), and (c) *Triton moritinctus* is a synonym of *R. cynocephalum*.

As with the following species, the specific epithet ("dog's head") is a noun, not to be declined to agree with the gender of the generic name. Similarly, "stoma" (mouth) is Greek neuter noun, not to be declined.

Dimensions.—Lectotype of *Triton cynocephalum* and of *Cymatium* (*Ranularia*) *caribbaeum*: H 89.6, D 40.6 mm; figured specimen, NMB 17563, El Manglillo Fm (Pleistocene), Isla Margarita, Venezuela, NMB H 17953: H (incomplete) 70.0, D 43.8 mm; Recent, St. Vincent, Cape Verde Islands, LACM.A-2777: H 58.3, D 32.0 mm; Recent, beach 10 km NE of Manaure, Goajira Peninsula, Colombia, R. von Cosel's material at SMF: H 90.3, D 48.2 mm; Recent, N of Choco, SW Conducia Bay, Mozambique, NMP H3440: H 91.3, D 50.4 mm.

Types.—*Triton cynocephalum*, lectotype MHNG 1099/96, designated by Beu & Cernohorsky (1986), the specimen illustrated by Kiener (1842: pl. 12, fig. 1), with two paralectotypes. This specimen was also designated the lectotype of *Cymatium* (*Ranularia*) *caribbaeum* by Beu & Cernohorsky (1986). *Triton moritinctus*, 3 syntypes BMNH 1967632, 1 syntype MCZ 188151, "Philippine Islands" (wrong; limited to the Indian and Atlantic Oceans); the specimen illustrated by Reeve (1844a: pl. 13, fig. 49) is the smallest one in BMNH 1967632, with a much shorter spire than the others and bearing its operculum (Pl. 45, Fig. 4). Clench & Turner (1957: 205) designated the type locality of *C. caribbaeum* as Bahia, Brazil, and this is also designated here as the type locality of both *T. cynocephalum* and *T. moritinctus*.

Other material examined.—**Recent: W Atlantic:** 83 lots examined at BMNH, GNS, LACM, NMB, RMNH, SMF, and ZMA (as with many other common species, many other lots have been examined at MCZ, ANSP, AMNH, USNM, and several private collections, but not listed), from Bahamas, Florida, E Mexico, Honduras, E Panama, Colombia, Jamaica, Haiti, Cuba, Puerto Rico, Aruba, Curaçao, Antillean islands (St. Croix, St. Thomas, Martinique, Guadeloupe, St. Martin, St. Vincent, British Virgin Islands), Venezuela, and Brazil (3 m, Barra, Salvador, GNS WM14013, 1; 20-25 m, Barra,

Salvador, GNS WM17260, 5). **E Atlantic: Canary Islands:** La Palma (TFMC 436, 1). **Cape Verde Islands:** "Cape Verde Islands, Dr Welwitsch" (BMNH; 1); "Cape Verde Islands" (BMNH; 1); *Talisman* sta. 107, 70 m, off of São Vicente, Cape Verde Islands (MNHN, 1; recorded as *Tritonium moritinctum* by Locard, 1897: 301); São Vicente, Cape Verde Islands (LACM A-2777, 1); São Vicente, Cape Verde Islands, L. J. Shackelford (NMP J.2328, 2); *Canap VI* sta. 6.131, Tydeman Cape Verde Islands Expedition 1982, 30-43 m, S of São Vicente, 16°47'N, 25°02'W (RMNH, 1). **São Thomé:** Espraina (GNS WM17596, 1). **Sénégal:** trawled, native fishermen, off of Sénégal (GNS WM17591, 1; smooth form). **Gabon:** Annobon Island, 360 km off of the Gabon coast, at 5 m, in an octopus "nest" (specimen illustrated by Bernard, 1982). **South Africa:** 66 lots examined at NMP, ranging from Mozambique S to beach drift, Mbotyi, eastern Transkei, South Africa (NMP G.8124, 6).

Fossils: Bermuda: Pleistocene: S shore of Bermuda (USNM; 1). **Venezuela: Pleistocene:** NMB 17563 (1, illustrated, NMB H 17953; Pl. 45, Fig. 8). **Holocene:** Tortuga Fm, Las Calderas Canyon, Cubagua Island, collection of Bernard Landau (3).

Distribution.—*Ranularia cynocephalum* lives now in the eastern and western Atlantic and in the eastern and western Indian Ocean, as far south as eastern South Africa, and to approximately Shark Bay in Western Australia. In the eastern Atlantic, it is recorded from Port Royal, South Carolina (Merrill & Petit, 1965; Shoemaker *et al.*, 1978: 126), USA, south to São Sebastião, Brazil, and Fernando de Noronha Island (Rios, 1994: 88). Matthews (1968) recorded specimens (as *Cymatium caribbaeum*) found rarely in the gut of the toadfish or "pacomon," *Amphychthys cryptocentrus*, caught off of Fortaleza, Ceará, Brazil. In the eastern Atlantic, it was reported (as *T. moritinctum*) by Locard (1897: 301) from *Talisman* sta. 107, off of São Vicente, Cape Verde Islands, by Bernard (1982) from Annobon Island, off of Gabon, West Africa, and by Ardovini & Cossignani (2004: 127, lower right fig.) from the Cape Verde Islands, and several specimens are listed above from the Cape Verde Islands, Canary Islands, São Thomé, and Sénégal, West Africa. In the eastern Indian Ocean, it occurs from eastern South Africa, as far south as the eastern Transkei (Kilburn & Rippey, 1982: 75; Kilburn, 1984: 3, pl. C, fig. j) to the Gulf of Arabia (Bosch *et al.*, 1995). A form occurs off of the northwestern coast of Western Australia, from approximately Darwin to Shark Bay (Wilson, 1993) and in New Guinea (specimen from Port Moresby examined in the collection of Dov Peled, Haifa) with wider, higher, and more closely spaced spiral cords than other specimens of *R. cynocephalum* that I have seen (24 lots examined at WAM and 4 at GNS). However, one of the large specimens from off of Sénégal, West Africa, at GNS (WM17591) also is this smoother form; I have

seen other specimens from Muscat, Oman (WM13277, 1; WM17593, 1), and Conducia Bay, Mozambique (WM17592, 1), and there is little doubt that it is part of the variation of *R. cynocephalum*. A normal specimen of *R. cynocephalum* at GNS is from North Borneo, Indonesia (5-10 m, on rocks, Rusakah Island, WM17603), and this species evidently occurs as far east as western Indonesia. Zhang & Ma (2004: 121) recently recorded *R. cynocephalum* from the coast of China, on the basis of three records from Taiwan (Zhang & Ma, 2005: map, fig. 77), and there is no doubt that their two colored figures show this species, although, again, one is the smoother form discussed above. I am not aware of any other authentic records of *R. cynocephalum* from any western Pacific localities; Reeve's type locality of "Philippines" for *Triton moritinctus* undoubtedly is wrong, because *R. cynocephalum* has not been found there again. Fossils are recorded only from Pleistocene deposits of Bermuda and of Isla Margarita, Venezuela.

Ranularia gallinago (Reeve, 1844)

Pl. 46, Figs 1-5, 8

Triton gallinago Reeve, 1844a: pl. 2, fig. 5; 1844c: 110; Küster & Kobelt, 1876: 235, pl. 65, fig. 4.

Triton aegrotus Reeve, 1844a: pl. 12, fig. 42; 1844c: 114; Küster & Kobelt, 1876: 214, pl. 60, fig. 4.

Triton (Gutturium) gallinago. Tryon, 1880: 21, pl. 11, fig. 89.

Triton (Gutturium) trilineatum. Tryon, 1880: 20, pl. 11, fig. 87 only (in part not *Triton trilineatus* Reeve, 1844).

Cymatium (Ranularia) mohorteri (sic) A. H. Verrill, 1952: 2, illus.

Ranularia gallinago. Kilburn, 1984: 3, pl. C, fig. h.

Cymatium (Ranularia) aegrotum. Beu, 1985: 59, fig. 19.

Cymatium (Ranularia) gallinago. Beu, 1985: 59; Piech, 1993: 80, figs 11-16; Henning & Hemmen, 1993: 78, pl. 16, fig. 8; Rios, 1994: 88; Piech, 1995: 12.

Remarks.—*Ranularia gallinago* is recognizable by (a) its small size for the genus (to 70 mm H), (b) its moderately short spire and moderately long, straight anterior canal, (c) its two or, on a few specimens, three very thick, prominent varices, (d) its prominent sculpture of narrowly rounded spiral cords raised into relatively few large, sharply compressed nodules around the periphery where they cross the sparse, narrow, high, widely spaced axial costae, (e) its narrow but well thickened, coarsely ridged lips, the outer one not reflected over the terminal varix at all, and (f) its almost completely white color, with two or more salmon to bright red-brown areas on each varix.

This species has been mentioned very few times in the literature, and even its geographical range has been very poorly known until recently. For instance, I gave (Beu, 1985) the range as "western Pacific," which is incorrect, despite Reeve's accurate-sounding type locality for *Ranularia gallinago*, "Cagayan, Province of Misamis, Island of Mindanao, Philippines" (no doubt more fiction by Hugh Cuming). The

application of the name and the range of variation have been clarified as a result of Betty Jean Piech's record of this species in the Atlantic (Piech, 1993). It is now clear that *R. gallinago* occurs only in the Indian and Atlantic Oceans, and that its variation includes the more weakly nodulose form named *Triton aegrotus* by Reeve (1844a). Nodule size is highly variable in the rather large lot (GNS WM13746, 10 specimens) collected at Mauritius by J. Closel, and this range certainly encompasses the type material of *T. aegrotus*. This was also the opinion of Henning & Hemmen (1993: 79), who as first revisers selected the name *Triton gallinago* for the species.

Verrill (1952) proposed the name *Cymatium (Ranularia) mohorteri* with a description that renders this name available in nomenclature, but with a poor drawing of a strange, distorted shell of a species of *Ranularia*. The name was proposed "in honour of Mrs Willard Mohorter of Cincinnati," and so should be spelled *mohorterae* (ICZN Article 31.1.2). The identity of this nominal species has never been commented on, Clench & Turner (1957) did not mention it, apparently regarding the name as not available, and the location of Verrill's type material is unknown. However, the figure of a narrow species of *Ranularia*, the small size, and Verrill's description of a "dull white" shell with "two or three pale orange or salmon colored blotches on dorsal varice (*sic*) nearest lip, a distinct orange-brown stripe on the summit of each varice of last whorl and extending to the tip of the siphonal canal" indicate that the name was almost certainly based on specimens of *R. gallinago*. His material consisted of "[t]hree specimens taken in a trap at Souffriere Bay, Island of Dominica, British West Indies in 75 to 100 fathoms [137-180 m]. Type - 67 mm in length. 38 mm in width. Siphonal canal 39 mm. Paratype - 48 mm in length. 24 mm in width. Siphonal canal 25 mm. Type and paratype in author's collection." If this is indeed based on specimens of *R. gallinago* (and any other species seems very unlikely), it extends the known range in the western Atlantic greatly to the north of the Brazilian records, all of which are from Todos Santos Bay, Bahia.

Dimensions.—*Triton aegrotus*, lectotype: H 48.0, D 23.3 mm; larger paralectotype: H 54.1, D 25.0 mm; smaller paralectotype: H 49.9, D 25.1 mm; *Triton gallinago*, lectotype: H 60.0, D 33.0 mm; larger paralectotype: H 53.1, D 28.4 mm; smaller paralectotype: H 52.0, D 27.7 mm; GNS WM17586, Nacala, Mozambique: H 69.5, D 36.7 mm; H 62.8, D 35.5 mm.

Types.—*Triton gallinago*, 3 syntypes BMNH 1967593, wrongly localized (see above); the type locality is here designated as Mauritius Island, Indian Ocean. The largest syntype (H 60.0 mm; Pl. 46, Figs 1, 3) is the specimen illustrated by Reeve (1844a: pl. 2, fig. 3), and is here designated the lectotype. *Triton aegrotus*, 3 syntypes BMNH 1967628, from "China" (wrong); the type locality also is here designated as

Mauritius. The smallest syntype (Pl. 46, Figs 4, 8) is the specimen illustrated by Reeve (1844a: pl. 12, fig. 42), identified by the letter "c" inside the outer lip, and is here designated the lectotype. I do not know the location of Verrill's type material of *Cymatium mohorterae*.

Other material examined.—**Recent: E Indian Ocean:** 29 lots examined at NMP, from Seychelles, Mozambique, and Durban, South Africa; Mauritius (GNS WM13746, 10; WM16426, 1; WM17610, 2); Natal, South Africa (GNS WM17608, 1); Tuléar, Madagascar (GNS WM17030, 3; WM15113, 1; WM17609, 1); Nacala, N Mozambique, H. Boswell (GNS WM17586, 2); Zanzibar (GNS WM13626, 2). **W Atlantic:** The records by Piech (1993), accompanied by photographs, are: Itaparica Island, Todos Santos Bay, Bahia, Brazil, beach wash, August 1991, Garcia collection (1); Todos Santos Bay, Bahia, coll. L. Trinchão, Piech collection (1); Itaparica Island, Todos Santos Bay, Bahia, beach wash, coll. B. J. Piech, August 1991, Piech collection (1; illustrated, Pl. 46, Figs 2, 5); Todos Santos Bay, Bahia, Trinchão collection (2); Todos Santos Bay, Bahia, beach wash, 1979-1980, Voss collection (2). Some of these specimens have been examined, through the generosity of Betty Jean Piech.

Distribution.—*Ranularia gallinago* is recorded only from the eastern Indian Ocean and from the islands of Madagascar, Réunion, and Mauritius, from South Africa (as far south as Durban; Kilburn, 1984: 3) and from Itaparica Island, Todos Santos Bay, Bahia, Brazil, in the western Atlantic. As noted above, Verrill's description of *Cymatium mohorterae* was apparently based on specimens of *R. gallinago* from Dominica, Lesser Antilles, but this record requires confirmation. This species definitely does not occur in the Philippine Islands, and a number of specimens labelled "Japan" in collections that I have examined also are mislocalized. *Ranularia gallinago* does not seem to occur at all in the western Pacific Ocean, and I have seen no material from the eastern Indian Ocean. I am also not aware of any fossil specimens.

***Ranularia rehderi* (A. H. Verrill, 1950)**

Pl. 46, Figs 6-7

Cymatium rehderi A. H. Verrill, 1950: 126, pl. 9, figs 1a-b.

Cymatium (Ranularia) pyrum rehderi. Clench & Turner, 1957: 208, pl. 119, figs 2-3; Kiliyas, 1973: 150.

Cymatium (Ranularia) testudinarium rehderi. Abbott, 1974: 165, fig. 1766; Piech, 1995: 13.

Cymatium (Ranularia) rehderi. Beu, 1985: 59; Henning & Hemmen, 1993: 83, pl. 18, fig. 5.

Cymatium testudinarium rehderi. de Jong & Coomans, 1988: 68; Paulmier, 1994: 18, illus.

Cymatium ridleyi. Leal, 1991: 115 (not *Triton ridleyi* E. A. Smith, 1890, = *Cymatium comptum* A. Adams, 1855).

Cymatium (Ranularia) pyrum. Rios, 1994: 88, pl. 29, fig. 343 (not *Cymatium pyrum* Linnaeus, 1758).

Remarks.—*Ranularia rehderi* is highly distinctive because of (a) its tan to pale yellow-brown exterior, (b) its moderately tall spire for the genus, (c) its moderately long, straight to lightly curved anterior canal, (d) the presence of two or three rather wide, prominent varices, (e) the sculpture of low, simple spiral cords raised into quite large, prominent nodules by the prominent axial folds and, in particular, (f) the dark brown to almost black inner lip crossed by many coarse, widely spaced, white transverse ridges. A specimen is illustrated excellently in color on a webpage (<http://www.femorale.com.br/shellphotos>, last accessed 28 April 2006).

Ranularia rehderi is an uncommon and little-known but endemic western Atlantic species. Clench & Turner (1957) thought it so similar to the Indo-West Pacific species *R. pyrum* (Linnaeus, 1758) that they ranked it as a subspecies of *R. pyrum*. Abbott (1974) and Piech (1995) were more impressed by the dark brown columella as an indicator of relationship, and ranked *R. rehderi* as a subspecies of the uncommon Indo-West Pacific species *R. testudinaria* (A. Adams & Reeve, 1850), which also has a dark brown area on the inner lip. The unusually large specimen collected at Bañes, Oriente, Cuba, by C. J. Finlay (Clench & Turner, 1957: pl. 119, fig. 2) and a similar Brazilian specimen illustrated by Rios (1994: pl. 29, fig. 343) show that the similarity to *R. testudinaria* is close, but they are not as closely similar as to be ranked as subspecies; only immature specimens of *R. rehderi* resemble *R. testudinaria*, and adults become much larger, wider, and shorter-spined than *R. testudinaria*. I pointed out above that *R. rehderi* is a member of a species group of large *Ranularia* species with a relatively large last whorl and spire, a relatively short, wide siphonal canal, a deeply excavated columella, and a weakly convex outer lip profile compared with the other species of the genus. The group comprises *R. pyrum*, *R. dunkeri*, and *R. rehderi*. The three also share similar sculpture of wide, well-raised, rounded spiral cords and small to quite large nodules, have similarly prominent, wide varices, and have similar large apertures with prominent ridges on both lips. *Ranularia pyrum* is the largest of the three species, and lacks a distinct parietal colored area, being pale to deep brownish orange or orange-red all over, including the aperture, with the apertural ridges markedly paler than the rest. *Ranularia dunkeri* has a more banded, paler, and darker red-brown color pattern than the other species, and has a red-brown parietal area, varying from diffuse and reddish tan to more clearly defined and dark tan. *Ranularia rehderi* differs from the two Pacific species in its uniform pale yellow-brown to pale tan exterior and in its striking dark brown to almost black inner lip, crossed by prominent white ridges, and in my opinion, is as different from the other two species as *R. pyrum* is from *R. dunkeri*, and is a distinct, endemic western Atlantic species. It is conceivable, however, that *R. rehderi* and *R. testudinaria* are sister species that evolved through the sub-

division of a formerly pan-tropical species by the uplift of the CAI, probably well before its final closure.

Dimensions.—Largest seen, Bañes Sands, Piñar del Río, Cuba, C. J. Finlay collection (now at FAU): H 89.4, D 47.0 mm; large Brazilian specimen: H 97, D 48 mm (Rios, 1994: 88); GNS WM17585, Fort de France, Martinique: H 67.3, D 33.9 mm; H 62.7, D 32.3 mm.

Types.—*Ranularia rehderi*, holotype USNM 594095 (Clench & Turner, 1957: pl. 119, fig. 3), from 50–80 m, off of Dominica, West Indies.

Other material examined.—**Recent:** **Florida:** dredged, Pompano Beach (ANSP 340275, 3); 10 m, dredged inside third reef off of Pompano Beach (ANSP 340272, 2); 20 m, under coral, off of Boynton Beach (ANSP 340271, 1). **Atlantic Panama:** dredged off of Portobello (GNS WM15276, 2). **Cuba:** dredged sand, Bañes Sands, Piñar del Río, C. J. Finlay collection (now at FAU, 1); channel dredgings, 12–16 m, Santiago de Cuba, C. J. Finlay collection (now at FAU, 1); Nuevitas, NE Camaguay (DMNH 105900, 1); Havana, C. Aguayo (MCZ 191389, 1); Bahía de Cienfuegos (GNS WM16030, 1). **Dominican Republic:** Puerto Plata (MCZ 188958, 1). **Puerto Rico:** Playa de Ponce (AMNH 112714, 1); W Puerto Rico (ANSP 340273, 1). **Curaçao:** St. Martha Bay, inner bay, 1960 (ZMA, 1 live). **Barbados:** 143 m, off of W coast (BMNH, 3). **Antillean islands:** St. Johns, Antigua (AMNH 190429, 1); Maid Island, Antigua (AMNH 190431, 1); 1.6 km N of Fredericksted, St. Croix (AMNH 190426, 3); Gallons Bay, St. Croix (AMNH 190430, 3); Charlotte Amelie, St. Thomas (AMNH 190427, 2); Vessups Bay, St. Thomas (AMNH 190432, 2); St. Barthelemy, harbor (AMNH 190428, 2); 8–12 m, Baie de Robert, Fort de France, Martinique (GNS WM17585, 2); Guadeloupe (GNS WM17001, 13).

Distribution.—*Ranularia rehderi* was recorded by Clench & Turner (1957) only from Cuba, the Dominican Republic, and the island of Dominica in the Lesser Antilles, but Betty Jean Piech (pers. comm., 1998) informed me of several specimens dredged off of the Atlantic coast of Panama; Paulmier (1995: 18) illustrated a living specimen from Bouillante, Guadeloupe, Antilles; Dominique Lamy presented GNS with several specimens from Guadeloupe; de Jong & Coomans (1988) recorded it from Curaçao and Aruba, and Rios (1994: 88) recorded it from Salvador, Bahia, Brazil. *Ranularia rehderi* evidently occurs uncommonly throughout the western Atlantic from southern Florida, USA, to Bahia, Brazil. I am not aware of any definite fossil records, but it seems likely that the record of “*Triton* aff. *sinensis* Reeve” from Pleistocene rocks of Curaçao by Rutten (1931: 644), citing two earlier publications that I have not seen, was based on this species, which is much the nearest of Atlantic species to the Indo-West Pacific species *R. sinensis* (Reeve, 1844) in appearance, size and sculpture.

Genus *RETICUTRITON* Habe & Kosuge, 1966

Reticutriton Habe & Kosuge, 1966b: 315, 330. Type species (by original designation): *Triton pfeifferianum* Reeve, 1844, Miocene to Recent, Indo-West Pacific and eastern and western Atlantic.

Remarks.—The genus *Reticutriton* comprises a small group of species of moderate size (60–100 mm H) with moderately to very elongate shells, with strongly convex whorls and deeply impressed sutures, with sculpture of many low, narrow, well-raised, closely spaced spiral cords (many more than in other members of Cymatiinae) crossed by many similarly spaced but lower and narrower axial costellae, with numerous (10–12) narrow, closely spaced, transverse ridges inside the outer lip, an operculum with an anterior terminal nucleus, and a large, wide, conical protoconch. All of the four or five species so far assigned to the genus occur in the study area.

Reticutriton carlottae (Ferreira & da Cunha, 1957)

Simpulum carlottae (sic) Ferreira & da Cunha, 1957: 41, pl. 3, fig. 11.

Cymatium (*Septra* [sic]) *carlottae*. Simone & Mezzalana, 1994: 36, pl. 9, fig. 260 (copy of Ferreira & da Cunha's figure).

Remarks.—*Reticutriton carlottae* is known only from the holotype, a rather crushed and incomplete specimen (natural mold?) available to me only as the original illustration. This shows a tall, narrow shell with several prominent varices down the entire spire, and sculpture of many narrow spiral cords and less prominent fine axial costellae. The aperture is incomplete and the anterior canal is missing. This specimen appears to belong in *Reticutriton* and, indeed, it does not display any characters by which it could be distinguished from *R. pfeifferianus* (Reeve, 1844). The reference by Simone & Mezzalana (1994) is merely a catalog of Brazilian fossils. Nothing more can be determined about the relationships and status of this species until better material can be compared with Recent specimens of *R. pfeifferianus*, but it seems likely to be a synonym of the latter.

The etymology of the specific epithet is clear, because the authors (Ferreira & da Cunha, 1957: 41) discussed the earlier work on Pirabas fossils by Carlotta Maury, and clearly named this species after her, although they spelled her name "Carlota" in their discussion, as well as spelling the species name "*carlottae*." The species name therefore is an error and should be emended to *carlottae*.

Dimensions.—Ferreira & da Cunha (1957: 42) stated the dimensions of the incomplete holotype as H 46, D 22 mm.

Types.—*Simpulum carlottae*, holotype cited by the authors (Ferreira & da Cunha, 1957: 41) as "tipo exemplar no. 367-I," Museu Paraense Emilio Goeldi, Estado do Pará, Brazil;

from Pirabas Fm (late Early Miocene), Ilha Fortaleza, Baía de Pirabas, Estado de Pará, Brazil. Only recorded specimen.

Reticutriton elsmerensis (English, 1914)

Pl. 47, Figs 2-4, 6-8

Gyrineum elsmerense English, 1914: 215, pl. 23, fig. 6; Kew, 1924: 78; Grant & Gale, 1931: 733.

Cymatium elsmerense. Kern, 1973: 89.

Cymatium (*Reticutriton*) *elsmerense*. Beu, 1998b: 132, figs 42h-l.

Remarks.—I pointed out (Beu, 1998b: 132) that *Reticutriton elsmerensis* is referable to *Reticutriton*, and illustrated some typical specimens from the Pliocene of the San Diego area, southern California. Although this species actually occurs just to the north of the study area, it is included here to demonstrate its close similarity to *R. lineatus* (Broderip, 1833), a species that is now limited to the Galápagos Islands. *Reticutriton elsmerensis* is small, short, and wide compared with *R. pfeifferianus*, and has numerous, very prominent varices, a subcircular aperture, the fine, closely spaced spiral and axial sculpture typical of the genus, and a few large, rounded nodes in each intervariceal interval. All specimens that I have seen are strongly dorsoventrally compressed (naturally, *i.e.*, not a taphonomic artifact), and have their varices placed to the sides of the flattened shell so that they are much more nearly aligned than in all other members of Cymatiinae. All specimens of *R. elsmerensis* examined also are consistently small, much smaller than normal adult *R. lineatus*. *Reticutriton elsmerensis* is very similar to *R. lineatus* in shape and sculpture, and the possibility needs consideration that it merely represents a range extension by *R. lineatus*. However, the smaller size, the dorsoventral flattening, and the lateral position of the varices distinguish *R. elsmerensis* from *R. lineatus*. Several species of tonnoideans occur both on the western coast of tropical America and at the Galápagos Islands at present, *e.g.*, *Semicassis centiquadrata* (Valenciennes, 1832), *Monoplex keenae*, *M. vestitus*, *Turritriton gibbosus* (Broderip, 1833), *Bursa corrugata*, and *B. rugosa*. It is therefore not surprising that *R. lineatus* formerly occurred both at the Galápagos Islands and along the tropical American mainland (see the record below from the Last Interglacial terrace near Mulegé, Baja California Sur), and became restricted to the Galápagos Islands as a result of Last Glacial cooling of waters along the mainland coast.

Dimensions.—*Gyrineum elsmerense*, holotype: H 26.4, D 22.0 mm; LACMIP loc. 305, K Ranch, Palm City, California: H 36.0, D 21.4 mm; H 27.3, D 16.2 mm; H 23.9, D 15.2 mm.

Types.—*Gyrineum elsmerense*, holotype UCMP-A.1802/11915, from Lower Fernando Fm, Elsmere Canyon, Los Angeles Co, California (Early Pliocene; Grant & Gale, 1931: 733).

Other material examined.—**Fossils: California: Pliocene:** LACMIP loc. 305, K Ranch, Palm City, near Mexican border, San Diego Co, San Diego Fm (collection 305, 33 specimens; 305A, 5; 305C, 2).

Distribution.—*Reticutriton elsmerensis* is recorded only from Pliocene rocks of southern California, USA (although this distribution suggests that it also occurs in northern Mexico). Besides the localities listed above, Kern (1973) recorded it from the Ventura Basin, California.

***Reticutriton lineatus* (Broderip, 1833)**

Pl. 47, Figs 1, 5

Triton lineatus Broderip, 1833: 6; Reeve, 1844a: pl. 2, figs 4a-b.

Triton (Simpulum) lineatus. Kobelt, 1878: 247; Tryon, 1880: 14, pl. 8, fig. 51.

Cymatium lineatum. Hertlein & Strong, 1955a: 135; Hertlein, 1972: 29 (list); Finet, 1991: 270 (list); Schneider, 1999: table 1; Hickman & Finet, 1999: 71, fig. 63.

Cymatium (Septa) lineatum. Keen, 1971: 507, fig. 958; Kilius, 1973: 173, fig. 127.

Cymatium (Reticutriton) lineatum. Beu, 1985: 59; Henning & Hemmen, 1993: 89, pl. 20, fig. 1; Piech, 1995: 13; Kaiser, 1997: 32.

Remarks.—*Reticutriton lineatus* is one of the most distinctive species in the family, because of its (a) much shorter and wider shape than *R. pfeifferianus*, (b) strongly inflated whorls and deeply impressed sutures, (c) sculpture of many narrow, chestnut brown to dark purplish brown spiral cords on a paler brown background, (d) prominent varices and the few rounded nodes in the intervariceal intervals, and (e) dark, purplish brown aperture with many narrow, stark white, transverse ridges on inner and outer lips. Numerous specimens are illustrated excellently in color on a webpage (<http://www.femorale.com.br/shellphotos>, last accessed 28 April 2006), providing a good appreciation of the unusual shape, sculpture, and coloration of *R. lineatus*.

Reticutriton lineatus is illustrated here because of the possibility that the southern Californian taxon *R. elsmerensis* is a synonym of *R. lineatus*. *Reticutriton lineatus* would then be a member of the Pliocene or earlier fauna of the mainland coast of tropical America, and certainly there is at least a close relationship between these species. Also, Schneider (1999: tables 1-2) reported a specimen of *R. lineatus* from Mulegé Terrace (Middle Pleistocene, oxygen isotope stage 5e, ca. 125,000-130,000 years old) at the northern end of Bahía Santa Inés, near Punta Chivato, on the inland coast of Baja California Sur, Mexico, demonstrating that this species extended its range to include mainland Mexico during at least the Last Interglacial period.

Dimensions.—Lectotype: H 57.1, D 31.2 mm; paralecto-

type: H 56.7, D 30.7 mm; N shore Cartago Bay, Albemarle Island, LACM-AHF 800-38: H 57.8, D 31.4 mm; H 49.9, D 27.8 mm; H 48.6, D 27.5 mm; largest seen, Sombrero Chino light, Galápagos Islands, AMNH 164536: H 94.0, D 47.4 mm.

Types.—*Triton lineatus*, 2 syntypes BMNH 1968526; the larger syntype, marked "25" (Pl. 47, Figs 1, 5), is the specimen illustrated by Reeve (1844a: pl. 2, fig. 4); from the Galápagos Islands.

Other material examined.—**Recent: Galápagos Islands:** Sombrero Chino light (AMNH 164536, 1); Baltra (AMNH 139458, 1); Academy Bay, Santa Cruz Island (AMNH 110422, 2; AMNH 139495, 1); 2-3 m, Sombrero, San Salvador (AMNH 111876, 1); dredged, 8-10 m, Rabida (James) Island (AMNH 117928, 1); 0-2 m, between Punta Tomayo and Academy Bay, S side Isla Santa Cruz (LACM 66-119, 1); Galápagos Islands (LACM 55034, 1); 0-3 m, Punta Tortuga, Canal Bolívar, Isla Isabella (LACM 66-123, 1); intertidal rocks, N shore of Cartago Bay, Albemarle Island (LACM-AHF 800-38, 3); under rocks at low tide, Academy Bay, Isla Santa Cruz, R. von Cosel's material in SMF (1 live-collected); Albemarle Island (BMNH, 1).

Fossils: Galápagos Islands: Pliocene: CAS loc. 1305, cliffs on SW side of Baltra (South Seymour) Island, Galápagos Islands (1; the specimen recorded by Hertlein, 1972: 29).

Distribution.—*Reticutriton lineatus* is limited at present to the Galápagos Islands. A Pliocene fossil specimen of *R. lineatus* also has been reported from the Galápagos Islands, and Schneider (1999: tables 1-2) recorded a late Middle Pleistocene (oxygen isotope stage 5e) fossil specimen from Baja California Sur, Mexico, indicating that its range has only recently been restricted to the Galápagos Islands.

***Reticutriton pfeifferianus* (Reeve, 1844)**

Pl. 47, Figs 10, 12

Triton pfeifferianus Reeve, 1844a: pl. 4, fig. 14; 1844c: 112; Küster & Kobelt, 1872: 194, pl. 55, figs 4-5.

Triton gracilis Reeve, 1844a: pl. 15, figs 58a-b; 1844c: 117; Küster & Kobelt, 1878: 243, pl. 67, fig. 5.

Triton (Simpulum) pfeifferianus. Kobelt, 1878: 247.

Triton (Guttarium) pfeifferianus. Tryon, 1880: 23, pl. 13, fig. 107.

Lampusia gracile. Dall, 1889: 227, pl. 29, fig. 2; 1903b: 132 (in part).

Cymatium pfeifferianum. Hedley, 1909: 360; Hinton, 1972: 12, pl. 6, fig. 11; 1978: 29, fig. 12; Drivas & Jay, 1988: 64, pl. 17, fig. 4; Oliveira & Trinchão, 1993: 314, figs 1(2), 2(3), 3-4.

Cymatium (Guttarium) pfeifferianum. van Regteren Altena, 1942: 103.

Cymatium (Guttarium) bayeri van Regteren Altena, 1942: 104, figs 2a-b.

Reticutriton pfeifferianum. Habe & Kosuge, 1966a: 43, pl. 15, fig. 14; Habe & Kosuge, 1966b: 315, 330.

Cymatium (Ranularia) pfeifferianum. Kilias, 1973: 145, fig. 107.
Cymatium gracile?. Popenoe & Kleinpell, 1978: pl. 5, figs 60, 63.
Cymatium (Septa) pfeifferianum. Kilburn, 1984: 2, pl. C, fig. f;
 Springsteen & Leobrera, 1986: 116, pl. 31, fig. 15; Rios, 1994:
 89, pl. 30, fig. 352.
Cymatium (Reticutriton) pfeifferianum. Beu, 1985: 59; 1998b: 130,
 figs 22h, 42a-g; 2005: 95, figs 252-257; Piech, 1993: 90, figs
 7-10; 1995: 13; Henning & Hemmen, 1993: 88, pl. 20, fig. 2;
 Wilson, 1993: 248, pl. 42, fig. 2; Zhang & Ma, 2004: 130, text-
 fig. 81; Beu & Segers in Poppe, 2008: 652, pl. 271, figs 2-5.

Remarks.—Although *Reticutriton pfeifferianus* has closely similar sculpture, a very similar aperture, and an almost identical protoconch to that of *R. lineatus*, the two species are strikingly different in overall appearance, and it seems likely that they represent long-separated lineages rather than sister species. *Reticutriton pfeifferianus* is consistently much taller and narrower than *R. lineatus*, and has a much paler color pattern of either uniform pale yellowish brown, or white to cream with spiral bands of pale red-brown. Although most specimens are very narrow, with a tall spire and a long, straight siphonal canal, the shape is quite variable, and markedly shorter and wider specimens are fairly common, although none is anywhere near as wide as *R. lineatus*. The holotype of *Cymatium bayeri* is one of these wide specimens, with fairly prominent intervariceal nodes. I reviewed (Beu, 1998b) the type material and synonymy of *R. pfeifferianus*, and this is merely summarized here.

Reticutriton pfeifferianus has turned out to be living from southern Florida to northern Brazil, so it is possible that *R. pfeifferianus* and *R. lineatus* constituted a species pair on either side of the CAI during Miocene and/or Pliocene time, but they are not related closely enough to comprise a geminate pair in the sense of one original species now subdivided as a result of the uplift of the CAI. Dall's (1889: pl. 29, fig. 2) illustration of a juvenile western Atlantic specimen of "*Lampusia gracile*" actually shows *R. pfeifferianus* but, unfortunately, Dall did not specify the locality of the illustrated shell. The four localities cited in the text by Dall (1889: 227) ("Barbados, 100 fms [180 m]. Cape Catoche, Yucatan, in 24 fms. [44 m], U.S. Fish Commission. Aspinwall, Dall. St. Thomas, Riis") might well refer to more than one species, and it is unclear which specimen was illustrated. M. G. Harasewych (USNM, pers. comm., 06 March 2007) reported that the specimens from Yucatan and Aspinwall are in the USNM collection, and are *Monoplex comptus*, so the specimen of *R. pfeifferianus* is from either Barbados or St. Thomas. The illustrated specimen also is not recognizable in MCZ (A. Baldinger, MCZ, pers. comm., 12 March 2007).

Dimensions.—*Triton pfeifferianus*, lectotype: H 66.0, D 27.5 mm, paralectotypes: H 82.5, D 34.0 mm, H 60.2, D 24.9 mm; *T. gracilis*, lectotype: H 27.7, D 13.0 mm, paralecto-

type: H 26.0, D 12.6 mm; SW Conducia Bay, Mozambique, NMP H.3614: H 60.8, D 25.9 mm; GNS WM13877, Gulf of Carpentaria, N Australia: H 73.7, D 27.4 mm; GNS WM18727, Kings Reef, N Queensland: H 68.9, D 31.0 mm.

Types.—*Triton pfeifferianus*, lectotype BMNH 1967596, designated by me (Beu, 1998b: 130), with 2 paralectotypes; the type locality was designated by me (Beu, 1998b) as Bohol Island, Philippine Islands. *Triton gracilis* (based on juvenile specimens of *R. pfeifferianus*), lectotype BMNH 1966543/1, designated by me (Beu, 1998b: 130), with 1 paralectotype, BMNH 1966543/2, from "Philippines." *Cymatium bayeri*, holotype RGM 456 888, a short, late Pliocene fossil specimen from locality M138 in the Kendeng beds of north-central Java (Beu 2005: 95).

Other material examined.—**Recent:** **W Atlantic:** None seen; reliable illustrated records have been published by Piech (1993: 90): **Florida:** DMNH 74116, 46 m, W of Egmont Key, Florida (2 small). **Brazil:** Todos Santos Bay, Bahia, Brazil, Trinchão collection (2); Todos Santos Bay, Bahia, Voss collection (1); and by Oliveira & Trinchão (1993): Itaparica Island, Todos Santos Bay, Bahia, collections of Oliveira and Trinchão (6); recorded also by Rios (1994: 90) from Itaparica Island, Todos Santos Bay, coll. B. Linhares.

Distribution.—*Reticutriton pfeifferianus* occurs throughout the Indo-West Pacific province, from East Africa (as far south as Durban, South Africa; 9 lots examined at NMP) and the Red Sea eastward to the western Pacific archipelagoes, and from Tanabe, Wakayama Prefecture, Honshu, Japan (GNS WM13844, 1) and Taiwan south to Kimberley in northern Western Australia and to approximately Townsville, Queensland (GNS WM18729, 1) and New Caledonia (Beu, 1998b). I am not aware of any records from east of New Caledonia. It is now recorded in the western Atlantic from southern Florida (Piech, 1993), USA, to northern Brazil (Rios, 1994: 89). Oliveira & Trinchão (1993) illustrated six specimens from Itaparica, Bahia. It presumably will prove to be uncommon but widespread in the tropical Atlantic. I am not aware of any American fossil records of *R. pfeifferianus*, apart from the possibility that the holotype of *R. carlottae* is a late Early Miocene specimen of *R. pfeifferianus*.

Reticutriton n. sp.?

Pl. 47, Figs 9, 11

Remarks.—A single small (H 15 mm) specimen from the Cantaure Fm (late Early Miocene) on Paraguaná Peninsula, northern Venezuela, appears to represent a further species of *Reticutriton*. It has the finely reticulate spiral and axial sculpture and the high, thin varices typical of *Reticutriton*, and the aperture has a similar appearance to those of *Reticutriton* spe-

cies. However, the interior of the outer lip bears seven pairs of narrow ridges rather than the 10-12 single ones present on other species of the genus, and the apex of the spire, where the missing protoconch would have been attached, is much too small to have supported the large, wide protoconch that is present on at least the two living species of *Reticutriton*. The relationships of this unnamed species will not be clear until better material is available. In view of the identical age, it is possible that this is a juvenile specimen of *R. carlottae*, if that is distinct from *R. pfeifferianus*. However, the spiral cords of the Cantaure specimen are considerably lower than those of *R. pfeifferianus*.

Dimensions.—Figured specimen, NMB H 17954, Cantaure, Venezuela: H 15.2, D 9.2 mm.

Material examined.—**Fossils: Venezuela: Late Early Miocene:** NMB 17520, upper shellbed, Cantaure Fm, near Casa Cantaure, Paraguaná Peninsula, Falcón, coll. J. & W. Gibson-Smith (1 small specimen, illustrated, NMB H 17954; Pl. 47, Figs 9, 11).

Genus *SEPTA* Perry, 1810

Septa Perry, 1810: signature B2, caption to pl. 3. Type species (by monotypy): *Septa scarlatina* Perry, 1810 (= *Murex rubecula* Linnaeus, 1758), Recent, Indo-West Pacific (see Petit, 2003: 24).

Simpulum Mörch, 1853: 108. Type species (by subsequent designation, Clench & Turner, 1957: 214): *Murex rubecula* Linnaeus, 1758 (not a junior homonym of *Simpulum* Fabricius, 1823, proposed in a work rejected as unpublished in ICZN Opinion 521, 1958).

Remarks.—The genus *Septa* contains a small group of species of small size – most do not exceed *ca.* 55 mm H, and none exceed *ca.* 65 mm – with sculpture predominantly of spiral cords crossed by close, regular axial costellae, with a color pattern of plain bright color or of bright spiral banding, with an operculum with an anterior terminal nucleus, and with an unusually short protoconch for the Cymatiinae. Most living species are confined to the Indo-West Pacific province (listed by me; Beu, 1998b) and only *S. occidentalis* (Möorch, 1877) lives now in the Atlantic, so it is surprising to find a distinctive new species in Miocene rocks of the Dominican Republic.

Septa landaui n. sp.

Pl. 48, Figs 1-2, 4-7, 10

Description.—Shell large and very wide for genus, with short, broadly conic, very weakly stepped spire, strongly inflated last whorl, weakly defined, gently sloping sutural ramp developed over last two whorls, and short, apparently straight (broken) siphonal canal (moderately long and straight in paratypes).

Last three intervariceal intervals of holotype with weakly distorted coiling caused by greater inflation of initial half of each interval than later half; coiling regular on juvenile paratypes. Varices as in other members of genus, low, rounded, wider at top (against upper suture) than elsewhere, the last significantly excavated on abapertural face and buttressed by spiral cords; situated at each 240°, but only four (on last two whorls) present on holotype; juvenile paratypes with 3-6 varices, commencing after less than one teleoconch whorl. Sculpture greatly dominated by spiral cords; with three major cords on spire whorls (but only two on whorl sides, and one subsutural cord; subsutural cord progressively reduced in prominence down spire), and six on last whorl, passing onto terminal varix; one fine spiral thread at center of each interspace, and 2-3 further fine threads on sutural ramp; 7-8 further low cords decreasing in prominence down siphonal canal. Axial sculpture of very numerous, closely spaced, fine costellae over entire teleoconch, 47 on penultimate intervariceal interval of holotype, but decreasing rapidly in number and increasing in spacing over last half-whorl of holotype, which bears only 17 costellae; four low, rounded axial folds and a weak fifth developed over last intervariceal interval of holotype, commencing abruptly at sutural ramp and fading out over base, forming low, rounded nodules where they cross uppermost four major spiral cords. Aperture broadly oval, with narrow, weakly reflected, strongly armed lips; interior of outer lip with seven prominent, short transverse ridges in holotype, each ridge subdivided over outer half into two diverging ridges; seven subdivided or single ridges in paratypes; inner lip with three prominent ridges on spiral cords of previous whorl in parietal area; remainder of inner lip bearing high, very prominent transverse ridges extending well into aperture and down onto top of siphonal canal. Protoconch (of paratypes) tall and narrow, with 5.5 weakly convex whorls; protoconch I poorly preserved, of one reticulate whorl; protoconch II with abraded remnants of sculpture on first *ca.* one whorl, smooth after that, showing sutural furrow between whorls resulting from dissolution of periostracal outer layer.

Dimensions.—Holotype: H 37.1, D 24.5 mm; figured small paratype, NMB H 17956, illustrated by SEM: H 20.6, D 11.1 mm; largest of small paratypes, NMB H 17957: H 23.9, D 13.3 mm.

Types.—Holotype NMB H 17955 (Pl. 48, Figs 1, 4), from NMB 19005 (= TU 1214), Gurabo Fm (Early Pliocene), Río Gurabo, bluffs 5-8 downstream from bridge on Los Quemados-Sabaneta road, Dominican Republic, coll. and pres. Bernard Landau; the only adult specimen that I have seen; NMB 18560 (= TU 1364), Baitoa Fm (late Early Miocene), Boca de Los Ríos, below waterfall in Arroyo Hondo, downstream from Baitoa, Río Yaque del Norte, Dominican Republic, collected by Emily & Harold Vokes, 6 small paratypes (NMB H

17956, paratype illustrated by SEM, Pl. 48, Figs 2, 5-7, 10; NMB H 17957-17961).

Distribution.—Known only by the type material, all from Early Miocene to Early Pliocene rocks of the Dominican Republic.

Remarks.—*Septa landaui* n. sp. is very distinctive, because is it much shorter and wider than any Recent species referred to the genus *Septa*. The shape, with strongly and evenly convex whorls apart from a narrow, slightly concave sutural ramp developed over the last two whorls, is so different from that of any Recent species that it is difficult to compare with the others, all of which are much narrower. Most other *Septa* species, including *S. occidentalis*, the only one now living in the western Atlantic, have eight major spiral cords on the last whorl, passing onto the terminal varix, whereas the holotype of *S. landaui* n. sp. has only six. The only other species recorded previously with only seven main spiral cords is *S. peasei* Beu (1987: 287), which is a very different species with a unique biconic shape caused by a protruding nodule on the posterior (adapical) shoulder of each varix, and is limited to Melanesia and Polynesia. The number of ridges inside the outer lip corresponds in all species of Cymatiinae to the number of spiral interspaces on the exterior, so the holotype of *S. landaui* n. sp. has only seven ridges compared with the 8-9 of all other species, other than *S. peasei*. The subdivision of these ridges into two toward the outer margin of the lip in the holotype of *S. landaui* also is unique. The low spire also contrasts with all other species in revealing only two main spiral cords on the sides of the spire whorls, rather than the three of all other species of the genus. Finally, *S. occidentalis* previously has been one of the species with the narrowest and most numerous axial costellae in the genus (ca. 35-37 on the penultimate intervariceal interval). The costellae are still finer on the spire whorls of *S. landaui* n. sp. (ca. 47 on the penultimate intervariceal interval), but over the last half-whorl, they become somewhat coarser and much more widely spaced (ca. 17 over last half-whorl), a character that I have not observed in any other species. As mentioned by me previously (Beu, 2005: 97), the most closely similar species of which I am aware is *S. dharmai* (Beu, 2005: 96, figs 264-266) from Late Miocene rocks at Citalahab, West Java, Indonesia. *Septa dharmai* has seven primary spiral ridges on the last whorl and is relatively short and wide as in *S. landaui* n. sp., but differs from *S. landaui* n. sp. in its coarser axial costellae (17-21 in each intervariceal interval, compared with 47 in the penultimate interval in *S. landaui* n. sp.) and is not so extremely short and wide as *S. landaui* n. sp. It is also significantly smaller (holotype, the largest specimen, H 28.6, D 18.4 mm) than *S. landaui* n. sp. (H 37.1 mm). Although similarly short and “plump,” the Indonesian species *S. dharmai* has an overall different appearance, because it has a markedly taller spire than *S. landaui* n. sp., with three

or, in places, even four primary spiral cords revealed on the spire whorls, and obvious, coarse axial costellae, unlike the almost invisibly fine ones of *S. landaui* n. sp. These Miocene fossils from Indonesia and the Dominican Republic introduce a greater range of shape and sculpture than is displayed by all the Recent species of the genus.

The specimens from the Baitoa Fm in Arroyo Hondo, Boca de Los Ríos, are referred to *Septa landaui* n. sp. at present, but are small juveniles, a little taller and narrower in proportion than the holotype, have varices starting on the first teleoconch whorl, and have only ca. 17-22 axial costellae on the penultimate intervariceal interval. However, they also have 1-3 or more very low, fine axial threads between the costellae, so these might well strengthen down the shell to produce a similar number of costellae on later whorls as on the holotype. These specimens also all have six main spiral cords (not including a prominent subsutural cord), but the seven ridges inside the outer lip can be subdivided or single, in various combinations in one specimen. The number of axial costellae and the subdivision of the ridges inside the outer lip therefore seem to be variable characters in this species, and at present, the Baitoa Fm specimens are all assumed to be small specimens of *S. landaui* n. sp.; more material is needed to evaluate the variation of *S. landaui* n. sp. before the identification of the Baitoa specimens is certain. One of the smallest Baitoa Fm specimens is significantly narrower and less inflated than the others, and resembles the Indo-West Pacific species *S. rubecula* (Linnaeus, 1758) in shape and proportions, but this specimen also has only six main spiral cords (again, not including a prominent subsutural cord) and seven ridges inside the outer lip like all the others, and seems likely to be part of the variation of *S. landaui* n. sp.

Distribution.—*Septa landaui* n. sp. is recorded only from Miocene and Pliocene rocks of the Dominican Republic.

Etymology.—It gives me great pleasure to name this species in honor of the collector of the holotype, Bernard Landau, whose excellent collections made a major contribution to this work.

Septa occidentalis (Mörch, 1877)

Pl. 48, Figs 3, 8-9, 11-12

Triton (Lampusia) rubecula occidentale Mörch, 1877: 29.

Triton rubeculum occidentale. Tryon, 1880: 12.

Septa? blacketi Iredale, 1936: 307, pl. 23, fig. 3; Iredale & McMichael, 1962: 54.

Cymatium (Septa) rubeculum occidentale. Clench & Turner, 1957: 214, pl. 110, fig. 3, pl. 113, fig. 5, pl. 121, figs 1-3; Kilius, 1973: 190, fig. 136; Abbott, 1974: 484, fig. 1759; Rios, 1975: 79, fig. 320; Coelho *et al.*, 1981: 121, fig. 7.

Cymatium rubeculum occidentale. Nowell-Usticke, 1959: 60, pl. 3, fig. 11; Matthews & Kempf, 1970: 28; Garcia-Talavera, 1983:

112, pl. 4, fig. 2.

Cymatium (Septa) beui Garcia-Talavera, 1985: 28, figs 1-2, 5.

Cymatium (Septa) occidentale. Arthur, 1983: 8, fig.; Beu, 1985: 59; 1987: 286, figs 37-45; 1998b: 134, fig. 23l; Rios, 1985: 76, pl. 27, fig. 333; 1994: 89, pl. 30, fig. 349; Garcia-Talavera, 1987: 250, pl. 1, fig. 2; Arthur & Garcia-Talavera, 1990: 7, row 2, figs A-F; Henning & Hemmen, 1993: 94, pl. 19, fig. 4; Piech, 1995: 13; Redfern, 2001: 62, pl. 31, figs 262A-B.

Cymatium occidentale. Leal, 1991: 118; Vega-Luz & Vega-Luz, 1995: 7; Ardovini & Cossignani, 2004: 128, center right fig.

Remarks.—*Septa occidentalis* is recognizable by its small size (rarely more than *ca.* 40 mm H), by its relatively elongate shape, which increases in height as the shell grows to be similar to that of *S. rubecula* (Linnaeus, 1758) in large adults, and by its very fine, close, regular axial costellae. Recent specimens are uniform pale brown, except for the paler peribasal band that is present on all *Septa* species other than *S. peasei*. The color is therefore the best guide to identification of Recent shells, because *S. rubecula* (Indo-West Pacific), *S. bibbeyi* Beu, 1987 (Philippine Islands), and *S. marerubra* Garcia-Talavera, 1985 (Red Sea), are bright scarlet to crimson red (with a wider peribasal white band in *S. bibbeyi* than in *S. rubecula*, and with much wider and more elevated spiral cords in *S. marerubra* than in the other two species); *S. closeli* Beu, 1987 (Indian Ocean), is medium brown with faint paler and darker spiral banding; *S. hepatica* (Röding, 1798) (Indo-West Pacific) has bright, narrow, alternating cream and dark red-brown spiral bands; *S. peasei* (Melanesia and Polynesia) has darker, black and bright red-brown spiral bands and *S. flaveola* (Röding, 1798) (western Pacific) is narrower than all the other species and has bright, broad, alternating cream and dark brown spiral bands. *Septa mixta* Arthur & Garcia-Talavera, 1990 (Indo-West Pacific), is banded as in *S. hepatica* and *S. peasei*, but less brightly, and has finer axial costellae than all other living species of the genus. As noted above, *S. peasei* differs from all the others by its large nodule on the shoulder of each varix, giving it a biconic shape.

Dimensions.—GNS WM18235, Rottneest Island, Western Australia: H 52.7, D 26.1 mm; GNS WM13668, Samar, Philippines (Pl. 48, Fig. 12): H 45.8, D 24.8 mm; TFMC 519, Punta Teno, Tenerife, Canary Islands: H 44.3, D 23.0 mm; NMB 17675, Borburata, Venezuela, largest of 19: H 34.9, D 19.6 mm.

Types.—*Triton rubecula occidentale*, holotype ANSP 36874, *ex* Swift collection, from St. Thomas, Virgin Islands, Caribbean. *Septa? blacketi*, holotype AMS C. 60662 (Pl. 48, Fig. 9), from Nielsen Park, Watsons Bay, Sydney Harbor, New South Wales, Australia. *Cymatium beui*, holotype TFMC 86, from Oahu, Hawaiian Islands.

Other material examined.—**Recent:** **Bahamas:** 2.5 m, off of Cat Island (GNS WM18233, 1); 21-24 m, off of Brown's

Cay (GNS WM18232, 1). **Florida:** wreckage in 25 m, off of Carysfort Reef, Key Largo (MCZ 238926, 1); 20 m, off of Pompano Beach (TFMC 517, 4; TFMC 510, 3; TFMC 509, 1; TFMC 514, 7; TFMC 516, 2; TFMC 511, 4; TFMC 512, 6); 20-25 m, spoil pile off of Hillsboro Light, Pompano Beach (TFMC 515, 3); 20 m, rock rubble off of Pompano Beach (GNS WM15002, 6; WM16541, 1); 20-22 m, off of Hillsboro Light, Pompano Beach (GNS WM18241, 2); 20 m, rock rubble, 3 km N of Boca Inlet (GNS WM13609, 2); 20 m, rubble, Dania Beach (GNS WM16539, 1); off of Delray Beach (GNS WM16540, 1); 15-20 m, rock rubble, N Broward Co and S Palm Beach Co (GNS WM18240, 1). **Puerto Rico:** 20 m, Bahia de Anasco (GNS WM18234, 1). **Cuba:** Carboneras, Matanzas (MCZ 202269, 1; MCZ 213477, 1); USNM 417842, Cable House, Guantanamo (1, illustrated, Pl. 48, Fig. 3); Cuba (TFMC 518, 1). **Antillean islands:** Altona Bay, N of Fredericksted, St. Croix, Virgin Islands (AMNH 190403, 17); Guadeloupe (GNS WM16988, 1; WM17000, 7). **Aruba:** [no further data] (AMNH 190406, 3; ZMA, 1). **Curaçao:** [no further data] (ZMA, 1). **Venezuela:** beach, Borburata, Estado Carabobo (NMB 17675, 19); dredged, Puerto La Cruz, Estado Anzoátegui (TFMC 508, 1). **E Mexico:** Isla Mujeres, Yucatan (MCZ 213476, 1). **Brazil:** off of Fortaleza, Ceará (MCZ 277231, 1); *R/V Chain* sta. 2, dredged, 30 m, 7°38.5'S, 34°37'W, 50 km NNE of Olindo (MCZ 274523, 1); 20-25 m, under rocks, off of Rio do Fogo, Rio Grande do Norte State (GNS WM17265, 2). **E Atlantic:** **Canary Islands:** La Palma (TFMC 436, with 1 *R. cynocephalum*, 1 *M. aquatilis*); La Palma (TFMC 520, Garcia-Talavera's (1983: 112, pl. 4, fig. 2) original figured specimen; illustrated, Pl. 48, Figs 8, 11); Punta Teno, Tenerife (TFMC 519, 1 large); 3-5 m, Playa del Hoyo Mazo, La Palma, Canary Islands (GNS WM17577, 1).

Fossils: **Atlantic Costa Rica:** **Late Pliocene:** Basal Moín Fm mudstone, Rte. 32, 3 km W of Puerto Limón, coll. J. A. Todd, February 1998 (BMNH Palaeontology Department, 1).

Distribution.—*Septa occidentalis* lives now throughout the Indo-West Pacific province from at least Mauritius to the Ryukyu Islands and the Philippines (GNS WM13668, Samar; Pl. 48, Fig. 12) and from Marmion Park, northern Western Australia (Wilson, 1993: 247) and Rottneest Island, southern Western Australia, around northern Australia to Sydney, New South Wales (holotype of *Septa? blacketi*; Pl. 48, Fig. 9), and eastward to Hawaii. It is moderately common in Hawaii, but rare in the rest of the region. Specimens in NMP are from Astov Island, Seychelles, Indian Ocean (NMP K.33, 1), and Port Blair, Andaman Islands (NMP F.5391, 3). In the western Atlantic, it is recorded from the Bahamas and southeastern Florida, USA, to Bahia, Brazil (Rios, 1994), and in the eastern Atlantic it is still recorded only from the Canary Islands

(Garcia-Talavera, 1983, 1987; Ardovini & Cossignani, 2004: 128, center right fig.). Matthews (1968) recorded specimens found commonly in the gut of the toadfish or "pacomon," *Amphychthus cryptocentrus*, caught off of Fortaleza, Ceará, Brazil. The one fossil specimen of which I am aware is from the Late Pliocene of Limón, Costa Rica.

Septa ogygia (Woodring, 1959)

Cymatium (*Septa*) *ogygium* Woodring, 1959: 204, pl. 27, figs 4, 6.

Remarks.—*Septa ogygia* is included here only to point out that Woodring (1959) referred it to the correct genus, and that this is the earliest known fossil record of *Septa*; the type locality is Late Oligocene in age. The holotype, the only known specimen, is much less inflated and has much lower spiral cords than in *S. landaui* n. sp., although it shares the unusual character of having only six main spiral cords and seven nodules inside the outer lip, rather than the seven exterior spiral cords and eight nodules inside the outer lip of most species of *Septa*. Although Woodring (1959) did not refer to the fine axial ridges, they clearly are visible in his illustrations (Woodring, 1959: pl. 27, figs 4, 6) and are very fine and closely spaced. In shape and the fineness of the axial ridges, this species is therefore most similar to *S. occidentalis*, differing in having six rather than seven main spiral cords. Although the specimen is an abraded, recrystallized calcite neomorph, it is important for indicating that *Septa* has been living in the tropical American region since at least Oligocene time.

Dimensions.—*Cymatium ogygium*, holotype, H 39.0, D 22.5 mm.

Types.—*Cymatium* (*Septa*) *ogygium*, holotype USNM 562573, from conglomerate lens in middle member of Caimito Fm (Late Oligocene), Pato Horqueto Island, Gatun Lake area, Panama; only known specimen.

Genus *TURRITRITON* Dall, 1904

Turritriton Dall, 1904: 134. Type species (by original designation): *Triton gibbosus* Broderip, 1833, Pliocene to Recent, eastern Pacific and western Atlantic.

Tritoniscus Dall, 1904: 134. Type species (by original designation): *Triton loraissii* Petit de la Saussaye, 1852 (= *Murex labiosus* Wood, 1828), Pliocene to Recent, Indo-West Pacific and eastern and western Atlantic.

Particymatium Iredale, 1936: 307. Type species (by original designation): *Triton strangei* A. Adams & Angas, 1864 (= *Murex labiosus* Wood, 1828).

Remarks.—The genus *Turritriton* was reserved by me (Beu, 1998b) for the smallest species of Cymatiinae (ca. 20-50 mm H), with three spiral threads on the crest of each spiral cord,

i.e., each cord is a fasciculate bundle of three narrow threads, the central the most elevated, with a short protoconch for the subfamily, and with an operculum with an anterior terminal nucleus. Beu & Knudsen (1987) reviewed the species and I reviewed (Beu, 1998b) the synonymy, type material, and range of *T. labiosus*. *Turritriton labiosus* has a highly distinctive radula (Bandel, 1984: text-fig. 158, pl. 10, fig. 2) with a central tooth that is higher than wide, with a tall, narrow, waisted basal plate quite different from that reported for any other species of Cymatiinae; Bandel (1984: 105) went as far as to state that "*Cymatium labiosum* does not belong to the genus *Cymatium*, but is close to the subgenus *Gyrineum* of the genus *Argobuccinum*." Although this central tooth shape seems likely to be a generic character, the radulae of the other living species assigned to *Turritriton* [*T. gibbosus* (Broderip, 1833), eastern Pacific and, rarely, western Atlantic, *T. fittkaui* Parth, 1991, Indo-West Pacific (doubtfully distinct from *T. tenuiliratus*), *T. kobelti* (von Maltzan, 1884), West Africa, and *T. tenuiliratus* (Lischke, 1873), Indo-West Pacific and Atlantic; see below] have not been described, so the taxonomic significance of the radula cannot be assessed.

At the time of writing the revisions by Beu & Knudsen (1987) and me (Beu, 1998b), I was not aware of any records of *Turritriton* species from the Cenozoic rocks of Europe or the Mediterranean area. I have since examined Hörnes & Auinger's (1879) type and illustrated material at NHMV, and found that the holotype (the only specimen known to Hörnes & Auinger) of *Triton* (*Simpulum*) *grundense* Hörnes & Auinger (1879: 177, pl. 21, figs 16a-c; NHMV 185/2/31) is a typical, small, fasciculate-ribbed species of *Turritriton*, closely resembling both *T. gibbosus* and *T. kobelti*. The drawing published by Hörnes & Auinger (1879) is not accurate, because it does not convey either the fasciculate nature of the spiral cords or the obvious, fine, regular axial costellae, and the peripheral keel is considerably narrower than the drawing indicates. The two main fasciculate cords around the periphery are closely spaced, as in most material of all the other species assigned here to *Turritriton*, and the other main spiral cords are more widely separated and have a single narrow thread in the center of each spiral interspace, as in all other *Turritriton* species. The specimen is from Grund, Vienna Basin (Badenian Stage, of the Central Paratethys stages; Middle Miocene; see Rögl, 1998: table 1). *Turritriton grundensis* has since been recorded correctly from the Korytnica clays (Middle Miocene, Badenian) in the Holy Cross Mountains, Poland, by Baluk (1995: 209, pl. 20, figs 3-4); the specimen in Baluk's figure (1995: pl. 20, fig. 3) closely resembles the holotype. This species therefore introduces a much more complex history to the record of *Turritriton* than seemed likely previously, indicating a possible ancestry for *T. gibbosus* and *T. kobelti* quite distinct from the origin from *T. domingensis* (Gabb, 1873) suggested

by Beu & Knudsen (1987). The relationships of *T. domingensis* are therefore now not as clear as they seemed previously, although the earliest records of *T. domingensis* (Baitoa Fm, Dominican Republic; Cantaure Fm, Paraguaná Peninsula, Venezuela) both are late Early Miocene in age, older than the Middle Miocene holotype of *T. grundensis*.

I recently modified (Beu, 2005: 100) the content of *Turritriton* further by transferring to it the species of the *T. tenuiliratus* (Lischke, 1873) species group. I pointed out that *T. tenuiliratus* (Indo-West Pacific), *T. pharcidus* (Dall, 1889) (Atlantic – concluded here to be a synonym of *T. tenuiliratus*), and *T. fittkau* Parth, 1991 (Indo-West Pacific), all have the diagnostic character of fasciculate spiral cords, and small (juvenile) specimens of *T. tenuiliratus* from Miocene and Pliocene rocks of Java resemble *T. domingensis* so closely that I initially identified them as *T. domingensis*. Atlantic material of this group is reassessed here. It seems likely now that there are three distinct species groups (lineages) within *Turritriton*. The more prominently spirally sculptured group of smaller species (*T. domingensis* and *T. labiosus*) apparently diverged before late Early Miocene time from the group of less strongly sculptured, very similar, slightly larger species (*T. grundensis*, *T. gibbosus*, and *T. kobelti*), whereas the taller and narrower *T. tenuiliratus* group (*T. tenuiliratus* and the doubtfully distinct form *T. fittkau*) seems to have been limited to the Indo-West Pacific province since Miocene time, before joining the Pleistocene-Holocene migrants into the Atlantic. The *T. domingensis-labiosus* group has a Caribbean and Tethyan distribution, whereas the *T. grundensis-gibbosus-kobelti* group is limited to the Paratethys in Europe, and today is limited to the eastern Pacific, western Atlantic, and West Africa, with a single record from the Pliocene(?) of Atlantic Colombia. The radula of species in the *T. tenuiliratus* species group needs to be checked to be sure that they have the tall, narrowly waisted central tooth characteristic of *T. labiosus*.

***Turritriton domingensis* (Gabb, 1873)**

Pl. 49, Figs 1-4, 8

Tritonium (*Ranularia*) *domingense* Gabb, 1873: 212.

Cymatium domingense. Pilsbry, 1922: 356, pl. 29, fig. 2.

Cymatium (*Turritriton*) *domingense*. Beu & Knudsen, 1987: 86, figs 31-32.

Remarks.—Beu & Knudsen (1987) pointed out that the Caribbean Miocene species *Turritriton domingensis* was the earliest species then referred to *Turritriton*, clearly having three spiral threads on each spiral cord (*i.e.*, fasciculate cords) crossed by many fine, close, regular axial costellae. It has a costal prominence similar to, but not quite as obvious as that of the strongly spirally sculptured Pliocene to living species, *T. labiosus*, and markedly more obvious than that of the weakly

spirally sculptured Pliocene to living species, *T. gibbosus*. It is taller and narrower than the living species *T. labiosus*, *T. gibbosus*, and *T. kobelti*, suggesting the possibility that it is an early species of the genus that had evolved from another group of tall *Turritriton* species not long before Miocene time. The other species newly assigned here, *T. tenuiliratus* and *T. fittkau*, are still taller and narrower than *T. domingensis*, and *T. tenuiliratus* has a fossil record from at least Late Miocene time onward in Indonesia (Beu, 2005: 102). The only species in Caribbean Miocene faunas with which *T. domingensis* might be confused is *Monoplex gurabonicus*, which is a similar size and shape to *T. domingensis* and has a similar aperture and similarly low, narrow varices. *Monoplex gurabonicus* is distinguished easily from *T. domingensis* by having a much more nearly smooth, finely reticulate shell surface, lacking the fasciculate spiral cord groups and many fine axial costellae of *T. domingensis*. Rather oddly, Maury (1917) did not mention *T. domingensis* in her monograph of the Dominican Republic fauna.

Two specimens collected from the Mataruca Member of Caujarao Fm (Late Miocene) at Carrizal, Falcón, Venezuela, by Jack and Win Gibson-Smith, are very similar to *Turritriton domingensis* in all characters, except that one develops a prominent median angulation on the last whorl, so that it begins to assume the shape of *T. gibbosus*. The other specimen in the sample (Pl. 49, Fig. 4) agrees well with Dominican Republic specimens, so this is assumed to be part of the variation of *T. domingensis*. A single small, elongate but immature specimen from the Gatun Fm (Late Miocene) of Colon, Panama, is narrower than any of the other species of the genus and also appears to be an immature specimen of *T. domingensis*.

Dimensions.—*Tritonium domingense*, lectotype: H (incomplete) 29.0, D 16.6 mm; paralectotype, ANSPIP 79195: H 25.0, D 16.4 mm; figured specimen, NMB H 18054, from NMB 16916, Cercado Fm, Río Mao, Dominican Republic: H 27.8, D 14.6 mm; figured specimen, NMB H 17962, from NMB 17530, Carrizal, Venezuela: H 25.9, D (incomplete) 15.8 mm.

Types.—*Tritonium domingense*, lectotype ANSPIP 3226 (Pl. 49, Fig. 1), designated by Pilsbry (1922: 356, pl. 29, fig. 2) by his action of identifying one of Gabb's (1873) specimens as "the type" (ICZN Article 74.6); with one paralectotype, ANSPIP 79195 (Pl. 49, Fig. 2), both from the Cibao Valley, Dominican Republic, Late Miocene or Early Pliocene, *ex* W. M. Gabb collection. The lectotype is now less complete than it was when Pilsbry (1922: pl. 29, fig. 2) illustrated it; it has lost the lower portion of the outer lip during the intervening years.

Other material examined.—**Fossils: Atlantic Panama: Late Miocene:** TU 962 (GNS WM18872, 1 small). **Dominican Republic: Late Early Miocene:** Baitoa Fm: TU 1363,

Boca de los Rios (GNS WM18874, 1); 1364, Boca de los Rios (GNS WM18873, 1). **Late Miocene:** Cercado Fm: NMB 15904 (1); 16983 (1); TU 1294 (GNS WM16937, 2); NMB 16982, Cercado Fm, Río Cana, collection of Bernard Landau (5); Gurabo Fm: NMB 16916 (1; illustrated, NMB H 18054; Pl. 49, Figs 3, 8); NMB 16928 (1); TU 1379 (GNS WM16945, 1). **Late Miocene/Early Pliocene:** USNM 112201, Dominican Republic, pres. W. M. Gabb (1). **Early Pliocene:** Gurabo Fm: TU 1215 (GNS WM16896, 1); 1227A = NMB 18582 (1). **Venezuela: Late Early Miocene:** NMB 17519 (1); Cantaure Fm, Casa Cantaure, Paraguaná Peninsula, collection of Bernard Landau (1). **Late Miocene:** NMB 17530, Carrizal (2; 1 illustrated, NMB H 17962; Pl. 49, Fig. 4). **Early Pliocene:** Cerro Negro Member, Cubagua Fm Cañon de las Calderas, Cubagua Island, collection of Bernard Landau (1).

Distribution.—*Turritriton domingensis* is apparently limited to late Early Miocene to Early Pliocene rocks of the Dominican Republic and northern Venezuela, apart from one record from the Gatun Fm (Late Miocene) of the Atlantic coast of Panama (a record possibly based on a small specimen of *T. gibbosus*). This distribution suggests that it formerly was much more widespread in the western Atlantic than these few records would seem to indicate.

***Turritriton gibbosus* (Broderip, 1833)**

Pl. 47, Figs 13-14; Pl. 49, Figs 6-7, 10-13

Triton gibbosus Broderip, 1833: 7; Reeve, 1844a: pl. 11, fig. 38a, pl. 14, figs 38b-c; Cooper, 1894: 32.

Triton (Gutturium) gibbosus. Tryon, 1880: 23, pl. 12, figs 101, 103.

Tritonium gibbosus. Arnold, 1903: 286.

Cymatium gibbosum. Dall, 1909b: 225; 1921: 141; Oldroyd, 1927: 243; Catarius, 1988: 10, figs 1-2; Finet, 1991: 270.

Cymatium adairense Dall, 1910: 33; 1925: 16, pl. 35, fig. 1.

Cabestana gibbosa. Grant & Gale, 1931: 733.

Cymatium (Turritriton) gibbosum. Emerson & Old, 1963b: 25; Keen, 1971: 507, fig. 961; Kilius, 1973: 99, fig. 73; Beu, 1985: 60 (in part); Beu & Knudsen, 1987: 80, figs 15-25; Garcia-Talavera, 1987: 253, pl. 2, fig. 4; Henning & Hemmen, 1993: 98, pl. 22, figs 6-7; López de la Fuente & Ramos, 2004: 86.

Eupleura sp. Aguilar & Fischer, 1986: 223, pl. 2, figs 15-16.

Cymatium (Turritriton) gibbosum gibbosum. Piech, 1995: 14; Kaiser, 1997: 32.

Remarks.—Beu & Knudsen (1987) reviewed the variation, types, and range of *Turritriton gibbosus*. This species reaches a considerably larger maximum size than *T. labiosus* (to 40 mm H, and a few specimens as large as 70 mm) and has much more subdued spiral cords, although the fasciculate effect (three riblets grouped together on each cord) is still clearly expressed. Most specimens have shouldered to strongly tabulate

or even narrowly keeled whorls, but Beu & Knudsen (1987) illustrated a large range of variation in height and shape, including a few specimens without strongly angled whorls. There is no doubt that the form *adairense* simply was based on a tall, strongly keeled specimen of *T. gibbosus*. All specimens have large, prominent, flat-faced, thin varices, similar to those of the Recent West African species *T. kobelti*, and much thinner and more prominent than those of either *T. domingensis* or *T. labiosus*. The protoconch [Beu & Knudsen (1987: figs 1-4) illustrated all those of the Recent species of this genus, although before *T. tenuiliratus* was referred here] is the tallest of the species in the genus, a little taller than that of *T. kobelti*. Specimens of *T. gibbosus* with a tall spire and strongly tabulate to narrowly keeled whorls make up a much lower proportion of the population than in *T. kobelti* and, along with the protoconch difference, this seems to indicate that *T. kobelti* is a distinct, if closely related species.

Dimensions.—LACM 66-28, Partida Bay, Baja California (Pl. 49, Figs 11, 13): H 48.5, D 32.4 mm; LACM 67-18, Punta Tormenta, E side Tiburon Island, Sonora, Mexico (Pl. 49, Fig. 12): H 54.5, D 29.4 mm; UCMP S-71, Point Canoas, Atlantic coast of Columbia (Pl. 49, Figs 6-7): H 24.6, D 17.1 mm; Puerto La Cruz, Venezuela, TFMC: H 38.6, D 23.7 mm; lectotype of *Triton gibbosus*: H 38.2, D 22.5 mm; paralectotypes: H 36.8, D 21.0 mm; H 34.6, D 19.4 mm; holotype of *Cymatium adairense* (Pl. 49, Fig. 10): H 32.7, D 18.3 mm.

Types.—*Triton gibbosus*, 3 syntypes BMNH 1968527/1-3, including the specimen illustrated by Reeve (1844a: pl. 14, figs 38b-c) and by Beu & Knudsen (1987: fig. 15) (these 3 specimens do not include the one illustrated by Reeve, 1844a: pl. 11, fig. 38a, which is not at BMNH); from "Panamam et ... Montem Christi"; the type locality is here designated as Panama Bay. *Cymatium adairense*, holotype USNM 214103 (Dall, 1925: 16, pl. 35, fig. 1; Pl. 49, Fig. 10), from U.S. Fish Commission sta. 3023, 18 m, Adair Bay, N Gulf of California, Mexico.

Other material examined.—**Recent: E Pacific:** 70 lots examined at LACM, 7 at GNS. Beu & Knudsen (1987) summarized the range as follows: anchorage N of Cedros Village pier, Cedros Island, W coast of Baja California peninsula, 20 m (LACM 67-64, 2) and Adair Bay, northernmost Gulf of California (LACM 23271, 3 specimens, and numerous other records) S to off of La Libertad, Ecuador, 2°12'30"S, in 6-10 m (LACM-AHF 9-33, 1), to Guayaquil, Ecuador (Dall, 1909b: 225) and to Negritos, N Peru (Olsson, 1924: 124). Dall (1921: 141) recorded specimens from as far north as San Diego and San Pedro, California State, USA, and a range as far north as Palos Verdes was confirmed by Catarius (1988: 10, figs 1-2). **W Atlantic:** Puerto La Cruz, Estado de Anzoátegui, Venezuela, dredged in shallow water, February

1976, F. Fernández (TFMC, 1 specimen).

Fossils: California: Pleistocene: Recorded from the “upper San Pedro Series” of San Pedro, Los Angeles Co, California, by Cooper (1894), Arnold (1903), and Grant & Gale (1931).

Pacific Costa Rica: Pleistocene: Recorded (as *Eupleura* sp.) from Montezuma Fm, Nicoya Peninsula, by Aguilar & Fischer (1986: pl. 2, figs 15-16). **Atlantic Panama: Middle Miocene:** lower Gatun Fm: NMB 18326 (1 small); bed 6 of Todd, 1999, quarry floor, Los Lomos Suites, Cativa, Colon (BMNH Palaeontology Department, GG22584, 1, elongate “*adairensis*” form; illustrated, Pl. 47, Figs 13-14). **Colombia:**

Pliocene: *Turritella* bed, Point Canoa, Departamento de Bolívar, Atlantic coast (UCMP S-71, 1 illustrated, Pl. 49, Figs 6-7; illustrated previously by Beu & Knudsen, 1987: figs 34-35); Beu & Knudsen (1987) identified this specimen as *Turritriton* cf. *kobelti*, and in many ways, it is more similar to the holotype of *T. grundensis* than to any other species.

A single small (juvenile) specimen from bed 1 of J. Todd, quarry floor, Los Lomos Suites, Cativa, Colon, Atlantic Panama (Lower Gatun Fm, Middle Miocene; BMNH Palaeontology Department, GG22585) might well be a further, aberrant specimen of *Turritriton gibbosus*, because it is identical in shape to the other Gatun Fm specimens, but it differs from all other *Turritriton* specimens that I have examined in having only two spiral threads on each primary spiral cord, rather than three. More material is needed to evaluate this form.

Distribution.—*Turritriton gibbosus* was recorded by Dall (1921) as ranging from “San Pedro and San Diego, California, to Panama,” although Dall himself (1909b: 225) earlier recorded it from as far south as Guayaquil, Ecuador. Catarius (1988: figs 1-2) reconfirmed the range of living specimens as far north as Palos Verdes, southern California State, USA, and Olsson (1924: 124) reported specimens collected at Lobitos, Mancora, and Negritos in Peru. Emerson & Old (1965) recorded the first specimens from the Galápagos Islands. This species therefore seems to have the most extensive range of any of the eastern Pacific Ranellidae. Garcia-Talavera (1987: 250, pl. 2, fig. 4) illustrated a Recent specimen from Puerto La Cruz, on the Caribbean coast of Venezuela, and I have examined this specimen, the first recorded from the western Atlantic. The protoconch is missing from the Venezuelan specimen, so it difficult to evaluate its possible relationship with the West African *T. kobelti*, but it has a very wide terminal varix and closely resembles eastern Pacific specimens. Fossils have been reported from Pleistocene rocks of the Los Angeles-San Diego area, California (Cooper, 1894; Arnold, 1903; Grant & Gale, 1931: 733), and from the Nicoya Peninsula, western Costa Rica. However, the most interesting for biogeography is the record from the Pliocene (or Pleistocene?) of the Atlantic coast of Colombia, because it implies that the CAI was still

open at the time that the *Turritella* shellbed at Point Canoa was deposited. It also helps to explain the (apparently rare) occurrence of *T. gibbosus* in the western Atlantic at present, as well as the close similarity between the living populations of *T. gibbosus*, *T. kobelti* in the eastern Atlantic, and *T. grundensis* in the Middle Miocene rocks of northern Europe. These are all similar enough that they are possibly conspecific.

Turritriton labiosus (Wood, 1828)

Pl. 49, Figs 5, 9; Pl. 53, Fig. 7

- Murex labiosus* Wood, 1828: 15, pl. 5, fig. 18.
Tritonium rutilum Menke, 1843: 25.
Triton labiosus. Reeve, 1844a: pl. 14, fig. 52; Küster & Kobelt, 1872: 203, pl. 57, figs 3-4; E. A. Smith, 1891: 413.
Triton lorisii Petit de la Saussaye, 1852b: 53, pl. 2, fig. 8.
Triton strangei A. Adams & Angas, 1864: 35; E. A. Smith, 1879: 816, pl. 4, figs 13-14; Iredale, 1915: 459.
Tritonium labiosum. Krebs, 1864: 23; Coomans, 1963: 64.
Triton loebbeckei Lischke, 1870: 23; 1871: 36, pl. 4, figs 13-14; Küster & Kobelt, 1876: 228, pl. 64, figs 2-3.
Triton (Guttarium) orientalis G. & H. Nevill, 1874: 29.
Triton (Cabestana?) labiosum. Mörch, 1877: 34; Coomans, 1963: 81.
Triton orientalis. Küster & Kobelt, 1878: 261, pl. 69, fig. 8.
Triton (Simpulum) labiosus. Tryon, 1880: 17, pl. 9, figs 64-68.
Lampusia labiosa. Dall, 1903b: 132.
Cymatium labiosum. Iredale, 1910: 73; Work, 1969: 661; Matthews & Kempf, 1970: 27; Cosel, 1982b: 54; Garcia-Talavera, 1983: 106; Bandel, 1984: 100, fig. 158, pl. 10, fig. 2; Drivas & Jay, 1988: 64, pl. 17, fig. 13; de Jong & Coomans, 1988: 68; Leal, 1991: 116; Vega-Luz & Vega-Luz, 1995: 7; Kubo in Kubo & Kurozumi, 1995: 75, fig. 5.
Triton (Cabestana) labiosus. Coulon, 1933: 127.
Cabestana labiosa. Powell, 1933: 159, pl. 26, fig. 9.
Particymatium strangei. Iredale, 1936: 307; Powell, 1952: 176.
Cymatium (Tritoniscus) labiosum. Abbott, 1954: 196, pl. 25, fig. m; Rios, 1975: 78, pl. 22, fig. 317; Nordsieck & Garcia-Talavera, 1979: 117, pl. 24, fig. 8; H. & E. Vokes, 1983: 23, pl. 11, fig. 7; Diaz & Puyana, 1994: 172, fig. 640.
Cymatium (Cabestana) labiosum. Clench & Turner, 1957: 201, pl. 111, figs 9-10, pl. 116, fig. 1; Warmke & Abbott, 1962: 100, pl. 18, fig. a; Humfrey, 1975: 121, pl. 13, fig. 8; Kiliyas, 1981: 703; Coelho *et al.*, 1981: 117, fig. 3; Kilburn, 1984: 2, pl. C, fig. b; Macsotay & Campos Villarreal, 2001: 66, pl. 12, fig. 4.
Tritoniscus labiosus. Habe, 1961: 45, pl. 22, fig. 4; 1964: 71, pl. 22, fig. 4; Habe & Kosuge, 1966a: 42, pl. 15, fig. 5; Kuroda *et al.*, 1971: 127, pl. 29, fig. 7; Okutani, 1986: 113, bottom right fig.
Turritriton labiosus. Beu, 1971: 109, figs 5-6; Hinton, 1978: 30, figs 10-10a; Powell, 1979: 164, pl. 33, fig. 3.
Cymatium (Ranularia) caribbaeum. van Regteren Altena, 1975: 36, pl. 2, fig. 5 (in part).
Cymatium (Tritoniscus) labiosus (sic). Abbott, 1974: 164, fig. 1763.
Cymatium (Turritriton) labiosum. Kay, 1979: 223, fig. 79F; Beu, 1985: 60, fig. 23; 1998b: 135, figs 33c, 42m-o; 1999: 42, figs 80-83 (with further synonymy); 2005: 101, figs 267-268;

Springsteen & Leobrera, 1986: 114, pl. 31, fig. 11; Garcia-Talavera, 1987: 253, pl. 2, fig. 7; Beu & Knudsen, 1987: 74, figs 3, 6-14; Lai, 1989: 124, figs 47-49; Henning & Hemmen, 1993: 102, pl. 22, figs 4-5; Wilson, 1993: 248, pl. 42, figs 4a-b; Piech, 1995: 14; Bosch *et al.*, 1995: 100, fig. 363; Hertz & Kaiser, 1998: 73, figs 1-2; Okutani, 2000: 289, pl. 143, fig. 26 (upper fig only); Redfern, 2001: 63, pl. 31, figs 264A-B; Zhang & Ma, 2004: 156, text-fig. 97; Beu & Segers in Poppe, 2008: 656, pl. 273, figs 1-3, 6-8.

Cymatium (Septa) labiosum. Rios, 1985: 76, pl. 27, fig. 331; 1994: 89, pl. 29, fig. 347.

Remarks.—The long synonymy of *Turritriton labiosus*, abbreviated above from my earlier version (Beu, 1998b), testifies to both the great range of variation and the great geographical range of this species. It is easily recognized by being the smallest *Turritriton* species (*ca.* 15–40 mm high, but few specimens are more than 25 mm), the short, wide shape of many specimens, the prominent spiral cords with three prominent lirae on the crest of each, the fine, regular, close, axial costellae that form a reticulate surface where they cross the spiral lirae, the short, stout protoconch with an olive green to greenish brown periostracum, and the short, stout, open anterior canal. When varices are present, they are thick and very prominent, but on most specimens, they are randomly disposed and many specimens have only the terminal varix present; some specimens in all large samples have prominent varices at each 240° all down the shell. The color is just as variable, from white to almost black through all shades of yellow, greenish yellow, orange, brown, red, and gray, and many specimens have narrow spiral banding of contrasting colors. The aperture is relatively large, and white in all specimens, with a row of prominent nodules inside the outer lip. Most but by no means all specimens have a weakly to very strongly developed peripheral angulation, and those with a very prominent shoulder angle are those with the most regular varices and, in many cases, a spirally banded color pattern. A few specimens in most populations are large, relatively tall-spined, with a long anterior canal, and with regularly placed varices, and in many cases with a uniform cream or pale brown color (the *loebbekei* form), but these intergrade with all other forms.

Dimensions.—*Triton strangei*, holotype, and *Murex labiosus*, neotype: H 36.1, D 25.4 mm; *T. loebbekei*, holotype: H 37.6, D 23.6 mm; GNS WM 15559, Black Island, Queensland, Australia: H 40.4, D 24.4 mm; GNS WM18703, trawled off of Southport, Queensland: H 41.5, D 29.2 mm; figured specimen, NMB H 17963, from NMB 18579, Limón, Costa Rica: H 17.5, D 11.6 mm.

Types.—*Triton strangei*, holotype BMNH 1870.10.26.99, from Moreton Bay, Queensland; this specimen was designated the neotype of *Murex labiosus* and of *Tritonium rutilum* by me (Beu, 1998b). The remains of Menke's collection

is now at SME, but does not contain any material identified as *Tritonium rutilum*. *Triton loroisii*, 5 syntypes at MNHN, from Guadaloupe, West Indies. *Triton loebbekei*, holotype at Löbbecke Museum und Aquazoo, Düsseldorf (Beu, 1998b: fig. 32c). *Triton orientalis*, types at the Indian Museum, Calcutta; not seen; from the Andaman Islands. Because of the neotype designation by me (Beu, 1998b), the type locality of *Turritriton labiosus* is Moreton Bay, Queensland.

Other material examined.—**Recent: W Atlantic:** 32 lots examined at GNS, LACM, NMB, RMNH, SME, and ZMA, from Bahamas (Browns Point, New Providence, LACM S-1368, 1), Florida, Puerto Rico, E Panama, Aruba, Curaçao, Antillean islands (St. Martin, St. Thomas, Guadeloupe – GNS, 3 lots), Colombia, Venezuela, and Guiana. As with most other common species, many other lots have been examined at MCZ, AMNH, ANSP, and USNM, but not listed. **E Atlantic: Cape Verde Islands:** beach, Baía Algodoeiro, Ilha Sal (1; R. von Cosel's material at MNHN). **Canary Islands:** La Palma (TFMC 1471, 1); Dázena comercial, Santa Cruz de Tenerife (TFMC 1470, 1 small).

Fossils: Jamaica: Late Pliocene: Bowden: USGS 2580 [USNM 135296, 1; the specimen recorded by Woodring (1928: 298) as "*Cymatium (Gutturnium)* species"]. **Atlantic Costa Rica: Late Pliocene-Early Pleistocene:** Moín: NMB 18274 (1); TU 1240 = NMB 19008 (2; 1 illustrated, NMB H 17963; Pl. 49, Figs 5, 9); locality same as last, collection of Bernard Landau (4). **Ecuador: Pleistocene:** NMB 19149, shellbed, road cuts on Manta-Montecristi road 5 km from Manta, Manabí Province (1 incomplete, illustrated, NMB H 18306; Pl. 53, Fig. 7).

Distribution.—*Turritriton labiosus* is probably the most widespread of all shallow-water benthic gastropods. It ranges from Jeffreys Bay, eastern Cape Province, South Africa (NMP A.3597, 1), East Africa, and the Red Sea eastward throughout the Indo-West Pacific province to Hawaii, and to the Marquesas Islands in eastern Polynesia (material at MNHN), and from central Honshu, Japan, southward to Albany, southern Western Australia (Wilson, 1993: 248) and to Auckland, northern New Zealand (Beu & Knudsen, 1987; Beu, 1998b). In the eastern Pacific, it has been reported recently from three localities along the Pacific coast of Mexico and Panama (Sayulita, Nayarit, western Mexico; Taboga Island, Panama; Pacific coast of Panama; Hertz & Kaiser, 1998), although of course, it is always difficult to be certain that such records from within the range of *T. gibbosus* are not based on short, weakly sculptured specimens of that very similar species. In the western Atlantic, *T. labiosus* ranges from Cape Hatteras, North Carolina (Porter, 1970), USA, southward throughout the Caribbean and northern South America to Bahia, Brazil, and Fernando de Noronha Island (Rios, 1994). Matthews (1968) recorded specimens found uncommonly in the gut of

the toadfish or “pacomon,” *Amphychthus cryptocentrus*, caught off of Fortaleza, Ceará, Brazil. In the eastern Atlantic, it is recorded from Madeira and the Canary and Cape Verde islands (Nordsieck & Garcia-Talavera, 1979; Cosel, 1982b; Garcia-Talavera, 1983, 1987). Fossils are recorded from the Pliocene of Java, and from the Late Pliocene of Jamaica, the Late Pliocene-Early Pleistocene of the Atlantic coast of Costa Rica, and the Pleistocene of the Pacific coast of Ecuador.

***Turritriton tenuiliratus* (Lischke, 1873)**

Pl. 43, Figs 1, 8

Triton tenuiliratus Lischke, 1873: 20; 1874: 30, pl. 2, figs 18-19; Küster & Kobelt, 1876: 230, pl. 64, figs 4-5; Yokoyama, 1922: 67, pl. 3, fig. 8; 1926: 341, pl. 41, fig. 14.

Triton (Gutturium) tenuiliratus. Kobelt, 1878a: 361; Tryon, 1880: 22, pl. 42, fig. 105.

Lampusia? pharcida Dall, 1889: 227, pl. 36, fig. 2; 1903b: 132.

Cymatium (Lampusia) pileare. Beets, 1941: 91 (not *Murex pilearis* Linnaeus, 1758; Beu, 2005: 102).

Cymatium (Cabestana) tenuiliratus. M. Smith, 1948: 9, pl. 4, fig. 2.

Cymatium tenuiliratum. Kuroda & Habe, 1952: 51; Vega-Luz & Vega-Luz, 1995: 7; Ardovini & Cossignani, 2004: 129, upper central fig.

Cymatium (Septa) tenuiliratum. Hatai & Nisiyama, 1952: 256; Masuda & Noda, 1976: 204; Springsteen & Leobrera, 1986: 113, pl. 31, fig. 1.

Cymatium (Septa) krebssii. Clench & Turner, 1957: 220, pl. 124, fig. 3 only (in part not *Triton krebssii* Mörch, 1877).

Turritriton tenuiliratum. Habe, 1961: 45, pl. 22, fig. 7; 1964: 72, pl. 22, fig. 8.

Reticutriton tenuiliratus. Kuroda *et al.*, 1971: 127, pl. 29, fig. 1.

Cymatium (Reticutriton) tenuiliratum. Oyama, 1973: 36, pl. 9, fig. 7; Lai, 1989: 122, fig. 29.

Cymatium (Cabestana) tenuiliratum. Nordsieck & Garcia-Talavera, 1979: 120, pl. 25, fig. 14.

Cymatium pharcidum. Garcia-Talavera, 1983: 115, pl. 4, fig. 4; Finlay & Vink, 1982: 123; Garcia-Talavera, 1987: 251, pl. 2, fig. 2; Petuch, 1987: 20, pl. 4, figs 4-5; Paulmier, 1994: 9, fig. 21; Gofas & Beu, 2002: 98, fig. 5C.

Cymatium (Turritriton) tenuiliratum. Beu, 1985: 60, fig. 22; 2005: 102, figs 222-223; Henning & Hemmen, 1993: 104, pl. 22, figs 1-2.

Murex sp. Noda, 1988: pl. 7, figs 3a-b.

Cymatium (Turritriton) pharcidum. Piech, 1995: 15.

Cymatium (Monoplex) tenuiliratum. Beu, 1998b: 101, figs 23g, 33a; 1999: 33, figs 65-67; Okutani, 2000: 287, pl. 142, fig. 15; Higo *et al.*, 2001: 158; Zhang & Ma, 2004: 145, pl. 3, fig. 9.

Cymatium (Monoplex) pharcidum. Beu, 1998b: 102.

Remarks.—Until recently, I have attempted to maintain an Atlantic species, *Turritriton pharcidus*, separate from the similar Indo-West Pacific species, *T. tenuiliratus*. I distinguished (Beu 1998b) *T. pharcidus* from *T. tenuiliratus* by a number of subtle but apparently consistent characters: all Atlantic speci-

mens that I had seen until recently are small (*ca.* 25–40 mm H, compared with up to at least 65 mm for Pacific material), and are relatively short and wide; the tan color spots on the spiral costae of the otherwise uniform cream shell are larger and more obvious than in *T. tenuiliratus*, and the fine axial grooves are fewer in number and further apart than in *T. tenuiliratus*, so that the rectangular lozenges that they cut into the secondary spiral sculpture are larger and fewer than in *T. tenuiliratus* (*ca.* 20 per intervartical interval, rather than *ca.* 30–33 per interval in *T. tenuiliratus*). However, examination of two further Canary Islands specimens and a range of Philippines material at TFMFC, and 11 South African lots examined at NMP (ranging from northern Zululand to off of the Transkei coast), demonstrate that Atlantic specimens reach at least 50 mm H, and all variants intergrade and can be found in any one area. Some Philippines specimens closely resemble Canary Islands ones, and several from the Philippines and South Africa are very coarsely sculptured and closely resemble typical Japanese shallow-water specimens. I am no longer in any doubt that this is one variable Indo-West Pacific and Atlantic species.

Turritriton tenuiliratus has been a little-known species in the Atlantic until recent years, when the material taken in fish traps off of Castle Roads, Bermuda, by Jack Lightbourn (see Finlay & Vink, 1982: 133, as *Cymatium pharcidum*) showed that the Atlantic form named *Lampusia pharcida* by Dall (1889) is a synonym of the Indo-West Pacific *T. tenuiliratus*. Within the Atlantic fauna, *T. tenuiliratus* is easily recognized by its distinctively tall, narrow shape, its large, tall and narrow protoconch, its large, prominent varices, including a particularly wide, flat-faced terminal varix, its long, straight anterior canal, and its fine spiral sculpture, arranged in the usual *Turritriton* fasciculate pattern. The holotype of *Lampusia pharcida* was illustrated well by Clench & Turner (1957: pl. 124, fig. 3) who, because they had seen no other material, assumed it was a synonym of *Monoplex krebssii*.

Dimensions.—*Lampusia pharcida*, holotype (Pl. 43, Fig. 1): H 23.6, D 11.5 mm; DMNH 96981, off S coast of Bermuda, 220 m: H 29.5, D 14.5 mm, H 30.4, D 14.7 mm, H 30.1, D 15.2 mm; GNS WM 12447, same locality as last: H 27.5, D 13.4 mm; TFMFC 368, Santa Cruz de Tenerife: H 49.2, D 20.9 (specimen with seven prominent spiral cords around last whorl, at and below periphery; but the seventh cord seems to be aberrant, due to injury); H 50.1, D 23.5 mm (normal *T. tenuiliratus* form, as in the Philippines); TFMFC 360, Panglao, Bohol: H 64.1, D 29.6 mm; TFMFC 359, Mactan Island, Bohol: H 58.1, D 22.6 mm.

Types.—*Triton tenuiliratus*, holotype (Beu, 1998b: 101, fig. 33a) at Löbbecke Museum und Aquazoo, Düsseldorf, from “Süd-Japan.” *Lampusia? pharcida*, holotype USNM 94887 (Pl. 43, Fig. 1), from Blake sta. 293, 150 m, off of Barbados.

Other material examined.—**Recent:** **W Atlantic:** 220 m, 4

km off of Castle Roads, S shore of Bermuda, coll. A. Guest and J. R. H. Lightbourn (DMNH 96981, 1); DMNH, same data (5); same data, pres. R. Jensen, DMNH (GNS WM12447, 1); *Luymes* Guiana Shelf Expedition sta. 1, off of Suriname, 130-140 m, 7°10'W, 53°35'W, 24 August 1970 (RMNH, 7, some collected alive; 1 illustrated, Pl. 43, Fig. 8). **E Atlantic: Lusitanian banks**, Seamount 1 cruise, sta. DW70, Seine Bank, 33°42.9'N, 14°23.9'W, 180-190 m, 9 October 1987 (MNHN, 1 empty shell; Gofas & Beu, 2002: fig. 5C). **Canary Islands**: TFM 369, La Palma (1, wide *pharcidum* shape); TFM 368, Santa Cruz, 100-200 m (2 large, resemble rather coarsely sculptured Philippines specimens, dimensions above).

Other material is reported from 85 m, off of Palm Beach, Florida (Petuch, 1987: pl. 4, figs 4-5), from 104-130 m, off of the coast of Suriname (Finlay & Vink, 1982; possibly based on the *Luymes* sta. 1 material listed above), from 125 m, off Martinique, Antilles (Paulmier, 1994: 9, fig. 21), and from La Palma, Canary Islands (Nordsieck & Garcia-Talavera, 1979: 120; Garcia-Talavera, 1983: 115; 1987: 251). Ardovini & Cossignani (2004: 129, upper central fig.) also illustrated a specimen from the Canary Islands.

Distribution.—The records listed above suggest that *Turritriton tenuiliratus* is an uncommon but widespread species in the living fauna from Bermuda and southern Florida, USA, throughout the Caribbean islands, to at least the northern coast of South America and perhaps to northern Brazil, and will be recognized more widely in the future. Gofas & Beu (2002) listed the first record from the central Atlantic banks, Nordsieck & Garcia-Talavera (1979) and Ardovini & Cossignani (2004: 129, upper central fig.) recorded it from the Canary Islands in the eastern Atlantic, and it probably occurs rarely at several of the other Atlantic banks and islands. Occurrences seem to be unusually “patchy,” and it is possible that all Atlantic records result from occasional spat-falls of larvae from the Indian Ocean. In the Indo-West Pacific, it occurs widely from Japan to New Caledonia (Beu, 1998b) and in the Indian Ocean as far south as the Transkei coast, South Africa (11 lots examined at NMP), although I am not aware of records from east of the main western Pacific archipelagos. Fossils are not reported from the study area, but are reported widely from Pliocene and Pleistocene rocks in Japan, and were recorded by me (Beu, 2005: 102, figs 222-223) from Miocene rocks of Indonesia.

Genus **SASSIA** Bellardi, 1873

Sassia Bellardi, 1873: 219. Type species (by subsequent designation, Cossmann, 1903: 93): *Triton apenninicum* Sassi, 1827, Miocene and Pliocene, Europe.

Austrotriton Cossmann, 1903: 98. Type species (by original designation): *Triton radialis* Tate, 1888, Miocene, Australia.

Cymatona Iredale, 1929b: 177. Type species (by original designation, Iredale, 1929b: 189): *Nassaria kampyla* Watson, 1885, Pliocene to Recent, circum-Southern Ocean.

Negyrina Iredale, 1929b: 177. Type species (by original designation): *Triton subdistortus* Lamarck, 1822, Pleistocene and Recent, southeastern Australia (September 1929).

Charoniella Thiele, 1929: 283. Type species (by original designation): *Triton subdistortus* Lamarck, 1822 (October 1929).

Charoniella Powell & Bartrum, 1929: 426. Type species (by original designation): *Charonia* (*Charoniella*) *arthritica* Powell & Bartrum, 1929, Early Miocene, New Zealand (November 1929; junior homonym of *Charoniella* Thiele, October 1929).

Austrosassia Finlay, 1931: 7. Type species (by original designation): *Septa parkinsonia* Perry, 1811, Pleistocene and Recent, southwestern Pacific.

Phanozesta Iredale, 1936: 309. Type species (by original designation, Iredale, 1936: 336): *Phanozesta remensa* Iredale, 1936, Recent, southwestern Pacific.

Proxicharonia Powell, 1938: 373. Replacement name for *Charoniella* Powell & Bartrum, 1929, preoccupied.

Remarks.—*Sassia* is much the most speciose genus in the family Ranellidae (more than 120 species have been named from the Cenozoic rocks of Europe alone), and encompasses a huge range of size and sculpture, as well as a time range from Campanian (Late Cretaceous) to Recent (Beu, 1988b). Most of the Neogene and all the living species are rather modest in size and are very generalized, elongate-fusiform, pale or uniformly colored species with simple sculpture of rows of low nodules, and most living species inhabit moderately deep to quite deep water (100-600+ m). In other words, they are the stem-group of the Ranellidae, and most have survived in environments where other similar, related taxa do not out-compete them, although *S. parkinsonia* (Perry, 1811) (= *S. lindneri* Parth, 1992: 48, first 4 unnumbered figs on p. 47; based on juvenile specimens) lives in a range of environments as shallow as intertidal rocky shores in southeastern Australia and northern New Zealand, and most of the Recent southern Australian species of the closely related genus *Cymatiella* can live as shallowly as the intertidal zone. Several living species are closely related to the type species of *Sassia*, *S. apenninica*, which occurs in the Miocene and Pliocene of Europe, and these have a large, dome-shaped protoconch with prominent, widely spaced, reticulate sculpture, *i.e.*, they have a typical, characteristic tonnoidean planktotrophic larva (Warén & Bouchet, 1990). The other Neogene and living species have one of three types of protoconchs. Two of these are essentially the same but differ in size. One species, *S. kampyla* (Watson, 1885), has a nearly smooth, turbiniform protoconch that is even larger than that of the *S. apenninica* group, and it is concluded below that it formerly lived (and possibly still lives) around the entire Southern Ocean. The other species have much smaller, turbiniform, smooth or at most weakly

sculptured protoconchs, and have more limited distributions than the species with large, smooth or reticulate protoconchs, *i.e.*, apparently they lack a planktotrophic larval stage; some apparently have a short-lived veliger stage. The third protoconch type is that of the southern Australian species formerly referred to *Sassia* (*Austrotriton*), now seen to probably be at least two distinct groups of *Sassia* species that have lost planktotrophy independently (Beu & Darragh, in prep.). They have direct, intracapsular development (B. J. Smith *et al.*, 1989), and consequently have either an irregular, partly calcified protoconch, or no calcified protoconch at all remaining on the teleoconch.

Two fossil *Sassia* species are recorded here from the Caribbean region for the first time. They both seem to be related to *S. apenninica* rather than to the one living species in the region, *S. lewisi* Harasewych & Petuch, 1980. Several other species reviewed here are present in the Neogene rocks of South America and belong in a group of large species that were widespread in the southern hemisphere during Paleogene to early Neogene time. The number of species of *Sassia* is so great that it is helpful to assess them within groups of similar, apparently phylogenetically related species ("stocks"), in cases where the groups seem obvious, rather than simply reviewing them in alphabetical order. Some *Sassia* species therefore are discussed here within species groups; one species with no obvious close relatives is treated at the end.

Sassia apenninica species group

Species of the *Sassia apenninica* group are the "typical" species of *Sassia*, in the literal sense of being closely related phylogenetically to the type species, *S. apenninica*. Taxa of this species group in the southwestern Pacific were studied by me (Beu, 1998b) and it was concluded that only one, highly variable species is present, *S. remensa* (Iredale, 1936). This is a small (to *ca.* 45 mm high), narrowly fusiform species, varying from strongly inflated, white, and with sculpture of low spiral cords only, through to weakly inflated, tan, and with sculpture of rows of small, narrowly rounded nodules over most of the shell surface. It has an identical protoconch to that of *S. apenninica*, dome-shaped, and entirely covered with fine, widely spaced, cancellate sculpture, and some of the more coarsely sculptured specimens are very similar indeed to *S. apenninica*. *Sassia remensa* and the other living members of this group [*S. semitorta* Kuroda & Habe in Habe, 1961 (Beu & Segers in Poppe, 2008: 656, pl. 273, figs 4-5); *S. nassariformis* G. B. Sowerby III, 1902; *S. melpangi* Harasewych & Beu, 2007, central western Pacific (illustrated by Beu, 1998b: fig. 411); and at least one still unnamed tropical Pacific species] seem likely to comprise a monophyletic group descended from *S. apenninica*.

Sassia cf. *apenninica* (Sassi, 1827)

Pl. 50, Fig. 1

cf. *Triton apenninicum* Sassi, 1827: 480.

cf. *Sassia apenninica*. Bellardi, 1873: 219, pl. 14, fig. 7; Landau *et al.*, 2004: 62, text-figs 3:1a- b, pl. 5, figs 1a-c, pl. 10, figs 3a- b; Chirli, 2007: 99, pl. 36, figs 1-11 (with long synonymy).

cf. *Charonia* (*Sassia*) *apenninica*. Cavallo & Repetto, 1992: 76, fig. 146.

Remarks.—A single, very incomplete specimen, little more than a small spire, from the Belmont Fm of Carriacou Island, closely resembles European Miocene and Pliocene specimens of *Sassia apenninica* in size, shape, evenly nodulose sculpture, protoconch size and shape, and finely reticulate teleoconch microsculpture. It has four rows of small, rounded nodules at the sculptural intersections on spire whorls, including two on the sutural ramp. The protoconch is similar in size and shape to that of *S. apenninica*, but lacks cancellate sculpture. However, in view of the fact that (like all the Grand Bay, Kendace, and Belmont Formations material) the specimen is preserved as a calcite neomorph, the preservation is remarkably detailed, but it would not be surprising if finely cancellate protoconch sculpture had been lost. Donovan *et al.* (2003) interpreted the Belmont Fm as deposited within a deep-water turbiditic basin, so it is not surprising that its aragonitic fossils have been altered to calcite. The protoconch termination is slightly narrower in diameter than the initial teleoconch whorl, suggesting that a periostracal layer has been lost from the protoconch. Such a loss would explain the lack of cancellate sculpture, but the protoconch surface appears to have been calcareous, rather than conchiolin, on Italian Pliocene specimens of *S. apenninica* that I have examined, and they retain the cancellate sculpture. The taxon in the Belmont Fm seems likely to be an unnamed species with a teleoconch resembling that of *S. apenninica* but with a smooth protoconch, but further material is needed for accurate comparison.

Bellardi (1873: pl. 14, fig. 7) illustrated only his Varieta B of *Sassia apenninica*, "testa crassior," with heavy varices and strongly inflated whorls. A better, more accessible modern figure of *S. apenninica* is that by Cavallo & Repetto (1992: 76, fig. 146), but even this shows a short, robust specimen; other good illustrations were provided by Landau *et al.* (2004: 62, pl. 5, figs 1a-c, pl. 10, figs 3a-b). The illustrations of *Triton granosum* (Bellardi, 1873: 221, pl. 14, figs 8a-b) particularly resemble the present specimen, but this also almost certainly is a large, finely sculptured variant of *S. apenninica*; it particularly resembles large Philippine Islands Recent specimens of *S. semitorta* (Kuroda & Habe in Habe, 1961). Vinassa de Regny (1902) illustrated the fullest range of variation of Italian fossil specimens of *S. apenninica*.

Dimensions.—Figured specimen, NMB H 18042, Carria-

cou: H (very incomplete) 25.6, D 16.6 mm.

Material examined.—**Fossil: Carriacou:** Grenadine Islands: **Middle Miocene:** NMB 13759, Kendace Siltstone Member, Belmont Fm, Kendace Point (1 frag, NMB H 18042; Pl. 50, Fig. 1).

Sassia warreni n. sp.

Pl. 50, Figs 2, 5, 8, 11-13; Pl. 63, Figs 9-10

Description.—Shell small to moderate-sized for genus (15-37 mm H), relatively short and wide for genus, with evenly convex whorls. Varices low, narrowly rounded, with narrow hollows along sides against remainder of shell surface, hollows weakly buttressed by spiral cords; varices regularly positioned each 240° down entire teleoconch. Teleoconch sculpture of many similar low, narrow, flat-topped to weakly bifid spiral cords, each interspace approximately twice as wide as one cord, with 1-3 low, narrow spiral threads in each interspace; four cords on spire whorls and eight on last whorl, passing onto terminal varix, with several more, narrower ones on canal, crossed by slightly more prominent, regular, narrow, round-crested axial costae, 15 on penultimate intervariceal interval and 17 on last one of holotype, forming very small, evenly spaced, rounded nodules at sculptural intersections, so that entire teleoconch surface bears small nodules, decreasing in size regularly over base and canal. Aperture oval, with slightly flared, narrow lips; inner lip slightly expanded over previous whorl in parietal area; interior of outer lip bearing seven small, narrowly rounded nodules; parietal area of inner lip bearing one elongate ridge on spiral cord of previous whorl, remainder wrinkled in conformity with underlying sculpture; lower part of inner lip with 5-6 low, widely spaced transverse ridges, one at base of columella slightly more elevated than others. Protoconch large for teleoconch but markedly smaller than in *Sassia apenninica*, tall and narrowly dome-shaped, height nearly twice diameter, of just under four weakly inflated whorls; protoconch I of one-half whorl bearing fine, irregularly reticulate microsculpture; protoconch II bearing cancellate, fine, widely spaced axial and spiral ridges.

Dimensions.—Holotype: H 15.2, D 8.9 mm; paratype, NMB H 17966, from NMB 15822, Dominican Republic: H 18.8, D (incomplete) 9.3 mm; largest paratype, TU 1215, collection of Bernard Landau: H 37.4, D 16.0 mm; paratype, TU 1215, collection of Bernard Landau: H 26.7, D 13.5 mm.

Types.—Holotype NMB H 17964 (Pl. 50, Figs 2, 5, 8, 11-13), from NMB 18581 (= TU 1215), Gurabo Fm (Early Pliocene), ca. 400 m above base, Maury's zone D, bluffs for ca. 1 km above Los Quemados, Río Gurabo, Dominican Republic, collected by Emily and Harold Vokes; with 1 paratype in same sample, NMB H 17965; 1 paratype NMB H

17966, from NMB 15822, base of Mao Fm (Early Pliocene), northern Río Gurabo, Dominican Republic, collected by P. Jung & A. Eva, 15 January 1978; 3 paratypes from TU 1215, type locality, Río Gurabo, collection of Bernard Landau (1 illustrated, Pl. 63, Figs 9-10); 2 paratypes GNS WM17698, from TU 1215, coll. and pres. Bernard Landau.

Remarks.—*Sassia warreni* n. sp. is similar in many characters to *S. apenninica*, but clearly is distinguished by its evenly inflated whorls rather than the obviously biangled whorls of most Italian Pliocene material of *S. apenninica*, by its finer and much more widely and evenly distributed nodulose teleoconch sculpture, and by its considerably smaller but relatively taller and narrower protoconch. The apertural characters, the protoconch sculpture, and the general appearance of *S. warreni* n. sp. are very similar to those of *S. apenninica*. The new species appears very similar at first glance to the small paratypes of *Septa landaui* n. sp., and was only separated tentatively before the protoconchs were examined. The five small to large paratypes from TU 1215 were collected by Bernard Landau long after the rest of the manuscript was completed, and are most useful for demonstrating that this species reaches a significantly larger size than is indicated by the original material. The largest paratype (H 37.4, D 16.0 mm; Pl. 63, Figs 9-10) also is significantly more elongate than the other specimens.

Distribution.—*Sassia warreni* n. sp. is recorded only from Early Pliocene rocks of the northern Dominican Republic.

Etymology.—The new species is named in memory of Warren Blow, thorough and committed curator of Cenozoic fossil collections at the USNM for many years, who died suddenly just as the present work was being completed. Warren helped me enormously with access to USNM collections while I was in Washington, and provided all of the information incorporated here on USGS collections. He was also very helpful with unpublished research, with MNHN, on the Kere River fauna in Vanuatu.

Sassia lewisi Harasewych & Petuch, 1980

Pl. 50, Fig. 9

Sassia lewisi Harasewych & Petuch, 1980: 121, figs 1-2; Abbott & Dance, 1982: 123; Gofas & Beu, 2002: 99, figs 6A-C.

Sassia (Sassia) lewisi. Beu, 1985: 61; Parth, 1992: 49; Henning & Hemmen, 1993: 116, pl. 24, fig. 1; Piech, 1995: 18.

Remarks.—*Sassia lewisi* is a small to moderate-sized species (to 38 mm H) with a tall, narrow shape, a tall spire and a moderately long, nearly straight siphonal canal, low, rounded varices at regular intervals of 240°, a subcircular aperture with lightly flared lips, six nodules inside the outer lip (with a weak seventh in some specimens), a parietal ridge and two or three small transverse ridges on the base of the columella, and can-

cellate sculpture of many fine spiral cords and axial costae, with small nodules at their intersections. In all of these characters, it is similar to the species of the *S. apenninica* species group. It differs from the *S. apenninica* group in its much smaller, turbiniform, smooth protoconch, in having a prominent, elevated white nodule forming a shoulder at the top of each varix, so that the outline of the upper (posterior) part of each varix is unusually horizontal and straight, and in having a wider and more clearly demarcated posterior excurrent notch inside the outer lip, interior to the prominent nodule at the top of the terminal varix. I have not observed this curiously shaped varix and wide posterior notch on any other ranellid. The largest of the eastern Atlantic specimens reported here (H 38 mm; from Seamount 2 cruise, sta. CP144, Meteor Bank; at MNHN) has a much less obviously protruding shoulder and a narrower posterior apertural notch than in the smaller specimens, but agrees in all other characters with *S. lewisi*; it indicates a closer relationship with *S. apenninica* than the small (probably all immature) specimens seemed to.

Garvie (1996: 71, pl. 15, figs 11-13) described and illustrated, as "*Distorsio (Personella) nucleoides*, a *Sassia* species from the Reklaw Fm (Lower Claibornian, Early Eocene) of Texas with the typical large, cancellate-sculptured protoconch of the *S. apenninica* group. This species has the varix projecting a little at the posterior end to produce a slight shoulder, and although it does not protrude quite as strongly as in small specimens of *S. lewisi*, *S. nucleoides* possibly is related to *S. lewisi*, and *S. nucleoides* is useful in demonstrating that *Sassia* species of this type have lived in the Americas since at least Ypresian (Early Eocene) time. I showed (Beu, 1988b) that *Personella septemdentata* (Gabb, 1860), type species of *Personella* Conrad, 1865, is a weakly distorted species of the Ranellidae, and ranked *Personella* as a subgenus of *Sassia*, replacing its usage in the Personidae with the new genus *Personopsis*. Although *S. nucleoides* is weakly distorted, it is no more so than many other *Sassia* species, and it appears to belong in *Sassia sensu stricto* rather than in *S. (Personella)*. Nevertheless, the phylogenetic position of this group of species deserves more study, and it is possible that both *S. nucleoides* and *S. lewisi* are weakly distorted species of *Sassia (Personella)*.

Dimensions.—Largest seen, Seamount 2 cruise, sta. CP144, Meteor Bank, eastern Atlantic, 335 m, MNHN: H 38.0, D 18.8 mm; sta. DW209, Banc Irving, 460 m, in MNHN: H 26.0, D 14.2 mm.

Types.—*Sassia lewisi*, holotype ANSP 352235, dredged in 60-80 m, N of Isla Contoy, Yucatan Peninsula, Atlantic coast of Mexico; 2 paratypes USNM 806061, dredged in 140 m off of St. James, Barbados.

Other material examined.—**Recent: W Atlantic:** Johnson-Smithsonian Deep-Sea Expedition sta. 96, 540-660 m, off of St. Thomas, West Indies (see Bartsch, 1933: 27) (USNM

429819, 1); SUI Expedition 1918, Barbados sta. 5, 200 m, off of Pelican Island, Barbados, J. B. Henderson (USNM 500132, 1); fish traps in 100 m, off of Sandy Lane, Barbados, West Indies (1, collection of B. J. Piech; now owned by K. Piech; Pl. 50, Fig. 9). **E Atlantic:** All material at MNHN, collected on *N/O Le Suroit* cruise Seamount 2, January 1993, by S. Gofas, B. Métivier, and A. Warén: sta. DW188, Hyères Bank, 31°30.0'N, 28°59.5'W, 310 m (2); sta. DW190, Hyères Bank, 31°29.0'N, 29°00'W, 750 m (2); sta. CP144, Meteor Bank, 30°09.90'N, 28°29.04'W, 335 m (1 large; Gofas & Beu, 2002: figs 6A-B); sta. DW215, Irving Bank, 31°53.60'N, 28°02.90'W, 275 m (1); sta. DW209, Irving Bank, 31°59.20'N, 27°55.90'W, 460 m (1).

Distribution.—In the western Atlantic, *Sassia lewisi* has been reported only from the Caribbean Sea, off of the Yucatan Peninsula, off of St. Thomas, and off of Barbados, but most records are from depths of more than 100 m, and it will almost certainly prove to be much more widespread in the western Atlantic when more intensive dredging is carried out in deep water. Material was reported from the eastern Atlantic for the first time by Gofas & Beu (2002: 99); specimens of *S. lewisi* were collected uncommonly during the Seamount 2 cruise on banks south of the Azores Islands in 275-750 m. *Sassia lewisi* probably is widespread in the Atlantic in more than 200 m. I am not aware of any fossil records of *S. lewisi*.

Sassia kampyla species group

The large, smooth protoconch of the taxa in the *Sassia kampyla* group is distinct from that of any other species of which I am aware. This is the group for which Iredale (1929b) proposed the "genus" *Cymatona*, based largely on the very large, turbiniform, multiwhorled protoconch of *S. kampyla*. Iredale (1936: pl. 24, fig. 2) described and illustrated an elaborately bristled protoconch for the type species, *S. kampyla*, but the rows of bristles that he described are a very transient periostacal character that is present on very few of the specimens that I have examined; a large, smooth, polished protoconch is present on almost all material. Other characters of the members of this group are the relatively small size (few specimens are over 50 mm H), the lightly shouldered whorls, the low, narrow varices, the moderately long, straight siphonal canal directed strongly to the left, the strongly excavated columella allowing the small aperture to be nearly circular, and the sculpture being similar to that of the *S. apenninica* species group, but with slightly more dominant axial costae, so that the many low nodules are situated on the costae. The members of the group are therefore similar to the *S. apenninica* group in most characters, differing in the thinner shell (probably resulting from the deeper-water habitat more than anything else), the less obvious varices, the more nearly circular aperture, the slightly more prominent axial costae, and, primarily, the larger pro-

toconch lacking the prominent cancellate sculpture of the *S. apenninica* group.

***Sassia kampyla* (Watson, 1885)**

Pl. 50, Figs 3-4

Nassaria kampyla Watson, 1885: 594; 1886: 405, pl. 14, fig. 12; Tomlin, 1948: 228, pl. 2, fig. 5.

Lampusia nodocostata Tate & May, 1901a: 90; 1901b: 355, pl. 23, fig. 2.

Lotorium nodocostatum. Kesteven, 1902: 463, 479, figs 1, 4.

Fusitriton kampylum. Hedley, 1918: M66.

Cymatona kampyla. Iredale, 1929b: 177; Iredale, 1936: 306, pl. 24, fig. 2 (protoconch); Cotton, 1957: 3, fig. 20; Iredale & McMichael, 1962: 55; Beu, 1967: 101, pl. 1, fig. 7; Powell, 1979: 166, pl. 33, fig. 4.

Cymatium (Ranularia) tenuilirata var. *nodocostata*. Bayer, 1933: 51.

Cymatium jobbernsi King, 1933: 341, pl. 35, fig. 1.

Cymatoma (sic) kampyla. Cotton, 1945: 255; Dell, 1956: 83, pl. 13, figs 126, 132.

Cymatona tomlini Powell, 1955: 97; 1979: 166, pl. 33, fig. 5.

Charonia (Negyriina) kampyla. Kiliyas, 1973: 83, fig. 62.

Cymatona kampyla kampyla. Beu, 1978a: 12, figs 4a-j, l-n, 6a-b, d-f, 7a-c, 12d-e; 1978b: 36.

Cymatona kampyla tomlini. Beu, 1978a: 18, figs 4q-r.

Cymatona kampyla jobbernsi. Beu, 1978a: 18, figs 4k, o-p.

Sassia (Sassia) kampyla kampyla. Beu, 1985: 61, fig. 28; Warén & Bouchet, 1990: fig. 28; Henning & Hemmen, 1993: 115, pl. 24, fig. 2; Piech, 1995: 18.

Sassia (Sassia) kampyla tomlini. Beu, 1985: 61; Henning & Hemmen, 1993: 115, pl. 24, fig. 3; Piech, 1995: 18.

Sassia (Sassia) philomelae. Pether, 1993: 278, fig. 2d (not *Triton philomelae* Watson, 1881).

Cymatium remotum Frassinetti & Covacevich, 1995: 58, pl. 2, figs 8-10.

Sassia leucostomoides. Nielsen & Valdovinos, 2008: 209, fig. 17 (not *Triton leucostomoides* G. B. Sowerby I, 1846).

Remarks.—Material from Pleistocene deposits on the shelf off of southwestern Africa was identified by Pether (1993) as *Sassia* “*philomelae*,” a species originally named from Nightingale Island in the South Atlantic (Watson, 1885). These specimens are reidentified here as the larger species *S. kampyla*. The naming of the synonym *Cymatium remotum* from southern Chile by Covacevich & Frassinetti (1995), the misidentification of the same species as *S. leucostomoides* by Nielsen & Valdovinos (2008: 209, fig. 17; 20 specimens from Tubul Fm, southern Chile), and the recognition of specimens of *S. kampyla* in collections from South Africa and Mozambique complete the circum-subantarctic circle for the species long known in New Zealand and southeastern Australia as “*Cymatona*” *kampyla*. Comparison of specimens from all of these localities made it clear that they all share the characters listed above as distinguishing the species group and, indeed, are conspecific.

The holotype of *Cymatium remotum*, from Pliocene rocks of Isla Guamblin in remote southern Chile, is indistinguishable from New Zealand Pliocene fossils and the very many Recent specimens dredged from around New Zealand and eastern Australia. Specimens of *S. kampyla* from Pleistocene deposits on the shelf off of southwestern Africa, sent by John Pether (South African Museum), and identified by Pether (1993: 278) as *S. philomelae*, also are closely similar to New Zealand material. Recent specimens from deep water off of South Africa and Western Australia also are reported here. However, the real *S. philomelae* from Nightingale Island and Tristan da Cunha is significantly smaller in all respects than *S. kampyla*, and in my opinion is a separate species (see below). Specimens of *S. kampyla* from shallow water (69-80 m) around Macquarie Island, the southernmost subantarctic island south of New Zealand, are a little shorter and wider than most others, but intergrade in most characters (compare Pl. 50, Fig. 3, lectotype of *S. kampyla*, with Pl. 50, Fig. 4, holotype of *Cymatona tomlini*) and probably are slightly shorter merely because of their shallow habitat. They apparently have tracked the isotherms southward into unusually shallow water for this otherwise bathyal species.

The concept of species that exist right around the Southern Ocean as benthic populations at each of the landmasses and intervening island groups, linked by the very widely dispersed larval population, is one that is now expected to apply to southern, cool-water tonnoidean taxa, as well as other mollusks with a planktotrophic larval stage. For some of these, the Southern Ocean constitutes their entire range, and most of these species occupy the temperate regions of the entire Southern Ocean, e.g., *Argobuccinum pustulosum*, *Fusitriton magellanicus*, *Semicassis labiata* (Perry, 1811), some other mollusks such as the chiton *Plaxiphora aurata* (Spalowski, 1795), and even the high-tidal lichens *Rinodina peloleuca* (Nylander) Müller Argoviensis, *Caloplaca sublobulata* (Nylander) Zahlbruckner, and *Verrucaria durietzii* Lamb (see Matzer et al., 1998: 180). For others, with ranges extending northward into the Atlantic and, in some cases, the Pacific, only part of the Southern Ocean has been colonizable (*Charonia lampas*, *Ranella olearium*, *Monoplex parthenopeus*, *M. exaratus*). It is no surprise, then, to now add *Sassia kampyla* to this group of circum-Southern Ocean dispersers. The populations of benthic adults that have been given different names in Australia and New Zealand (*S. kampyla kampyla*), Macquarie Island (*S. kampyla tomlini*), and southern Chile (the Pliocene fossil *C. remotum* and the Tubul Fm specimen wrongly identified as *Sassia leucostomoides* by Nielsen & Valdovinos, 2008: 209, fig. 17), and now recorded from South Africa, are judged to be so similar that, at least in the recent past, they have been linked by a continuous larval population. In my opinion, this is all one species. It is still quite feasible that deep-water sampling

will bring to light living material of *S. kampfyla* off of southern Chile or other parts of southern South America, where little oceanographic research has been carried out, particularly below the shelf edge.

A single specimen of a small, unnamed species closely resembling *Sassia kampfyla*, but with more prominent and complex sculpture, is known from New Zealand Late Miocene rocks of deep-water facies; the rest of the fauna was described by Beu (1970a). *Sassia kampfyla* evidently has had a long history in the New Zealand area, at least. *Sassia kampfyla* is common around New Zealand at present in ca. 300–600 m, and particularly on the Campbell Plateau in 400–600 m, but empty shells are quite common in lesser depths, ca. 200–400 m. I suggested (Beu, 1978a) that when *Fusitriton magellanicus* arrived in the New Zealand region late in Pleistocene (or perhaps even during Holocene) time, it supplanted *S. kampfyla* in its former environment, forcing the latter to live in deeper water and further to the south than it had formerly. If this happened also at the other southern continents, it is conceivable that *S. kampfyla* lives at them still in deep water (ca. 300–600 m), or even has been unable to compete at all (e.g., possibly in southern South America) in areas where *F. magellanicus* was the first of the two to arrive, and is bypassed by the planktotrophic larval population of *S. kampfyla*.

Dimensions.—*Nassaria kampfyla*, lectotype: H 39.0, D 20.7 mm; largest paralectotype, BMNH 1889.10.26.12: H 42.1, D 20.0 mm; NMP E3985, off of Neill Peak, Zululand: H 34.7, D 17.6 mm; H 27.1, D 14.5 mm.

Types.—*Nassaria kampfyla*, lectotype (Pl. 50, Fig. 3; designated by me, Beu, 1978a: 10, fig. 4a), the syntype figured by Watson (1886: pl. 14, fig. 12), and 1 paralectotype, BMNH 1887.2.9.1246/1–2, 4 paralectotypes BMNH 1889.10.26.12–15, 16 paralectotypes at NMW, all from *HMS Challenger* sta. 164b, off of Sydney, Australia. *Lampusia nodocostata*, “holotype” at Tasmanian Museum, Hobart, E571/7912 (Turner & Dartnall, 1971: 47; not seen), from off of the eastern coast of Tasmania [but note that Tate & May (1901a) referred to two original specimens; the location of the other is unknown]. *Cymatium jobbernsi*, holotype GNS TM3958, from cliffs east of Lake Ferry, Palliser Bay, southern North Island, New Zealand, Nukumaruan Stage (Late Pliocene). *Cymatona tomlini*, holotype BMNH 1994145 (Pl. 50, Fig. 4), with 1 paratype BMNH 1951.6.13.93, from British, Australian, and New Zealand Antarctic Research Expedition sta. 83, 69 m, off of Lusitania Bay, Macquarie Island, subantarctic islands south of New Zealand; the holotype is the specimen illustrated by Tomlin (1948: pl. 2, fig. 5) as *Nassaria kampfyla*. *Cymatium remotum*, holotype SGO.PI 4208, from Late Pliocene rocks at Puerto Llave, Isla Guamblin, Los Chonos Archipelago, southern Chile, coll. V. Covacevich & D. Frassinetti, September 1984.

Other material examined.—**Recent:** There is little point in listing the huge collections of *Sassia kampfyla* dredged around New Zealand and southeastern Australia in recent years, and examined at AMS and NMNZ. **Western Australia:** HMAS *Diamantina* 1976 sta. 24, W of Rottneest Island, 225–220 m, 31°47'S, 115°58'E (WAM, 1 incomplete). **South Africa:** trawled S of Durban Bluff, 220 m (NMP 9925, 1); *R/V Meiring Naudé* sta. P13, off of Nthlonyane River, Transkei, 32°18.2'S, 29°06.2'E, 550 m (NMP C.8671, 1); *R/V Meiring Naudé* sta. ZP5, off of Neill Peak, Zululand, 28°44.4'S, 32°32.2'E, 320–340 m (NMP E.3985, 2 good, 1 colored, with 1 juvenile *Fusitriton magellanicus*); “trawl haul Natal coast [146 m] July 1919, leg H. W. Bell Marley” (NMP, 1 incomplete). **Mozambique:** Trawled in 375–450 m off of Barra Falsa, June 2003, coll. and pres. José Rosado (GNS WM17463, 1 specimen). Rosado reported (pers. comm., November 2003) that he has further material from off of Barra Falsa.

Fossils: **Chile: Late Oligocene–Early Miocene?:** One of Philippi's (1887: 56) syntypes of *Tritonium thersites* (see above, under *Distorsio ringens*), SGO.PI 4557, from Ranquil, coast south of Concepción, south-central Chile (Early Pliocene), is an incomplete specimen of a *Sassia* species, identified by Sven Nielsen (pers. comm., May 2009) as *S. kampfyla* (the other specimens are *Distorsio ringens*). The record by Frassinetti (2000) of *S. leucostomoides* (G. B. Sowerby I, 1846) from Arauco (see below) is also based on *S. kampfyla* (Sven Nielsen, pers. comm., May 2009). **South Africa: Postglacial sequence:** western coast continental shelf, 30°30'–31°30'S, 17°00'–17°30'E, De Beers Marine, don. J. Pether, April 1993 (NMP S.9936, 13); continental shelf between Walvis Bay and Luderitz, Namibia, leg. Gemcor, 1994 (NMP V.297, 1); postglacial sequence dredged by diamond miners, western coast continental shelf (Orange Shelf) off of Kleinsee, SW Africa, pres. J. Pether, January 1993 (GNS WM17488, 7).

Distribution.—*Sassia kampfyla* is abundant in the New Zealand region in depths of ca. 300–900+ m, from the far north to throughout the Campbell Plateau in the south, around all of the outlying islands, and a few specimens have been collected as far south as Macquarie Island (type locality of *Cymatona tomlini*). Around Australia, it is common in the same depth range as in New Zealand, at least from northern New South Wales southward and eastward to off of Tasmania, Victoria, and South Australia, and occurs much less commonly off of southern Western Australia. Pether (1993) reported that *S. kampfyla* (under the name *S. philomelae*) is common in relatively shallow water (ca. 130 m) in postglacial deposits (radiocarbon-dated at 13,500 years BP) mined for diamonds off of Kleinsee, southwestern Africa, indicating deposition during a cool period when sea level was higher than it is at present. It is therefore not surprising to find that there also are a few Recent specimens from the southern coast of South

Africa in the Natal Museum, and late in 2003, José Rosado sent me a specimen trawled off of Barra Falsa, Mozambique. Until recently, the sole record from South America (apart from the possible specimen in Philippi's Ranquil material) has been the Pliocene holotype of *Cymatium remotum*, but Nielsen & Valdovinos (2008: 209, fig. 17) illustrated a specimen from the Tubul Fm (Early Pleistocene) as *S. leucostomoides*, and *S. kampyla* can be expected to be found more widely in this little-studied region. It is likely that this species still lives at all the landmasses in the Southern Ocean, and it will probably be found much more commonly in the future off of southern Africa and South America once more detailed sampling is undertaken in deep water in these areas.

Late Pliocene fossils of *Sassia kampyla* are recorded from Palliser Bay, southern North Island, New Zealand (King, 1933, as *Cymatium jobbernsi*), in bathyal mudstone at the mouth of Wairoa River, northern Hawke's Bay, and in an isolated deep-water Late Pliocene deposit in inland central Hawke's Bay, central North Island (Beu *et al.*, 1977). These and the holotype of *C. remotum* are the only fossil records of this species, apart from the possible specimen in Philippi's material from Ranquil, south-central Chile, and Pether's (1993) Holocene material from off of Namibia, southwestern Africa.

***Sassia philomelae* (Watson, 1881)**

Pl. 50, Figs 6-7, 10

Triton philomelae Watson, 1881: 268; 1886: 391, pl. 14, fig. 10.

Sassia (Sassia) philomelae. Beu, 1985: 61; Piech, 1995: 18.

Remarks.—The three syntypes of *Sassia philomelae* and the two other lots of specimens that I have examined agree in virtually all characters with specimens of *S. kampyla* from Australia, New Zealand, southern Chile, and South Africa. However, they are markedly smaller in all characters, including the protoconch, and the teleoconch sculpture is a little more prominent than in *S. kampyla*. The protoconch and teleoconch remain in the same proportions as in *S. kampyla*, but the Tristan da Cunha specimens are simply diminutive overall, about two-thirds the size of *S. kampyla*. The lot of 10 live-collected specimens at NMP demonstrates that this really is a small species restricted to the area around the Tristan da Cunha Group. Presumably it evolved from the closely similar species *S. kampyla* as a result of Pleistocene disruption of a formerly continuous geographical range, and subsequent genetic drift of a small population (allopatric speciation).

Dimensions.—*Triton philomelae*, syntypes: H 28.8, D 14.8 mm, H 27.4, D 15.0 mm; NMP K.5633, Inaccessible Island: H 26.5, D 13.8 mm; H 23.4, D 14.0 mm; H 22.3, D 12.5 mm.

Types.—*Triton philomelae*, 2 syntypes BMNH 1887.2.9. 1188-1189, from 200-300 m, off of Nightingale Island,

Tristan da Cunha Group, South Atlantic, *HMS Challenger* (1 illustrated, Pl. 50, Fig. 6); 1 syntype USNM 118764 (Pl. 50, Figs 7, 10), all data as above.

Other material examined.—Lobster traps, 80-150 m, Inaccessible Island, Tristan da Cunha Group, South Atlantic, April 1989 (NMP K5633, 10 specimens, live-collected; GNS WM17137, 2 specimens from the NMP lot); lobster traps in 80 m, off of Tristan da Cunha Island, *ex* A. Arthur collection (GNS WM17512, 2).

Distribution.—*Sassia philomelae* presumably is restricted to the small shelf area around the Tristan da Cunha Group, where it inhabits much shallower water than *S. kampyla* does around the southern landmasses. There is no fossil record.

***Sassia zealta* species group**

Beu & Maxwell (1990: 426) referred to this group of giant *Sassia* species in New Zealand Oligocene and Early Miocene rocks when explaining the complications of the name *Sassia minima* (Hutton, 1873), and Beu & Griffin (1997) and Beu *et al.* (1997) discussed the South American members of this group and the possible transport of larvae of species between New Zealand and South America. The group has been identified informally by the name of one of the most distinctive New Zealand members, *S. zealta* (Laws, 1939), which occurs in Early Miocene and early Middle Miocene rocks throughout New Zealand. Members of this group are characterized by their large size (up to *ca.* 200 mm H for *S. minima*), by their moderately to very tall, narrow shape, with a tall, stepped spire and a long anterior canal, and by the biangled whorl profile brought about by the consistent presence of two prominent rows of nodules, one at the shoulder angle and the other on an almost equally prominent peribasal angulation. Although these nodules are very long and pointed in *S. zealta*, they are smaller and more rounded in most of the really large, Oligocene species. The aperture also is distinctive, because of the deeply excavated columella and the smooth lips of most species. The only Eocene and earlier record of this species group of which I am aware is in New Zealand, where the earliest known species occurs in the earliest Eocene Red Bluff Tuff of Pitt Island, Chatham Islands, and at least two other species are known in Eocene rocks of the South Island. The group then seems to have become widespread in the Southern Ocean during Oligocene and Miocene times, only to become extinct with the cooling of Southern Ocean waters from Middle Miocene time onward. This record appears to imply an early development in New Zealand, followed by larval dispersal in the Antarctic Circumpolar Current to the other southern hemisphere land masses, reflecting the development of circum-Antarctic circulation following the opening of Drake Passage at approximately 34-30 Ma (Beu & Griffin, 1997; Beu *et al.*, 1997; Livermore *et al.*, 2004).

Species of which I am aware in the *Sassia zealta* species group are:

- *abbotti* (Tennison Woods, 1875), Early Miocene, northern Tasmania.
- *armata* (Hupé, 1854) (= *bicegoi* Ihering, 1897), Late Oligocene/Early Miocene (displaced into Late Miocene/Early Pliocene rocks), Chile; Late Oligocene/Early Miocene, Argentina.
- *minima* (Hutton, 1873), Oligocene, New Zealand, and Torquay, Victoria, Australia.
- *morgani* (Ortmann, 1902), Late Oligocene/Early Miocene, Argentina.
- *zealta* (Laws, 1939), Early and early Middle Miocene, New Zealand.
- n. sp. A, Early Eocene, Chatham Islands, New Zealand.
- n. sp. B, Early Eocene, New Zealand.
- n. sp. C, Middle Eocene, New Zealand.
- n. sp. D, aff. *S. minima*, Oligocene, New Zealand.
- n. spp. E-F, aff. *S. minima*, Early Miocene, New Zealand.

***Sassia armata* (Hupé, 1854)**

Pl. 52, Figs 1-6, 12; Pl. 53, Figs 3, 5-6

Triton armatum Hupé, 1854: 182, pl. Conquiliologia 3, fig. 1.

Tritonium exiguum Philippi, 1887: 54, pl. 3, fig. 23 (in part).

Tritonium verruculosum. Philippi, 1887: 57, pl. 4, fig. 10 (in part not *Triton verruculosus* G. B. Sowerby I, 1846).

Siphonalia aff. *nodosa*. Ihering, 1897: 299 [Ihering, 1907: 193; not *Siphonalia nodosa* "Martyn," i.e., *Austrofusius glans* (Röding, 1798), a buccinid restricted to New Zealand].

Tritonium bicegoi Ihering, 1899: 29, pl. 1, fig. 8; 1907: 177; Ortmann, 1902: 206, pl. 33, fig. 15.

Siphonalia nodosocincta Ihering, 1907: 193, pl. 6, fig. 37.

Siphonalia matthewsi Ihering, 1914: 102, pl. 3, fig. 14.

"*Tritonium*" (*Lotorium*) *bicegoi*. Tavera, 1979: pl. 19, figs 66a-b.

Sassia armata. Nielsen, 2003: 94, pl. 17, figs 8-12; Griffin & Nielsen, 2008: 291, pl. 17, figs 11-12.

Remarks.—*Sassia armata* is a large species (to ca. 120 mm H) and is relatively wide for a member of this species group, with a moderately tall, weakly stepped spire. Almost all specimens have a short siphonal canal, but this is the result of damage; it is moderately long in the one complete adult specimen seen (Pl. 53, Fig. 5). In shape and proportions and in the fine surface sculpture, Chilean specimens closely resemble specimens identified as *S. bicegoi* (Ihering, 1899) from the Late Oligocene or Early Miocene of Argentina. The few specimens that I have examined from Argentina differ from most Chilean ones in having longer, narrower nodules, particularly in the upper, peripheral row, and some of them have a low, wide spiral cord in the center of the concave area between the two rows of large nodules; I have not observed such a median cord on Chilean specimens. However, the large lots of specimens from

the Río Rapel area, Chile, loaned by Sven Nielsen (material at SGO.PI and SMF) include long-noduled specimens with the penultimate varix close to the left side of the aperture (closely resembling Argentinean specimens) and short-noduled specimens with the penultimate varix situated further to the left (the common form seen from Chile) and, in my opinion, this is one species. *Sassia bicegoi* is regarded as a synonym of *S. armata*. Tavera (1979) identified his Chilean material as "*Tritonium*" *bicegoi*, and in general Chilean authors seem not to have been aware of Hupé's species name. The holotype was illustrated by Nielsen (2003: pl. 17, figs 8-9) and Griffin & Nielsen (2008: 291, pl. 17, figs 11-12).

Hupé's species name *Triton armatum* is a senior primary homonym of *T. armatus* Tate (1888: 121, pl. 5, fig. 3), proposed for an Australian fossil (Bookpurnong fauna, Bairnsdalian Stage, Middle Miocene; "well sinking in the Murray Desert," South Australia). The replacement name *Sassia tatei* is provided here for *Triton armatus* Tate, 1888, because it is a junior homonym of *T. armatum* Hupé, 1854. The replacement name commemorates Professor Ralph Tate, author of the replaced species name, and describer of most of the common Cenozoic fossil mollusks of southern Australia.

Dimensions.—Holotype: H 65.1, D 40.2 mm (both very incomplete); Purdue University, Indiana, loc. 265, Matanzas, Chile: H (incomplete) 70.8, D 40.5 mm; Purdue University, Indiana, Paleontology collection, PU.P 675a, mouth of Santa Cruz River, incomplete specimen illustrated by Ortmann (1902: pl. 33, fig. 15): H 74.8, D 45.3 mm; PU.P 675b, second specimen mentioned by Ortmann (1902): H 67.9, D 40.3 mm (PU.P material is now at PRI).

Types.—It recently has been realized (Agnes Lauriat-Rage, MNHN, pers. comm., October 2001) that Gay's collection, described by Hupé (who was curator of collections in the Département de Paléontologie, MNHN, during the middle years of the 19th century) is at the Département de l'Histoire de la Terre, MNHN. The holotype [because it is the only specimen present, and is the one in Hupé's (1854) illustration] of *Triton armatus* is registered as MNHN Géologie Gg2001/21, in the Gay/Hupé collection. Casts have been presented by Emmanuelle Vennin (Département de l'Histoire de la Terre, MNHN) to Sven Nielsen, Institut für Geowissenschaften, Christian-Albrechts-Universität Kiel, and to GNS (WM17378) (Nielsen, 2003: pl. 17, figs 8-9; Griffin & Nielsen, 2008: 291, pl. 17, figs 11-12). A photographic copy of Hupé's original figure is provided here (Pl. 52, Figs 1-2). Hupé (1854: 183) stated the type locality as "Habita fósil en los terrenos terciarios de Coquimbo," Chile (Pliocene), and the holotype was found in a collection of species that otherwise occur only at Coquimbo, but a Pliocene locality is most unlikely for this otherwise Oligocene and Miocene species, and the preservation and matrix of the holotype resemble those of

Navidad Oligocene/Miocene specimens rather than Coquimbo Pliocene ones. Because *Sassia armata* is common along the coast north of Río Rapel, north of Navidad (Oligocene-Early Miocene fossils displaced into Late Miocene-early Pliocene rocks; Nielsen *et al.*, 2003; Finger *et al.*, 2007), this is likely to be the real provenance of the holotype; it evidently was associated accidentally with Coquimbo specimens at a very early date, perhaps by Gay. *Tritonium exiguum*, 4 syntypes at SGO.PI: (1) SGO.PI 4567, Navidad, central Chile, Oligocene-Early Miocene, a small specimen of *S. armata* with complete outline and complete protoconch, apparently the original of Philippi's (1887: pl. 3, fig. 23) illustration; this specimen is here designated the lectotype of *Tritonium exiguum*; (2) SGO.PI 734, (3) SGO.PI 4565, and (4) SGO.PI 4566, 1 paralectotype each, all from Navidad; all are small, juvenile specimens of *Ameranella verruculosa* (G. B. Sowerby I, 1846). *Tritonium verruculosum* "Sowerby" of Philippi, 1887, 2 lots of specimens present at SGO.PI: (1) SGO.PI 839, 6 specimens, from Navidad; 2 are large, excellent specimens of *S. armata*, including the specimen illustrated by Philippi (1887: pl. 4, fig. 10), and the other 4 are specimens of *A. verruculosa*, ranging from complete specimens *ca.* 30 mm H to large, incomplete specimens *ca.* 70 mm H; (2) SGO.PI 741, from Matanzas, near Navidad, central Chile, Late Miocene, 2 good small specimens of *S. armata*. *Tritonium bicegoi*, holotype MACN Ihering type collection no. 790 (Pl. 52, Fig. 6), with 1 paratype (Pl. 52, Fig. 12), from Mount Entrance (Monte Entrada) Member, Monte Leone Fm (Late Oligocene or, more probably, Early-Middle Miocene), bluff on the southern side of the Santa Cruz River, a short distance upstream from the mouth, Patagonia, southern Argentina. *Siphonalia nodosocincta*, holotype, MACN Ihering type collection no. 841, from Cabo Tres Puntas, Golfo San Jorge, Patagonia, "Patagonico medio," now classified in Chenque Fm, Early-Middle Miocene; a calcite neomorph from greenish sandstone, an incomplete specimen of *S. armata*. This specimen at first appears to be taller and narrower than *S. armata*, but this is because part of the shell is missing from the internal mold on the sides of the specimen, artificially making it appear narrow. The fine surface spiral sculpture and two rows of large nodules agree exactly with those of *S. armata*. *Siphonalia matthewsi*, holotype MACN Ihering type collection no. 845a (Pl. 52, Fig. 5), from "Golfo San Jorge, Patagonico"; a very poor, crushed, calcite neomorph of *Sassia armata* in concretionary sandstone, also from Chenque Fm (Early-Middle Miocene).

Other material examined.—Fossils: Chile: Late Oligocene-Early Miocene: Collections examined at SGO.PI, January 1998: Navidad, miembro Navidad (1); Estero Maitenlahue, near Navidad (1); beach-front cliff and wave-cut platform at Matanzas, near Navidad (1); Punta Perro, Navidad, *ca.* 400 m N of puebla La Boca (5); between Punta Perro and puebla

La Boca (3); also material at SGO.PI among that identified by Philippi (1887) as "*Tritonium verruculosum*," listed above: SGO.PI 839, from Navidad (2 specimens of *S. armata*); SGO.PI 741, from Matanzas (2 specimens, both *S. armata*); collections at Purdue University, Indiana, USA: W. J. Zinsmeister loc. 255, Navidad, central Chile (1); W. J. Zinsmeister loc. 265, coastal cliff N of Río Rapel, N of Navidad (1); material collected by Sven Nielsen, now at SGO.PI and SMF: loc. RAP, Río Rapel, N of Matanzas, Oligocene-Early Miocene fossils reworked into Late Miocene-Early Pliocene rocks (24; 1 illustrated, Pl. 53, Fig. 6, now SGO.PI 6448; 1 illustrated, pl. 53, Figs 3, 5, now SGO.PI 6447; 1 at Universidad de Concepción); loc. PPN, Punta Perro (1); loc. LBZ, Las Brizas (1); loc. RAN, Ranquil (5); loc. RQK 008, Ranquil, coast S of Arauco, S of Concepción, south-central Chile, Ranquil Fm (Oligocene-Early Miocene fossils displaced into Pliocene rocks; Finger *et al.*, 2007) (4). **Argentina: Late Oligocene/Early-Middle Miocene:** Cerro Chenque, small hill immediately behind city of Comodoro Rivadavia, Chubut Province, from Chenque Fm, lateral equivalent of Monte Leon Fm, coll. J. Frenguelli (MLP 1180, 1; identified as *Siphonalia nodosocostata* Ihering); material formerly at Department of Earth and Atmospheric Sciences, Purdue University, Indiana, collection formerly at Princeton University, Department of Geological and Geophysical Sciences, now at PRI; PU.P.675, Monte Leon Fm, bluff on S side of Santa Cruz River a short distance upstream from mouth, Patagonia (2; PU.P.675a, specimen illustrated by Ortmann, 1902: pl. 33, fig. 15; illustrated, Pl. 52, Fig. 4; PU.P.675b, second specimen from type locality mentioned by Ortmann, 1902: 206; illustrated, Pl. 52, Fig. 3).

Distribution.—In Chile, *Sassia armata* is recorded from the Matanzas-Navidad area, on the coast of central Chile southwest of Santiago, and from Ranquil, south of Concepción, south-central Chile (all Chilean localities consist of Oligocene-Early Miocene fossils displaced into Late Miocene-Early Pliocene rocks; Nielsen *et al.*, 2003; Finger *et al.*, 2007); the supposed type locality of Coquimbo (Pliocene) is certainly an error. In Argentina, *S. armata* seems to be a rare species, which Miguel Griffin and I were unable to recollect at the mouth of the Santa Cruz River, Argentina. It is recorded from Monte Leon Fm (Late Oligocene/Early-Middle Miocene, poorly constrained) at the mouth of the Santa Cruz River, and the laterally equivalent Chenque Fm at Cerro Chenque (a hill behind the city of Comodoro Rivadavia) and at Cabo Tres Puntas, Golfo San Jorge.

Sassia morgani (Ortmann, 1900)
Pl. 52, Figs 7, 9-10; Pl. 53, Fig. 4

Tritonium morgani Ortmann, 1900: 374; 1902: 207, pl. 33, fig. 16.
Litorium morgani. Ihering, 1907: 177.

Remarks.—*Sassia morgani* is a very different species from *S. armata*, because it is much the tallest and narrowest member of the *S. zealta* species group and, indeed, is probably the narrowest species of the entire, highly speciose genus (*ca.* 160 species of *Sassia* have been named to date). The spire is very tall and narrow and, because the nodules are low, its outline is unusually weakly stepped for a member of this group. The siphonal canal also is correspondingly long, weakly curved, and narrow, and the aperture is correspondingly small. The surface sculpture of spiral cords is, however, much coarser than the fine, close spiral cords and threads making up much of the surface of *S. armata*. The most striking thing about this species, though, is its small nodules, because they are reduced to low, rounded swellings on the shoulder angle, and on some specimens are particularly small on the base. *Sassia morgani* resembles the New Zealand Oligocene species *S. minima* particularly closely in nodule size and in the strong spiral cords, but adults are much taller and narrower than adult *S. minima*, and resemble immature specimens of *S. minima*, *ca.* 60–80 mm H. This suggests that *S. morgani* might have evolved from *S. minima* or a similar species by a heterochronic process such as paedomorphosis.

The name *Sassia morgani* (Ortmann, 1902) is a senior secondary homonym of *S. morgani* (Marwick, 1931: 103, pl. 10, fig. 183; proposed in *Austrotriton*), from Miocene rocks of the Gisborne district, New Zealand. However, a replacement name is not required for *S. morgani* (Marwick), because it is a synonym of *S. tortirostris* (Tate, 1886), a species now known to occur in both Australia and New Zealand (Beu & Maxwell, 1990).

Dimensions.—*Tritonium morgani*, holotype, H 63, D 28 mm (Ortmann, 1902: 207), H actually 62.3 mm; GNS WM15880, Monte Leon Beach, H 100.1, D 39.8 mm; BMNH Palaeontology Department, G11963, “Monte Leone,” H (incomplete) 75.1, D 43.5 mm.

Types.—*Tritonium morgani*, holotype (Pl. 52, Fig. 7) formerly at Department of Earth and Atmospheric Sciences, Purdue University, Indiana, now at PRI, from Monte Leon Fm (late Oligocene–Early or Middle Miocene), “mouth of the Santa Cruz River,” Argentina, but probably actually from Monte Leon Beach, *ca.* 40 km south of the Santa Cruz River (see below).

Other material examined.—**Fossils: Argentina: Late Oligocene/Early–Middle Miocene:** “Santa Cruz Fm, Monte Leone, Patagonia,” *i.e.*, presumably from Monte Leon Beach, as below, purchased from R. F. Damon, July 1899 (BMNH Palaeontology Department, G11963, 1, illustrated, Pl. 52, Figs 9–10); Mount Entrance (lower) Member, Monte Leon Fm, Monte Leon Beach, *ca.* 2 km N of Punta Lobos, coast *ca.* 40 km S of mouth of Santa Cruz River, coll. M. Griffin, January 1995 (GNS WM15880, 1, illustrated, Pl. 53, Fig. 4);

and *ca.* 10 specimens observed and (in part) collected by me and M. Griffin from wave-cut platform at this same locality, February 1998. Because *S. morgani* is common at this locality, and has not been recollected at the supposed type locality (bluff on S side of Santa Cruz River a short distance upstream from mouth, *ca.* 40 km to the N), it seems likely that Monte Leon Beach is the real provenance of the type material (which was collected for Ortmann by Hatcher; it is now known that Hatcher’s “Santa Cruz” locality covered a wide area; Del Rio, 2004).

Distribution.—*Sassia morgani* has been reported only from Monte Leon Fm (Late Oligocene/Early or Middle Miocene) at the mouth of the Santa Cruz River (probably spurious) and at Monte Leon Beach 40 km to the south, in southeastern Patagonia.

Remaining species, not assigned to a group

Sassia leucostomoides (G. B. Sowerby I, 1846)

Pl. 52, Figs 8, 11

Triton leucostomoides G. B. Sowerby I, 1846: 618, pl. 4, fig. 64.

Sassia leucostomoides. Frassinetti, 2000: 136, pl. 1, figs 11–14; Griffin & Nielsen, 2008: 299, pl. 21, figs 9–12 (in part; not figs 13–14).

Remarks.—“*Triton*” *leucostomoides* has been one of the least well-known species of the family since it was named by G. B. Sowerby I (1846) from material collected at Isla Guafo, southern Chile, by Charles Darwin. Daniel Frassinetti and the late Vladimir Covacevich recollected this remote locality in August 1984 during a cruise by *R/V Hero* (see description of Cenozoic geology of the southern Chilean islands by DeVries *et al.*, 1984, based on this cruise), and the characters and relationships of this species are now clear (Frassinetti, 2000). *Sassia leucostomoides* is a small (to *ca.* 35 mm H), moderately tall and narrow, finely sculptured species of *Sassia*, not unlike *S. philomelae* in many characters. Its protoconch is small and turbiniform, only about a third of the size of that of *S. philomelae*, and is apparently smooth (not well preserved on specimens examined). The varices are low and narrow, and are unusual in being only *ca.* 200–220° apart around the whorls, rather than the usual 240°. A weakly concave, moderately sloping sutural ramp occupies half of the whorl height on spire whorls, and the spiral cord at the shoulder angle protrudes as a carina, and bears slightly larger nodules than the other cords. Five narrow, rather low, widely spaced spiral cords extend onto the terminal varix on the last whorl, and the uppermost two of these are visible on spire whorls; the three uppermost ones on the last whorl are spaced more closely than the others, and their interspaces each bear a single secondary cord. Lower interspaces have two or three narrow

secondary cords, further similar ones are present on the canal, and three narrow cords of intermediate width occupy the sutural ramp. These are crossed by many low, narrow, widely spaced axial costae extending the whole height of the last whorl, 10 in both penultimate and last intervariceal intervals of the specimen examined. The aperture is subcircular, with narrow, weakly reflected lips; the interior of the outer lip bears six low, rounded nodules and a weak seventh at the base; the inner lip is smooth except for sculpture of the previous whorl visible in the parietal area, and two short, narrow transverse ridges on the base of the columella.

Sassia leucostomoides is similar to both *S. apenninica* and *S. philomelae* in a general way, but differs from them both in its smaller size, its much smaller protoconch, its taller spire, its unusually arranged varices, its slightly more prominently keeled whorls, and its finer sculpture. I am not aware of any closely similar species.

Dimensions.—Lectotype, H 26 mm (Griffin & Nielsen, 2008: 298), figured specimen (Pl. 52, Figs 8, 11): H 24.2, D 14.5 mm.

Types.—*Triton leucostomoides*, lectotype BMNH Palaeontology Department, G26337, 2 paralectotypes, G26338 and G26365, all from Guafo Island, southern Chile, Pliocene; collected by Charles Darwin on *HMS Beagle*. The situation with these specimens is complex, because one (G26338, possibly the specimen illustrated by G. B. Sowerby I, 1846: pl. 4, fig. 64; Griffin & Nielsen, 2008: pl. 21, figs 13-14) has a much larger and taller protoconch than the other two, of mammillate shape with several whorls, and appears to be the one genuine southern hemisphere pre-Holocene fossil record of *Fusitriton*. If it is a species of *Fusitriton*, it is an extremely small juvenile specimen, and at this size at least, it is not distinguishable from *F. magellanicus*. The other two specimens have more obviously shouldered whorls, much smaller protoconchs, and slightly finer and more nodulose sculpture than the illustrated syntype, and clearly are the *Sassia* species collected in large numbers at Guafo Island by Covacevich and Frassinetti (see below). The best-preserved of the *Sassia* specimens, BMNH Palaeontology Department G26337, was designated the lectotype of *T. leucostomoides* by Griffin & Nielsen (2008: 299, pl. 21, figs 11-12), ensuring that this name is retained for the *Sassia* species rather than applying to *Fusitriton magellanicus*, because the *Sassia* species then would require a new name.

Other material examined.—**Fossils: Chile: Pliocene:** Almost all material is at SGO.PI, and all was collected by V. Covacevich and D. Frassinetti on the *R/V Hero* during August 1984, from Estero Tres Calles Bay, on NE Isla Guafo, SW of Chiloé Island, southern Chile; this was thought likely to be Darwin's type locality, because it is the only area where it is easy to land on the island (see description of the locality and expedition by DeVries *et al.*, 1984). However, Griffin

& Nielsen (2008: 299) pointed out that Darwin's material is in hard sandstone, whereas the new material collected by Covacevich and Frassinetti is in soft mudstone, so the new material evidently is not from the type locality, in the strictest sense. Specimens were found at 12 of the 13 discrete localities collected within the bay (locality names are generalized here): (a) Punta Yanez, loc. 1 (10 specimens); (b) Punta Yanez, loc. 2 (1); (c) S of Caleta Samuel (12); (d) Punta Torro, N side (1); (e) Punta Torro, N side, further E (9); (f) Estero Chilconal (3); (g) N of Punta Caleta, loc. 1 (15); (h) N of Punta Caleta, loc. 2 (5); (i) Estero Tres Calles (7); (j) E of mouth of Estero Tres Calles (5); (k) Punta Caleta, loc. 1 (7); (l) Punta Caleta, loc. 2 (3); 78 specimens in total; one specimen from loc. j, E of mouth of Estero Tres Calles, field no. 280884.2, is at GNS (WM15954; Pl. 52, Figs 8, 11).

Distribution.—*Sassia leucostomoides* is recorded here and by Frassinetti (2000) from Pliocene mudstone cropping out in Estero Tres Calles Bay, northeastern Isla Guafo, southwest of Chiloé Island, southern Chile. Frassinetti (2000: 137) also recorded two specimens from the Tubul Fm (Miocene?) at Arauco, near Concepción, southern mainland Chile, but Sven Nielsen (Christian-Albrechts-Universität Kiel, pers. comm., May 2009) advised me that these are specimens of *S. kampyla*. Frassinetti (2000: 137) pointed out that Philippi (1887: 45) confused *S. leucostomoides* with his species *Fusus sowerbyanus*, from Matanzas, central Chile, but Frassinetti confirmed that this is incorrect, and that *S. leucostomoides* does not occur at Matanzas.

Genus *CYMATIELLA* Iredale, 1924

Cymatiella Iredale, 1924: 253. Type species (by original designation): *Triton quoyi* Reeve, 1844 (= *T. verrucosus* Reeve, 1844), Pliocene to Recent, southern Western Australia to southern New South Wales, Australia.

Vernotriton Iredale, 1936: 308. Type species (by original designation, Iredale, 1936: 336): *Charonia pumilio* Hedley, 1903, Recent, southern Queensland and northern New South Wales, Australia.

Remarks.—The genus *Cymatiella* contains the smallest ranelids, few exceeding 20 mm H, with a relatively tall, straight-sided spire and a short, rounded last whorl and short, open siphonal canal, simple sculpture of spiral and axial ridges, and a correspondingly small, smooth, turbiniform protoconch. This genus seems a suitable position for many of the small, generalized, relatively tall-spined species from the Paris Basin Eocene named by Lamarck (1803) and Deshayes (1864-1865), although some of the shorter and wider species named by these same authors are not so easily classified. *Triton parvulum* Michelotti, 1847, from the Miocene of Italy and the Middle Miocene (Badenian) of Lapugy, Transylvania (NHMV

1854/35/165, 46 specimens from Lapugy examined), and its possible synonym *Cymatiella tritonea* (Grateloup, 1847) from Chattian-Aquitainian (Oligocene-Early Miocene) rocks of the Aquitaine Basin, France, clearly also are further younger species in European Cenozoic rocks, so it is likely that there are other European species referable to this genus. *Cymatiella tritonea* is particularly similar to *C. verrucosa* (Reeve, 1844), type species of *Cymatiella* Iredale, 1924. Also, *Triton fenemai* Martin (1899: 141, pl. 22, fig. 322) and *C. menkrawiensis* (Beets, 1941) are further species of *Cymatiella* (Beu, 2005: 104-105) occurring in the Miocene rocks of Java, and Bunjamin Dharma (Jakarta, pers. comm., 2002) has shown me specimens of another unnamed *Cymatiella* species more similar to *C. verrucosa* in Indonesian Miocene rocks. However, I am aware of few other species that seem to belong here, apart from the moderately diverse assemblage of species in southern Australia. In Australia, there is one Miocene species, four or five Pliocene species, two of which are still living, and a further three or four species known only in the living fauna. Until now, the two quite diverse assemblages from Europe and Australia have seemed isolated from each other, and the genus therefore possibly polyphyletic. I record here a single species of apparently typical *Cymatiella* from the Miocene of Trinidad and the Dominican Republic, the only record of the genus of which I am aware from the Americas. Of previously named species, the new species is most similar to the Australian Pliocene to living species *C. verrucosa*. This species therefore helps to fill the gap in the time and geographical range of the genus, and with the addition of the Miocene species from Java, makes *Cymatiella* likely a monophyletic group that formerly was much more widespread in the tropical realm than present records would suggest. Like several other genera, *Cymatiella* seems to be a genus whose current restriction to southern Australia is a relic of a formerly much wider, Paris Basin and then Indo-Pacific distribution.

Cymatiella vokesorum n. sp.

Pl. 54, Figs 1-10

Description.—Shell small (to ca. 17 mm high), with a moderately tall, straight-sided spire, short, moderately well-inflated last whorl and short, straight, open anterior siphonal canal. Varices low and rounded, situated at approximately every 240° down entire teleoconch. Teleoconch sculpture of low, rounded spiral cords with interspaces each approximately equal to the width of one cord, with one or two low, narrow spiral threads in each interspace, 3-4 additional, low, closely spaced threads below suture, and 5-6 additional, closely spaced cords on canal; with two major spiral cords on spire whorls and a weak third at center of sutural ramp, seven main cords on last whorl, passing onto terminal varix, including weaker cord at

center of sutural ramp; all crossed by many low, rounded axial costae slightly more widely spaced than spiral cords, extending for whole height of last whorl, 10 costae on penultimate intervariceal interval and nine on last interval of most specimens; most cords low, narrow, similar in proportions to spiral costae, but on most specimens with two or three costae on dorsum of last whorl and immediately following each varix on preceding 2-3 intervariceal spaces considerably higher and wider than others, forming large, nodulose ridges; all forming very small, rounded nodules at sculptural intersections, and on coarse axial costae forming slightly larger nodules that angulate whorl profile. Aperture evenly oval, with weakly flared lips; interior of outer lip bearing seven short, narrow transverse ridges or, on some specimens, two rows of very short ridges separated by narrow smooth zone parallel to lip margin; inner lip bearing one low, narrow parietal ridge and 4-6 low, narrow transverse ridges on columellar area. Protoconch very small, low-turbiniform, of 2.2 strongly inflated whorls with deeply impressed suture, apparently smooth but not well preserved on available material.

Dimensions.—Holotype: H 14.0, D 7.3 mm; figured paratype, NMB H 17968, from TU 1249 (NMB 19010), road cut W of San Cristobal: H 12.2, D 6.5 mm; figured paratype, NMB H 17970, from TU 1364 (NMB 18650), Boca de Los Ríos: H 11.6, D 6.4 mm; largest paratype, NMB H 17971, locality same as last: H 14.2, D 7.8 mm.

Types.—Holotype NMB H 17967 (Pl. 54, Figs 1, 4, 9), from TU 1249 (= NMB 19010), road cut 8.6 km W of plaza at San Cristobal, on road to Bani, S Dominican Republic; from unnamed Middle Miocene formation, planktic foram zone N.11, discussed by E. Vokes (in E. & H. Vokes, 1989: 66-67): “on the south coast of the Dominican Republic there is a small outcrop, perhaps 15 m in length, along the highway west of San Cristobal”, with 2 paratypes, NMB H 17968 (illustrated, Pl. 54, Figs 2-3), H 17969; TU 1364 (= NMB 18560), Baitoa Fm (late Early Miocene), Boca de Los Ríos, below waterfall in Arroyo Hondo, downstream from Baitoa, Río Yaque del Norte, N Dominican Republic, 2 paratypes NMB H 17970-17971 (1 illustrated, Pl. 54, Fig. 7); all collected by Emily and Harold Vokes.

Other material examined.—**Fossils:** **Trinidad:** **Miocene:** USGS 9219, Brasso Fm, Guaico-Tamana Road, 40 m E of mile 13 [20 km] (1 small specimen, at USNM; illustrated, Pl. 54, Figs 5-6, 8, 10).

Remarks.—*Cymatiella vokesorum* n. sp. is remarkably similar in size, overall appearance, and coarseness of sculpture to the most common southern Australian living species, *C. verrucosa*, type species of the genus. The largest Australian specimens reach a considerably larger size (to ca. 25 mm H) than any of the available specimens of *C. vokesorum* n. sp., and besides minor differences in the details of the sculpture and

the apertural ridges, the obvious character separating them is that *C. verrucosa* does not form the few wide, elevated ridges on the dorsum of the last whorl that are so prominent on *C. vokesorum* n. sp. There can be little doubt that the two species are closely related phylogenetically. The other common, widespread southern Australian living species, *C. eburnea* (Reeve, 1844) (= *C. lesueuri* Iredale, 1929), is much more finely sculptured than either *C. verrucosa* or *C. vokesorum* n. sp., and the other moderately common, southern Australian, living, coarsely sculptured species, *C. sexcostata* (Tate, 1888) (= *C. gaimardi* Iredale, 1929), has a significantly taller spire and fewer, coarser axial costae than either *C. verrucosa* or *C. vokesorum* n. sp. The Paris Basin Eocene species seem all to be smaller, narrower, and more finely sculptured than the Australian, Italian, Javanese, and tropical American species, and more nearly resemble the Australian Miocene species *C. pratti* (Tenison Woods, 1879), suggesting that the evolution and migration of *Cymatiella* has been complex.

Distribution.—*Cymatiella vokesorum* n. sp. is recorded only from late Early Miocene to Late Miocene rocks of Trinidad and the Dominican Republic.

Etymology.—It is a great pleasure to name this species in honor of Emeritus Professors Emily and Harold Vokes, after their retirement from Tulane University and the lamented death of Harold. Emily and Harold collected a considerable proportion of the material studied here, including the type material of *Cymatiella vokesorum* n. sp., and the advanced state of knowledge of tropical American Cenozoic molluscan paleontology results to a large degree from their collecting and publishing vigor. They provided generous help and guidance, as well as huge collections of valuable specimens, to an entire generation of students (in the broadest sense) of American paleontology, and their influence and friendliness have made an enormous, unique contribution to the science.

Family **CASSIDAE** Latreille, 1825

Remarks.—The classification used here follows my earlier classifications (Beu, 2005, 2008) and differs from that of Riedel (1995, 2000) in recognizing Cassidae as a family distinct from Tonnidae. This follows largely from the comments by Andrews *et al.* (1999: 13), who pointed out the distinctive anterior gut glands of Tonnidae and the significantly different salivary glands of the tonnoidean families, and commented that “all this evidence demonstrates that Tonnidae is further removed from Cassidae than is implied by Riedel’s classification.”

The correct Latin spelling for a family name based on *Cassis* is Cassidae, and this has been the accepted name for the family until recently. The family group name Cassidae formally was adopted for this family in ICZN Opinion 1023

(1974), to avoid homonymy with the family Cassididae in Insecta.

Subfamily **CASSINAE** Latreille, 1825

Remarks.—This subfamily includes the taxa of Cassidae with an oval operculum with a subcentral or anterior nucleus, or with the nucleus near the center of the right (abaxial) margin, against the *outer* lip, and with a subspherical to moderately elongate, inflated shell in which the anterior siphonal canal is straight or at most moderately twisted, except for the strongly twisted canal of adult specimens of *Cypraecassis* Stutchbury, 1837 (but note that the canal is straight in juvenile specimens of *Cypraecassis* spp.).

The genera included in the subfamily are *Cassis* Scopoli, 1777, *Cypraecassis* Stutchbury, 1837, *Galeodea* Link, 1807, *Microconsia* Beu, 2008, and *Sconsia* Gray, 1847. The status of some apparent members is still to be determined, such as *Menthafontia* MacNeil in MacNeil & Dockery (1984: 111); based on *Phalium* (*Menthafontia*) *menthafons* MacNeil in MacNeil & Dockery (1984: 112, pl. 17, figs 10-13), which to judge from its untwisted anterior siphonal canal seems to be a very tall-spined relative of *Cassis*, related to *Cassis* and *Galeodea* rather than to *Phalium* and *Echinophoria*. Subfamily Oocorythinae was recognized by me (Beu, 2008) to include *Dalium* Dall, 1889, *Eucorys* Beu, 2008, and *Oocorys* Fischer, 1884, genera that some authors (including me) previously have included in the Cassinae.

Genus **CASSIS** Scopoli, 1777

Cassida Brünnich, 1772: 248. No included species (junior homonym of *Cassida* Linnaeus, 1758).

Cassis Scopoli, 1777: 393. Type species (by subsequent designation, Dall, 1909a: 60): *Buccinum cornutum* Linnaeus, 1758, Recent, Indo-West Pacific.

Cassidea Bruguière, 1792a: 414. Type species (by subsequent designation, Cossmann, 1903: 123): *Buccinum cornutum* Linnaeus, 1758.

Cassinia Rafinesque, 1815: 45 (emendation of *Cassis* Scopoli, 1771).

Goniogalea Mörch, 1857: 21; 1877: 37. Type species (by subsequent designation, Cossmann, 1903: 124): *Cassis madagascariensis* Lamarck, 1822, Pliocene-Recent, western Atlantic.

Galeodocassis Sacco, 1890: 18. Type species (by original designation): *Cassis* (*Galeodocassis*) *anceps* Sacco, 1890 (junior secondary homonym of *C. anceps* H. & A. Adams, 1858), = *Cassisola saccoi* Rovereto, 1900, Oligocene, Italy.

Cassisola Rovereto, 1899: 107 (unnecessary replacement name for *Cassis* Klein, 1753, pre-Linnean).

Coalingodea Durham, 1942: 186. Type species (by original designation): *Galeodea tuberculiformis* Hanna, 1924, Eocene, California.

Hypocassis Iredale, 1927a: 322. Type species (by original designation, Iredale, 1927a: 329): *Cassis bicarinata* var. *decrensensis* Hedley, 1923 (= *C. fimbriata* Quoy & Gaimard, 1833), Recent, southern Australia.

Nannocassis Iredale, 1927a: 322. Type species (by original designation, Iredale, 1927a: 328): *Cassis nana* Tenison Woods, 1879, Recent, northern New South Wales and southern Queensland, Australia.

Remarks.—*Cassis* contains the Cassinae of small to very large size [*C. cornuta* (Linnaeus, 1758) reaches more than 350 mm H, whereas adult specimens of the restricted Western Australian Recent species *C. patamakanthini* Parth, 2000, are about one tenth of this size] with a thin to large and massive apertural shield covering much or all of the venter of the shell, with varices retained at positions of growth pauses, with a weakly to moderately twisted anterior siphonal canal, and with a small, narrowly oval operculum, much smaller than the aperture of the shell, with a subcentral nucleus or the nucleus at the center of the right margin, against the *outer* lip of the aperture.

Cassis abbotti Bouchet, 1988, from the Chesterfield Plateau, in the Coral Sea midway between New Caledonia and Queensland, Australia, is a small (40 mm H), completely smooth, polished species with varices retained all down the shell, pale coloration (largely white, with faint yellowish spots), the ventral callus limited to the columellar base and a collar to its left over the siphonal fasciole, a narrow aperture with both lips evenly and finely ridged for their full height, and a moderately strongly twisted siphonal canal (Bouchet, 1988; Kreipl, 1997: pl. 5, fig. 7). This combination of characters is not known in any other species of Cassinae, and at first glance, this species seems to belong in an unnamed genus. It resembles *Sconsia* spp. (particularly the unusual, smooth Recent Caribbean species *S. alexarthuri* Parth, 1994) most in overall appearance, but is shaped much more like a juvenile specimen of a *Cassis*, and is unique in completely lacking sculpture and in having the ventral callus limited to a thick collar over the siphonal fasciole. However, the recently described species *C. kreipli* Morrison, 2003, is quite similar to *C. abbotti* in its smooth surface and in having a small callus shield limited to the columellar base and to a collar over the siphonal canal, and [if this is not just a smooth juvenile form of *C. fimbriata* (Quoy & Gaimard, 1835)] suggests that *C. abbotti* is correctly regarded as a pedomorphic species of *Cassis*.

The subgenus *Hypocassis* Iredale, 1927, was maintained by Abbott (1968) for the relatively small living Australian species *Cassis fimbriata* (Quoy & Gaimard, 1833) and *C. nana* Tenison Woods, 1879, even though he stated that it “differs little from true *Cassis*” and “could be ... synonymised with

Cassis.” I synonymized (Beu, 2005, 2008) *Hypocassis* and *Nannocassis* Iredale, 1927, with *Cassis*, on the grounds that their sole distinguishing character, the large paucispiral protoconch, is a developmental difference of no phylogenetic significance. *Cassis fimbriata* and, in particular, *C. patamakanthini* seem to be more closely related to European Miocene fossil species such as *C. mammillaris* (Gratoloup, 1827) rather than to the other Australian species. Other species that have been placed in this subgenus (apparently mainly because they occur in Australia) are *C. torva* Iredale (1927b: 335, pl. 46, fig. 7; Abbott, 1968: pl. 40), a rare Recent species from southern Queensland (not fossil, as claimed by Abbott; no fossiliferous marine Cenozoic deposits occur near Caloundra) and *C. kreipli*. Although *C. kreipli* is little different from a smooth, orange-brown juvenile form of *C. fimbriata*, *C. torva* is widely sundered from all other Australian species; its elaborate spiral and axial sculpture suggests that it could be more nearly related to Paris Basin Eocene fossil species than to *C. fimbriata*. *Hypocassis* is not a monophyletic Australian clade, but a haphazard assemblage of unrelated species that have arrived in Australia after evolving in other parts of the world, and independently have lost planktotrophic development.

One genus-group taxon that safely can be removed from all relationship with *Cassis* is *Mangkalia* Beets, 1941 (type species: *Cassis?* (*Mangkalia*) *martini* Beets, 1941: 87, pl. 5, figs 187–192; Miocene of Mangkalihat Peninsula, eastern Borneo). The few, enormous fragments on which Beets based this species (examined at RGM; Beu, 2005: 152, figs 325–327) demonstrate no characters in common with *Cassis*, and have several highly distinctive characters, such as resorbed internal shell walls and an almost flat, *Conus*-like spire with a tall, narrow central “spike” of early whorls. The anterior end has the remains of a low, wide, smooth siphonal fasciole. The lack of any characters of the columella and aperture make its classification difficult. However, the thick shell (up to 10 mm thick in places), the smooth exterior apart from prominent growth lines, the weakly wavy shoulder outline (with few, very low, wide swellings rather than actual nodules), and the long, gradually tapering last whorl suggest that this is a huge (300–350 mm H), very distinctive, low-spired species of *Turbinella* Röding, 1798.

Illustrations, synonymies, and descriptions of the living western Atlantic *Cassis* species can be found in the monographs by Clench (1944) and Abbott (1968), and some of this information is not repeated here. However, the opportunity is taken to clarify the type specimens of the early species names, and to clarify synonymies in some cases. Excellent colored illustrations were also provided by Kreipl (1997), and are referred to where relevant.

Cassis altispira n. sp.

Pl. 55, Figs 1-3; Pl. 56, Figs 1, 3, 7

?*Cassis flammea*. Gabb, 1881: 356; Olsson, 1922: 307 (not *C. flammea* Linnaeus, 1758).

?*Cassis* sp. cf. *tuberosa*. Vokes, 1990b: 121, pl. 2, figs 2a-d.

Description.—Moderately large for genus (largest seen 155 mm H), tall and narrow, with moderately high spire for genus, moderately wide, gently sloping sutural ramp, and long, weakly inflated, gradually tapering last whorl. Sutural margin of sutural ramp located at shoulder angle (*i.e.*, extending around crests of shoulder nodules) on juvenile specimens and on early whorls of adults, descending below shoulder angle slightly, but increasingly further, over last three intervariceal intervals of adults, to reveal adapical edge of callus shield progressively with increasing size, producing unusually tall, weakly stepped spire. Major spiral sculpture of adult specimens of three low, rounded, vaguely defined spiral ridges, one at shoulder angle and two almost evenly spaced between shoulder and siphonal canal, raised into small to large, narrowly rounded, anteroposteriorly compressed nodules, 9-12 small, almost even-sized ones on last intervariceal interval on immature specimens, and 6-8 on adults, some much larger and more compressed than others and curved adapically, particularly one at mid-dorsum; lower major cords weak on or absent from immature specimens, moderately prominent on adults, bearing 4-6 low, rounded, widely spaced nodules on last intervariceal interval on adults. Minor spiral sculpture of *ca.* 20 low, rounded, weakly defined, closely spaced cords occupying entire last whorl below shoulder angle on immature specimens, moderately prominent on small juvenile specimens, and decreasing in prominence with increasing size; spiral cords narrow, weakly defined and widely spaced on adults; 2-4 low, very narrow, widely spaced spiral threads at center of sutural ramp on juvenile specimens, fading out over medium-sized immature specimens, not present on last two whorls. Axial sculpture of low but obvious, narrow, closely but irregularly spaced ridges, *ca.* 20 on last intervariceal interval of juvenile specimens and *ca.* 50 on moderately large immature specimens, less well-defined on large adults, more-or-less evenly rounded over earlier half of last intervariceal interval and sharp-edged, bevelled with abapertural shorter face and adapertural longer face over latter half of last intervariceal interval; ridges markedly more prominent over narrow basal zone, above siphonal fasciole, than higher up; ridges prominent and narrow on sutural ramp of all specimens. Ventral callus shield moderately thin, with two anterior major spiral cords of previous whorl showing through, rounded-triangular in outline, extending only to just below shoulder angle adapically, to just beyond previous varix at left edge, and narrowly thickened and reflected at right edge; interior of outer lip

thickened into widely callused lip extending laterally over aperture from adapical end to basal quarter, merging into curved shell wall over basal quarter, lightly convex in outline to be widest at center of aperture, bearing 10-11 narrow, well raised nodules ("teeth") on inner margin, weakest at adapical and abapical ends and highest at center of lip, 4-5 at center of lip extended slightly into low transverse ridges over inner quarter of lip width, at adapical end widely spaced and commencing well below adapical end of aperture; inner lip with 16-18 prominent, long, narrow, widely spaced transverse ridges over full height of lip in juvenile specimens, more prominent over siphonal fasciole than higher up, with one larger at adapical end forming parietal ridge; ridges weakening over adapical half of lip with increasing size; adults with only 2-3 low, narrow, short, closely spaced parietal ridges, adapical half of lip otherwise smooth; basal half of lip bearing many prominent, long, narrow, weakly anastomosing ridges extending well into aperture, 4-5 on inner edge of basal half of columella prominently thickened into wide, square-edged ridges. Siphonal canal moderately long, rather weakly twisted, separated from base of whorl by wide, almost smooth depressed area, prominently demarcated by strongly and abruptly depressed adapical margin in juvenile specimens, weakly defined in adults; canal inclined strongly towards dorsum and moderately to right in basal view, forming large, very prominent, evenly rounded siphonal fasciole. Inner lip with large central pale brown area (presumably faded from dark brown), and two red-brown spots near left edge where previous varix shows through callus; terminal varix with five large red-brown spots on both outer edge and ventral face, two over sutural ramp and shoulder angle and one between each pair of major spiral cords and between lowest cord and siphonal canal. Protoconch small, tall, narrowly conical, with weakly impressed sutures, of 2.5 smooth whorls.

Dimensions.—Holotype: H 155.2, D (including shoulder nodules) 118.7 mm, D (parallel to aperture) 113.2 mm; largest paratype, NMB H 17974: H 146.9, D 100.9 mm; juvenile paratype, NMB H 17975: H 53.0, D 40.8 mm; NMB H 17981, from NMB 16824, Dominican Republic: H (incomplete) 142 mm, D 107 mm.

Types.—Holotype NMB H 17972 (Pl. 55, Figs 1-2), from NMB 18734, Cayo Agua Fm (Pliocene), 300 m WNW of Punta Piedro Roja, Bocas del Toro Basin, Atlantic Panama, coll. P. Jung and A. Heitz, 1995, with 1 large paratype, NMB H 17974, similar in size and preservation to holotype, 1 incomplete medium-sized paratype, NMB H 17975, and 1 complete immature paratype, NMB H 17973 (illustrated, Pl. 55, Fig. 3; Pl. 56, Fig. 7), all from the same locality as the holotype.

Other material examined.—**Fossils: Atlantic Costa Rica: Late Pliocene-Early Pleistocene**, Moín: NMB 18278 (2

frags, base of whorls with prominent spiral cords; assigned tentatively); NMB 18084 (1, incomplete); 18113 (1 complete juvenile, similar to that figured by Vokes, 1990b: pl. 2, figs 2a-d); Moín Fm, Limón, collection of Bernard Landau (4, small). Gabb (1881: 356) also recorded specimens of *Cassis flammea* (Linnaeus, 1758) from Limón, presumably referring to this species. **Atlantic Panama: Pliocene:** Cayo Agua Fm: NMB 17808, Cayo Agua (1 poor); 18373, Cayo Agua (2); Shark Hole Point Fm?: NMB 18387, E coast of Fish Hole, E coast Isla Bastimentos, Bocas del Toro Basin (2 large frags and 1 apex); 18388, locality same as last (1 medium-sized, incomplete, with prominent spiral cords). Olsson (1922) also recorded specimens of *C. flammea* from Atlantic Panama, again presumably referring to this species. **Panama, Darien: Late Miocene:** NMB 18510, Tuirá Fm, Río Tuquesa, between village of Marraganti and Boca Marraganti (1, incomplete, medium-sized, with prominent, widely spaced spiral cords). **Dominican Republic: Early Pliocene:** NMB 16824, Gurabo Fm, Río Cana, bluff at upstream end of bends near mouth of Cañada de Zamba (1 incomplete, illustrated, NMB H 17981; Pl. 56, Figs 1, 3); much larger than but with much narrower apertural shield than specimens of *C. sulcifera* G. B. Sowerby I, 1850). **Venezuela: Late Pliocene,** Mare Fm, Cabo Blanco: NMB 13355 (1, incomplete; color showing on exposed outer lip); NMB 17512 (4 large frags, canal inclined to right). **Ecuador: Late Miocene:** NMB 19122, Angostura Fm, shellbed 2.5 m below oyster bed, Punta Verde, 30 km ENE of Esmeraldas, Esmeraldas Province (1, abraded small spire, not certainly identifiable). **Pliocene:** Onzole Fm, Quebrada Camarones [BMNH Palaeontology Department, GG22469, 1, incomplete, figured by Vokes (1990b: pl. 1, fig. 1), not certainly identifiable].

Other fragments that might well belong to this species, but are not identifiable with certainty, have been seen from: **Atlantic Costa Rica: Late Pliocene-Early Pleistocene,** Moín: NMB 18276 (2 frags). Robinson (1991) also recorded specimens that I have not seen, and that are probably juveniles of this species, from the Moín Fm at Limón (TU 953, 1 specimen; TU 954, 11 specimens; TU 956, 1 specimen; TU 1240, 2 frags; TU 1489, 3 frags). **Atlantic Panama: Pliocene:** NMB 18681, Escudo de Veraguas Fm, E end of Escudo de Veraguas, Bocas del Toro Basin (1 frag); NMB 18976, Shark Hole Point Fm?, E coast of Fish Hole, E coast of Isla Bastimentos, Bocas del Toro Basin (1 frag).

Remarks.—*Cassis altispira* n. sp. evidently is the species that Gabb (1881) recorded from Limón as *C. flammea*, that Olsson (1922) recorded from Atlantic Panama as *C. flammea*, and that Vokes (1990b) recognized as a new species in juvenile material from Limón, Costa Rica, and from Bowden, Jamaica. The incomplete, immature specimen from Bowden illustrated by Woodring (1928: 304, pl. 19, figs 5-6; as *C.*

sulcifera) is wider at the shoulder, producing a more triangular overall shape, and has weaker spiral sculpture than all specimens that I have seen of the *C. flammea-altispira* group, and more nearly resembles *C. tuberosa* (Linnaeus, 1758) and Dominican Republic specimens of *C. sulcifera*. Robinson (1991) also recorded juvenile specimens from Limón, under a manuscript name that remains unpublished. Seven juvenile specimens from Bowden, Jamaica (Late Pliocene), at NMB all have prominent, relatively widely spaced axial ridges similar to the type material of *C. altispira* n. sp.; two have prominent, relatively widely spaced spiral cords, and could well be specimens of *C. altispira* n. sp., whereas the other five all completely lack spiral sculpture and evidently represent still another unnamed *Cassis* species, not described here, although it is possible that they are juvenile specimens of *C. costulifera* n. sp. All are too small for certain identification, and identification of all the Limón and Bowden *Cassis* species must await the collection of larger (preferably adult) specimens. A juvenile specimen and several fragments from Limón at NMB are identified as *C. altispira* n. sp. (listed above), if a little hesitantly because of their small size.

Cassis altispira n. sp. is easily recognized among western Atlantic *Cassis* species because of the tall, elongate shape of adult specimens, resembling that of the living Cape Verde Islands species *C. norai* Prati Musetti, 1995 (Prati Musetti, 1995; Kreipl, 1997: pl. 3, fig. 4), newly reported here also from Curaçao (Pl. 55, Figs 4-5). *Cassis altispira* n. sp. differs strongly from *C. norai* in having much weaker, more widely spaced axial ridgelets and more prominent spiral cords. The spire of *C. altispira* n. sp. is taller than in all other fossil or living *Cassis* species, except the Floridian Plio-Pleistocene species *C. ketteri* Parodiz & Tripp, 1992 (see below); the high spire is caused by the suture progressively descending further over the last three intervariceal intervals, below the top of the callus shield of the previous whorl, gradually revealing more and more of the top of the callus of previous growth pauses. In contrast, the high spire of *C. ketteri* is caused by the convex sutural ramp and the increasing angle of slope of the ramp with increasing size. Juvenile specimens of *C. altispira* n. sp. have prominent, sharp-topped, closely spaced axial ridges as in most other *Cassis* species, and the angular ridges persist but are weaker, more irregular, and less well-defined in adults. Juvenile specimens also have prominent, rather wide, closely spaced spiral cords all over the exterior, resembling those of juvenile specimens of *C. madagascariensis* (Lamarck, 1822), but the spiral sculpture of adults is much weaker than in *C. madagascariensis*, consisting of a few narrow, widely spaced angling ridges in a narrow zone below the lowest row of nodules but well above the siphonal canal, and vague, weak, widely and irregularly spaced spiral sulci between the three nodule rows; the sutural ramp lacks spiral sculpture over the last

two whorls. *Cassis altispira* therefore differs further from the Floridian Plio-Pleistocene species *C. ketteri* in having much weaker spiral sculpture, because the latter species has the same 18-20 prominent, widely spaced spiral cords on the last whorl as *C. floridensis* Tucker & Wilson, 1932 (see below). A further distinctive character of *C. altispira* is the siphonal canal directed to the right (in basal view) much more strongly than in any other *Cassis* species of which I am aware, other than the West African species *C. tessellata* (Gmelin, 1791). *Cassis altispira* n. sp. differs from *C. tessellata* in its much smaller size, its larger shoulder nodules, and its more prominent spiral cords. *C. altispira* n. sp. differs further from *C. tuberosa* in the much thinner ventral callus shield, which does not develop into the very thick, wide, triangular shield of *C. tuberosa*, in lacking the prominent, finely reticulate microsculpture that covers the exterior of *C. tuberosa*, in lacking the large parietal nodule on the inner lip of *C. tuberosa*, in the ridges inside the outer lip commencing further down the aperture as in *C. ketteri*, and in lacking dark brown areas between the ridges on the inner edge of the outer lip. It differs further from *C. flammea* in its much larger size and larger dorsal nodules (perhaps limited to male specimens), and in having obvious, if weakly defined, spiral sculpture. It differs further from *C. madagascariensis* in its smaller size, in the development of large shoulder nodules in some specimens, and in lacking the dark brown areas between the ridges on the inner edge of the outer lip.

Distribution.—*Cassis altispira* n. sp. is recorded so far from Early to Late Pliocene or Early Pleistocene rocks of the Caribbean region, at Limón, Costa Rica, along the Atlantic coast of Panama, and in the lower Mare Fm of Venezuela. It possibly occurs also at Bowden, Jamaica, but Bowden specimens (which belong to at least two species) are too small for certain identification. A single specimen is recorded also from Late Miocene rocks of Darien, in the eastern Pacific; this is only the fourth specimen of *Cassis* recorded from Cenozoic rocks of western America. The specimen recorded by Vokes (1990b) from the Onzole Fm (Pliocene) in Ecuador could well belong to *C. altispira* n. sp. also, but is too incomplete for certain identification; another Late Miocene specimen from Ecuador is recorded here, but also is too incomplete for certain identification. Also, a single specimen from Early Pliocene rocks of the Dominican Republic (NMB H 17981, from NMB 16824; Pl. 56, Figs 1, 3) is much larger than all of the specimens of *C. sulcifera* from there, has a much narrower and thinner apertural shield than specimens of *C. sulcifera*, and is referred to *C. altispira* n. sp.

Etymology.—The specific name (Latin, “tall-spined”) refers to the most distinctive character of this new species.

Cassis costulifera n. sp.

Pl. 56, Figs 2, 4-6

Description.—Shell moderate-sized for genus (largest 108 mm H; immature?), with low, weakly dome-shaped spire, long weakly convex last whorl, thin, rounded-triangular callus shield, numerous small nodules on shoulder angle, and narrow, sharp-edged, prominent axial ridges over entire exterior of teleoconch of all specimens. Shoulder angle sharply rounded, bearing 5-10 small, moderately widely spaced, narrowly rounded, slightly axially elongate nodules over part or most of last intervariceal interval, very small on or absent from last third of each intervariceal interval, to produce weakly sculptured area coinciding with adapical area of callus shield of succeeding whorl; two very faint, low, vaguely defined spiral cords anterior to shoulder angle on two largest available specimens, bearing very faint, low swellings on one specimen, lacking nodules in all others, cords absent from juvenile specimens. Minor spiral sculpture of 7-10 low, rounded, closely spaced, moderately prominent cords over basal quarter of last whorl on juvenile specimens, commencing abruptly at adapical sharply defined edge of depressed groove above siphonal fasciole, decreasing in prominence rapidly and progressively adapically; cords remaining prominent on some larger specimens, weakening somewhat on others; spire of most specimens bearing 2-5 low, very narrow, widely spaced spiral threads in center of sutural ramp. Axial sculpture of many narrow, closely spaced, sharp-edged axial costellae, ca. 53-58 on last intervariceal interval, becoming lower, wider, more widely spaced and bevelled, with short abapertural face and long adapertural face, over latter half of last intervariceal interval of two largest specimens available; costellae passing consistently and regularly across sutural ramp, shoulder angle, and last whorl of all complete specimens, except where shoulder angle bears nodules. Ventral callus shield thin, rounded-triangular, extending only to shoulder angle adapically, to previous varix at left edge, weakly and narrowly reflected over whorl surface at outer lip, smooth and polished except for 16-20 long, narrow, prominent, widely spaced, weakly anastomosing transverse ridges on inner lip, without differentiated parietal ridge; 4-6 ridges markedly more prominent than others on base, interior to siphonal fasciole; interior of outer lip strongly thickened internally to form wide lip extending across outer edge of aperture, bearing 10-11 narrow, prominent transverse ridges (“teeth”) on inner margin, of similar prominence down entire lip on some specimens, uppermost three weaker than others on some; central 6-7 ridges raised into prominent, inclined, transverse ridges over up to inner half of lip on most specimens, ridges descending toward anterior (abapically) and toward exterior. Siphonal canal moderately strongly twisted toward dorsum and weakly toward right, producing promi-

nent, evenly rounded siphonal fasciole separated from previous whorl by moderately wide, almost smooth groove. Color pattern largely faded from available specimens, apparently with five red-brown spots on at least outer edge of terminal varix. Protoconch small, as in *Cassis altispira* n. sp., but with slightly wider apex.

Dimensions.—Holotype: H 89.0, D 67.9 mm; largest paratype, NMB H 17979: H 107.8, D 75.8 mm; paratype, NMB H 17978: H 76.3, D 57.1 mm; juvenile paratype, NMB H 17977: H 47.7, D 36.7 mm.

Type material.—Holotype NMB H 17976 (Pl. 56, Figs 4-5), from NMB 18668, Escudo de Veraguas Fm (Pliocene), N coast of Escudo de Veraguas Island, Bocas del Toro Basin, Atlantic Panama, coll. P. Jung, A. Heitz, and J. Todd, 1995; with 1 juvenile paratype NMB H 17977 (Pl. 56, Figs 2, 6); 2 paratypes NMB H 17978 and 17979, from NMB 17829, Cayo Agua Fm (Pliocene), E coast of Cayo Agua, Bocas del Toro Basin, Atlantic Panama (1 moderately small, resembling holotype; 1 moderately large, poorly preserved, larger and more elongate than holotype but slightly incomplete).

Other material examined.—**Fossils: Atlantic Costa Rica: Pliocene:** NMB 17450, Río Banáno, near Limón (1 frag). **Atlantic Panama: Pliocene:** NMB 18733, Cayo Agua Fm, 1 km SE of Punta de Tiburón, Cayo Agua (1 frag); 18738, Cayo Agua Fm, small island off of coast W of Punta de Nispero, Cayo Agua (1 poor). Bernard Landau (pers. comm., 2006) also collected a specimen (not seen) from Cayo Agua Fm near Punta Nispero (Coates, Appendix A in Collins & Coates, 1999: 292, map 6), 10°32.2'N, 82°02'32.0" to 00°42.1"W.

Remarks.—*Cassis costulifera* n. sp. is easily distinguished from all other *Cassis* species in (a) retaining the thin, sharp, closely spaced axial costellae at a large size, (b) having numerous very small nodules around the shoulder angle but only faint expressions of nodules lower down the shell, (c) having little spiral sculpture, even on juvenile specimens, except in a narrow zone immediately above the shallow spiral sulcus between the last whorl and the siphonal canal, (d) retaining its low, dome-shaped spire and rounded-conic shape at a relatively large size, and (e) having prominent ridges inside the outer lip and on the inner lip, closely resembling those of *C. sulcifera* but with a group of larger, coarser ridges on the base of the inner lip, on the interior of the siphonal fasciole, that is not as well developed as in *C. sulcifera*. The axial ridgelets, although more prominent than in any other American *Cassis* species, are fewer, coarser, and more widely spaced than in *C. norai* Prati Musetti, 1995 (Pl. 55, Figs 4-5), in which a fine microsculpture of very close axial ridgelets is one of the most distinctive characters. The relatively large size, the small nodules at the shoulder angle, the lack of nodules lower down the shell, and the more prominent, persistent, and more closely spaced axial ridges distinguish it from *C. flammea*. A few Recent

specimens of *C. flammea* have been examined with sculpture consisting only of narrow axial ridges as in *C. costulifera* n. sp. (most notably SMF 306002/4, unlocalized, Caribbean, H 56.9, D 42.0 mm, with 35 regular, bevelled axial ridges on last whorl, long face of ridges toward aperture, short face away from aperture), suggesting the possibility that *C. costulifera* n. sp. was directly ancestral to *C. flammea*. The axial costae are even sharper, narrower, and more consistently present than on *C. sulcifera*; *C. costulifera* n. sp. reaches a larger size than *C. sulcifera* and it differs very obviously from *C. sulcifera* in its very much smaller nodules and smaller ventral callus shield. The much smaller size of available specimens of *C. costulifera* n. sp., the very much smaller nodules, and the much weaker development of the ventral callus shield distinguish it immediately from *C. madagascariensis*, *C. jameshoubrieki* Petuch, 2004, and *C. tuberosa*, but these characters probably result at least partly from all the available material being immature. Nevertheless, the small nodules, the weak development of spiral sculpture, and the prominence of the axial ridges clearly distinguish it from both *C. madagascariensis* and *C. tuberosa*. Clearly, the weak spiral sculpture distinguishes it also from the Floridian Plio-Pleistocene species *C. floridensis* and *C. ketteri*, both of which have very prominent spiral sculpture. More large, adult specimens of *C. costulifera* n. sp. will help to define the characters of adults, but the essential differentiating characters are displayed well by the available material.

Distribution.—*Cassis costulifera* n. sp. is recorded so far only from Pliocene rocks along the Atlantic coast of Costa Rica and Panama, although it is quite possible that some of the juvenile *Cassis* specimens from Bowden, Jamaica, that lack spiral sculpture belong to this new species (NMB10635, 10651, and 11146, 5 specimens). Larger specimens are required from Bowden before their identification can be confirmed.

Etymology.—The specific name (Latin, “bearing little ribs”) refers to the retention of many narrow axial ridges throughout ontogeny, the most distinctive character of this species.

Cassis delta Parker, 1948

Cassis delta Parker, 1948: 91, pl. 6, figs 1-1b, 2-2b; Abbott, 1968: 51, pl. 24 (copy of Parker's plate); Vokes, 1997: 212.

Remarks.—Abbott (1968: 51) suggested that *Cassis delta* from the Chipola Fm (late Early Miocene) of Florida might be a synonym of *C. sulcifera*. However, Parker (1948) correctly pointed out that *C. delta* differs from *C. sulcifera* in several significant characters. First, it reaches a much larger size – 138 mm H, rather than 80 mm in *C. sulcifera*. Also, the inner edge of the outer lip bear 8-10 or more very prominent, high, narrow teeth that extend as ridges a short way across the lip or even, in large specimens, up to halfway across the lip in *C.*

sulcifera, whereas *C. delta* has eight short denticles, very much smaller than those of *C. sulcifera*. Similarly, *C. sulcifera* has 16-24 prominent, narrow ridges on the inner lip that extend well across the callus shield; the number of ridges increases with age, and both number of ridges and the distance they extend across the shield increase with increasing callus thickness. In contrast, *C. delta* has only 10 small teeth on the inner margin of the lip, not extending across the callus at all. A further difference not noted by Parker (1948) is that the aperture is much wider in *C. delta* than in *C. sulcifera*, particularly in small, weakly callused specimens. Also, the narrow axial ridges are much more numerous and prominent in *C. sulcifera* than in *C. delta* and, although both species produce a very extreme, wide, triangular callus shield in some adult (presumably male) specimens, the left top extremity of the callus shield (in conventional spire-upward apertural orientation) of *C. delta* has a more rounded margin and a more sinuous posterior margin than that of *C. sulcifera*. There is no doubt that these are distinct species.

Dimensions.—Holotype: H 138, D 97, “greatest width” of apertural shield 140 mm; paratypes: H 134, D 101 mm; H 44.7, D 32.7; H 41.2, D 27.5 mm (Parker, 1948: 92).

Types.—Holotype and one paratype USNM 543482; two paratypes ANSP 18680 (Parker, 1948: 92; not seen), from Chipola Fm, bank of Ten Mile Creek “on the east side of the bridge of Florida highway no. 84”, 7.6 km N of Clarkesville, Calhoun Co, Florida. I have not seen material of this species.

Distribution.—To my knowledge, *Cassia delta* is limited to the Chipola Fm in Florida, USA.

Cassia flammea (Linnaeus, 1758)

Pl. 61, Figs 1-2

Buccinum flammeum Linnaeus, 1758: 736; 1767: 1199; Gmelin, 1791: 3473.

Cassidea flammea. Bruguière, 1792a: 429; Lamarck, 1816: pl. 406, figs 3a-b; “Liste des objets”: 3.

Cassia marmorata Röding, 1798: 29.

Cassia alba Perry, 1811: pl. 33, fig. 2.

Cassia flammea. Lamarck, 1822: 220; Kiener, 1835b: 6, pl. 3, figs 5, 5a; Deshayes, 1844: 23; Reeve, 1848b: pl. 5, figs 12a-b; Küster, 1847: 20, pl. 43, fig. 5; Trechman, 1933: 39; Clench, 1944: 12, pl. 6; Abbott, 1968: 51, pl. 3, figs 7-8; 1974: 162, fig. 1746; Warmke & Abbott, 1962: 98, pl. 1, fig. e; Work, 1969: 659; H. & E. Vokes, 1983: pl. 9, figs 14, 14a; Diaz & Götting, 1988: 156; Lipe & Abbott, 1991: 4, illus.; Diaz & Puyana, 1994: 170, fig. 631; Kreipl, 1997: pl. 2, figs 2, 2a-b; Redfern, 2001: 58, pl. 29, figs 248A-B.

Cassia (Goniogalea) flammea. Mörch, 1877: 37.

Remarks.—Abbott (1968) and Kreipl (1997: pl. 2, figs 2-2b) provided excellent colored illustrations. *Cassia flammea* is the smallest of the living western Atlantic *Cassia* species, reaching

ca. 130 mm H, with a taller spire than all other living western Atlantic species (other than *C. norai*), and without the fine reticulate sculpture of most other species and, indeed, most specimens lack spiral sculpture altogether, even when juvenile. The figure by Clench (1944: pl. 6) shows weak spiral cords between the main nodule rows, and the Pleistocene specimen from the La Isabella Fm (Pleistocene) of the Dominican Republic, in Bernard Landau's collection, has weak spiral cords over the basal area, below the lowest row of nodules and above the sulcus margining the siphonal canal. *Cassia flammea* has an oval callus shield that does not develop the extensive projections beyond the shell outlines of the other Recent western Atlantic species, and without the dark brown coloration of the interior of the outer lip, between the transverse ridges, that characterizes both *C. madagascariensis* and *C. tuberosa*.

I agree with Vokes (1990b: 124) that *Cassia subtuberosa* Hanna (1926: 444, pl. 20, fig. 8, pl. 29, figs 2-3; Schenck, 1926: 75, pl. 12, figs 2, 4; Abbott, 1968: 51, pl. 25) is based on a specimen very closely similar to, if not conspecific with, *C. flammea*. Schenck (1926: 75) stated that it differs from *C. tuberosa* in having smaller nodules, in the absence of posterior denticles on the inner lip, and in having the callus shield expanded further anteriorly. The oval shape, small exterior nodules, and oval callus shield extending well anteriorly are characters agreeing with those of *C. flammea*. The locality is an unexpected one: Alverson Canyon, Coyote Mountains, Imperial Co, California, USA, Latrania Fm (Late Miocene) (G. Vermeij, pers. comm., April 2008; Demere & Rugh, 2006). Vokes (1990b) also recorded *C. cf. subtuberosa* from the Onzole Fm (Pliocene) at Punta Camarones, Ecuador, but the specimen she recorded probably belongs to *C. altispira* n. sp.

Dimensions.—Clench (1944: 13) provided dimensions of a range of three adult specimens: large, Grand Bahama Island: H 135, D 100 mm; “average,” Cat Island, Bahamas: H 109, D 82 mm; small, Puerto Sosúa, Hispaniola: H 72, D 50 mm; lectotype of *Buccinum flammeum*, UUZM 931: H 90.4, D 63.8 (Mats Eriksson, UUZM, pers. comm., 25 August 2008); GSN WM19026, off of St. François, Guadeloupe, 20-25 m: H 113.0, D 83.2 mm, H 111.6, D 79.1 mm.

Types.—No specimens representing *Buccinum flammeum* are present in Linnaeus' collection, housed by the Linnean Society of London. Clench (1944: 13) selected a “type figure,” that by Rumphius (1705: pl. 23, fig. 2), in effect designating the illustrated specimen as the lectotype of *B. flammeum*, although not formally. However, a type specimen has not been clarified. Linnaeus (1758: 736) cited for *B. flammeum* only the illustrations by Buonanni (1681, vol. 3: pl. 161) and Rumphius (1705: pl. 23, fig. 2). Neither of these illustrated specimens is available in collections today, and that illustrated by Buonanni appears to be a specimen of *Cypraecassis testiculus*

(Linnaeus, 1758) rather than *Cassis flammea* [note that this figure was also cited by Linnaeus (1758: 735) for *B. plicatum*]. Wallin (1993: 50) listed three putative syntypes of *B. flammeum* at the Uppsala University Zoological Museum, no. UUZM 931 (identity confirmed by the well-known malacologist Nils Odhner) and UUZM 1118a-b. Olle Israelsson (UUZM) kindly sent digital images of these specimens in October 2004, confirming that all three are, indeed, *C. flammea* of all authors after Linnaeus (1758). I have previously assumed (Beu, 1998b: caption to fig. 22) that there is no evidence that any of the Thunberg or other of Queen Ulrica's specimens was an original syntype available to Linnaeus (1758). However, Mats Eriksson (UUZM) recently informed my colleague Gijs Kronenberg (Eindhoven, The Netherlands, in e-mail 02 December 2007) that "the manuscript of this work ["Museum Ludovicae Ulricae"] was written long before its publication. Linnaeus visited the Queen's collection several times starting 1751 ... The publication was however postponed several times ... Linnaeus ... financed the publication himself in 1764. Linnaeus refers to the manuscript already in the tenth edition of *Systema Naturae* ... He continued to visit the Queen's collection until 1770 ... Unfortunately Linnaeus did not label any specimens in the collection. The Queen's collection was donated to Uppsala University by King Gustav IV Adolf in 1804. Some of the specimens in the Queen's collection were considered duplicates and sold to private collectors. ... By a financial donation of King Carl XIII the University was able to buy these collections [back] from the private collectors. The written labels were made by Carl Peter Thunberg when the collections were merged with the University collection." It therefore seems likely (although it is difficult to prove) that the specimens labeled by Thunberg were seen by Linnaeus and that at least most specimens from Queen Ulrica's collection are, therefore, authentic syntypes of Linnaeus' species. In view of the lack of evidence to the contrary, specimen UUZM 931 (Pl. 61, Figs 1-2) is assumed to be a syntype of *B. flammeum*, and is here designated the lectotype. Specimens illustrated by me (Beu, 1998b: caption to fig. 22) will require reconsideration in the light of Eriksson's evidence. The type locality of *C. flammea* is here designated as Grand Bahama Island. The same reasoning as is followed here also applies to the lectotype selection for *C. tuberosa*, below.

Other material examined.—**Fossils:** **California:** **Early Pliocene:** Possibly represented by the record of *Cassis subtuberosa* Hanna (1926: 444; Abbott, 1968: 51, pl. 25) from Latrania Fm (formerly classified as Imperial Fm), Alverson Canyon, Coyote Mountains, Imperial Co. **Barbados:** **Pleistocene:** BMNH Palaeontology Department, G69048, post-Coral Rock, Highgate, coll. C. T. Trechman (1; Trechman, 1937); BMNH Palaeontology Department, GG4095, Coral Rock, Highgate, coll. C. T. Trechman (1 large and several small spec-

imens). **Venezuela:** **Late Pliocene/Pleistocene:** NMB 17515, Mare Fm upper shellbed, Punta Gorda, Cabo Blanco, coll. J. & W. Gibson-Smith (1, cf.). **Pleistocene:** La Isabella Fm, El Castillo, La Isabella, collection of Bernard Landau (1). Two fragmentary specimens from NMB 17531, Punta Gavilán Fm (Early Pliocene) at Punta Gavilán, northern Venezuela, coll. J. & W. Gibson Smith, lack diagnostic characters and could belong to *C. flammea*, *C. costulifera* n. sp., or another species altogether.

Distribution.—*Cassis flammea* lives now in the western Atlantic from the Bahamas south through the Caribbean Sea and Yucatan (H. & E. Vokes, 1983: pl. 9, figs 14, 14a) to the northern coast of Venezuela. There seem to be no records from Brazil. Fossils are recorded only from Pleistocene localities and from the Mare Fm (Late Pliocene/Pleistocene) in Venezuela, unless the holotype of *C. subtuberosa* (from California, USA) is a specimen of *C. flammea*, a point that can be decided only by collecting more material from the Latrania Fm.

Cassis flintensis Mansfield, 1940

Cassis sulcifera. Dall, 1916: 508, pl. 86, fig. 4; Abbott, 1968: 53 (not *C. sulcifera* G. B. Sowerby I, 1850).

Cassis flintensis Mansfield, 1940: 214, pl. 27, figs 47-49; MacNeil & Dockery, 1984: 103, pl. 17, figs 5-8, pl. 49, fig. 6.

Remarks.—Abbott (1968: 53) synonymized *Cassis flintensis* with *C. sulcifera*, but there is no doubt that this is incorrect, as was also concluded by Vokes (1990b). It is included here mainly to point out the distinction. *Cassis flintensis* was proposed for the specimen from the Flint River, Georgia (Oligocene), which Dall (1916: 508, pl. 86, fig. 4) assigned to *C. sulcifera*, although Mansfield's (1940) holotype is another, much more complete specimen, also a silicified one from the Flint River. Dall's (1916) illustration shows a very different species from *C. sulcifera*, with a taller spire than in *C. sulcifera*, very prominent, narrow, clearly defined axial costae all over, much more prominent than those of *C. sulcifera*, crossed by narrow, widely spaced, regular but rather weak spiral costae, much more prominent than those present on *C. sulcifera*, and with at least two rows of moderately large, prominent, rounded nodules, one at the shoulder angle and the other just below, which are much more regular and uniform in size than those on specimens of *C. sulcifera* that I have observed. MacNeil & Dockery (1984: 103, pl. 17, figs 5-8, pl. 49, fig. 6) redescribed and illustrated an excellent specimen and fragments of *C. flintensis* from the Oligocene Mint Spring Fm of Mississippi, demonstrating that it is a very distinctive species with prominent, narrow spiral sculpture, and 2-3 rows of nodules below the peripheral ones, more nearly resembling European Eocene fossil species of *Cassis*, such as *C. elegans* Grateloup, 1835

(MacNeil & Dockery, 1984: pl. 49, figs 7-8), than any other American species.

Dimensions.—Holotype: H 48.5, D 33 mm; paratype 70 mm H (Mansfield, 1940: 215); specimen illustrated by MacNeil & Dockery (1984: pl. 17, figs 5-6): H 58.6, D 46.0 mm.

Types.—Holotype USNM 498499 (not seen), from USGS 14083, Flint River Fm (Oligocene; probably a Pleistocene weathering remnant of several Oligocene formations in Georgia; MacNeil & Dockery, 1984: 103), Flint River near Bainbridge, Georgia; paratype USNM 198500 (not seen), a mold from USGS 12723, Suwannee Limestone, upper bed, Parish Farm, 5 km SE of Wausau, Washington Co, Florida (MacNeil & Dockery, 1984: 103-104).

Distribution.—Mansfield (1940: 214) recorded *Cassidulinopsis flintensis* also from USGS 14281, 2.5 km north of Waynesboro, Mississippi (illustrated last whorl, USNM 498672), from ten further localities in Georgia, from the Suwannee Limestone at one locality in Florida, from one locality in the lower Chickasawhay Marl in Alabama, and from one locality in the Chickasawhay Marl in Mississippi. MacNeil & Dockery (1984: 104) recorded it from the Flint River Fm in Georgia, the Suwannee Limestone in Florida, and the Mint Spring Fm, Marianna Limestone, and Chickasawhay Limestone at five localities in Mississippi. Most localities are Oligocene, but MacNeil & Dockery (1984) suspected that a few might be Late Eocene. I have not seen material of *C. flintensis*.

***Cassidulinopsis floridensis* Tucker & Wilson, 1932**
Pl. 57, Figs 2-3

Cassidulinopsis floridensis Tucker & Wilson, 1932: 11, pl. 2, figs 2, 5, pl. 5, fig. 2; Parodiz & Tripp, 1992: 322, figs 1, 3, 5, 7, 9, 11; ?Petuch, 1994: pl. 37, fig. F (?not of Tucker & Wilson, 1932); 1997: fig. 66, fig. I.

Cassidulinopsis spinella. Petuch, 1994: pl. 36, fig. I, pl. 37, figs A-B (not *C. madagascariensis spinella* Clench, 1944).

Cassidulinopsis schneireli Petuch, 1994: 271, pl. 36, fig. J, pl. 37, figs C-D.

Remarks.—Examination of the figures by Parodiz & Tripp (1992) and Petuch (1994) and of the excellent collection of Bernard Landau has demonstrated that there are only two fossil *Cassidulinopsis* species in Florida Pliocene-Pleistocene rocks (apart from the recently named *C. jameshoubrieki* Petuch, 2004, which is known from only one locality). The more common is *C. floridensis*, which is very similar to *C. madagascariensis*, but differs in its fewer, more prominent, more widely spaced spiral cords. The shape, the range of nodule sizes (from the small-noduled *spinella* form, probably female, to the large-noduled “typical *madagascariensis*” form, probably male), and the nodules and ridges inside the inner and outer lips are all closely similar in both species, and the largest specimen of *C.*

floridensis seen, in Bernard Landau’s collection, is comparable with the largest *C. madagascariensis*. A juvenile specimen (59 mm H) in Landau’s collection agrees with the illustration of the holotype of *C. floridensis* by Tucker & Wilson (1932: pl. 2, figs 2, 5) in all characters, and particularly in the distinctive species characters, the relatively tall spire and the very prominent spiral cords. The other nine adult specimens in Landau’s collection, ranging from 146-229 mm H, all have 18-20 wide, prominent spiral cords, with clearly defined edges, and with interspaces each about equal in width to one cord. There are no consistent characters distinguishing the “species” separated by Petuch (1994), *C. spinella* (not of Clench, 1944) and *C. schneireli*, and in my opinion these are based on trivial shape and sculptural variants of *C. floridensis*.

Dimensions.—Bermont Fm, Palm Beach Rock pit: H 229, D 174 mm; H 163, D 123 mm; H 169, D 128 mm; H 146, D 110 mm; H 59, D 42 mm; Caloosahatchee Fm, Griffin Brothers pit: H 151, D 108 mm (all collection of B. Landau; dimensions kindly provided by Landau).

Types.—*Cassidulinopsis floridensis*, holotype not seen, supposedly in “Paleontology Mus., Cornell University” (Tucker & Wilson, 1932: 11), but never received by PRI; not present at USNM, or at Field Museum of Natural History, Chicago (where it was reported to be by Druid Wilson, pers. comm., 2000); from Acline, Florida, USA, Pinecrest Beds, middle Pliocene (Vokes, 1990b: 122). This type specimen presumably still exists in an American museum, but is not recognized at present. *Cassidulinopsis schneireli*, holotype (not seen) UF 66233, from Bermont Fm (Pleistocene), Palm Beach Rock Pit, Loxahatchee area, off State Road 80, W of West Palm Beach, Florida, USA (Petuch, 1994: 271).

Other material examined.—**Fossils: Florida: Pleistocene:** Bermont Fm, Palm Beach Aggregates Rock Pit, 3 km W of Loxahatchee on Florida Hwy 441, Palm Beach Co, collection of Bernard Landau (10, from juvenile of H 59 mm to adult of H 229 mm; Pl. 57, Figs 2-3). **Latest Pliocene:** Upper Caloosahatchee Fm, Griffin Brothers Pit, Holey Land area, Palm Beach/Broward Co line, collection of Bernard Landau (1 adult, H 151 mm).

Distribution.—*Cassidulinopsis floridensis* is recorded from several stratigraphical units of Late Pliocene and possible Early Pleistocene age from southern Florida, USA. (The stratigraphical positions assigned by various authors are difficult to resolve.) It differs from *C. madagascariensis* only in its more prominent spiral cords, and seems likely to have been the immediate ancestor of *C. madagascariensis*.

***Cassidulinopsis jameshoubrieki* Petuch, 2004**

Cassidulinopsis jameshoubrieki Petuch, 2004: 281, pl. 85, figs B-C.

Remarks.—*Cassis jameshoubrieki* was described by Petuch (2004: 281) as having a “triangular body cross-section and wide, sharply angled parietal shield.” Petuch consequently compared it only with *C. tuberosa*, but pointed out that it differs from *C. tuberosa* in lacking the fine, reticulate ornament and in having larger, more numerous nodules. In fact, the sculpture of low, wide, closely spaced, ill-defined spiral cords with three rows of nodules on the last whorl is much more like that of *C. madagascariensis* and *C. floridensis* than of *C. tuberosa*. It seems to be a relative of *C. madagascariensis* with a heavier and more triangular parietal shield than is present in Recent specimens. The relationship to *C. floridensis* is unclear, and it is possible that most material of *C. floridensis* is female, and that *C. jameshoubrieki* was based upon a male specimen of *C. floridensis*, which occurs in the same locality and formation. More material, preferably of a larger size, is needed to evaluate this species fully.

Dimensions.—Holotype: H 183, D 144 mm; paratypes: H 187 and H 172 mm (Petuch, 2004: 281).

Types.—Holotype AMNH.IP 50666, from “Holey Land Member equivalent, lower Bermont Fm [Pleistocene], in the Palm Beach Aggregates, Inc. quarry, Loxahatchee, Palm Beach County, Florida” (Petuch, 2004: 281; not seen); 2 paratypes from the same locality in Petuch collection.

Distribution.—*Cassis jameshoubrieki* is known only by the type material. It may well be limited to the lower Bermont Fm. However, it also seems possible that it is based on male specimens of *C. floridensis*.

***Cassis ketteri* Parodiz & Tripp, 1992**

Pl. 57, Figs 1, 4

Cassis ketteri Parodiz & Tripp, 1992: 318, figs 2, 4, 6, 8, 10, 12.

Cassis floridensis ketteri. Petuch, 1994: pl. 37, figs E, G.

?*Cassis floridensis*. Petuch, 1994: pl. 37, fig. F (?not *C. floridensis* Tucker & Wilson, 1932).

?*Cassis schnireli*. Petuch, 2004: 233, pl. 85, figs E-F (?not *C. schnireli* Petuch, 1994).

Remarks.—The only other *Cassis* species, besides *C. floridensis* and *C. jameshoubrieki*, that appears to occur in the Pliocene of Florida is *C. ketteri*. This species differs from *C. floridensis* in having a much taller, domed spire, in having much smaller nodules inside the outer lip, and in having weaker ridges and nodules on the inner lip, largely limited to the lower half of the lip. The interior of the outer lip bears ca. 10 small nodules along the actual lip edge, commencing well below the posterior (adapical) end of the aperture as in *C. altispira* n. sp., and contrasting strongly with the 10–12 prominent, wide nodules passing into transverse ridges that cross at least the inner half of the lip face and commence high on the lip in *C. floridensis*, as they do in *C. madagascariensis*. Petuch

(1994: pl. 37, figs E-F) did not illustrate the critical apertural characters of two of the specimens that he figured, but the high, domed spires of these two specimens suggest that both are *C. ketteri* [identified by Petuch (1994) as *C. floridensis* and *C. floridensis ketteri*, respectively]. The prominent, widely spaced spiral cords of *C. ketteri* are closely similar to those of *C. floridensis*.

Dimensions.—Pinecrest beds, APAC pit: H 145, D 107 mm; D 62, H 47 mm (collection of Bernard Landau; dimensions supplied by Landau); holotype: H 141, D 85 mm (Parodiz & Tripp, 1992: 322); larger specimen in a private collection: H 166, D 123 mm (Parodiz & Tripp, 1992: 322).

Types.—*Cassis ketteri*, holotype at Invertebrate Zoology Section, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, CM 47209, from Buckingham Fm (Pliocene), APAC Florida Inc. pit, Honore Road, Sarasota, Florida (Parodiz & Tripp, 1992: 322; not seen).

Other material examined.—**Fossils: Florida: middle Pliocene**, Pinecrest Fm, unit 10, TU 1000, Quality Aggregates phase 6 (APAC) pit, Sarasota, collection of Bernard Landau (2; 1 juvenile, 1 adult; Pl. 57, Figs 1, 4).

Distribution.—*Cassis ketteri* is recorded only from Pliocene rocks of Florida, USA, where it is less common than *C. floridensis*. It appears not to have produced any successors, and does not seem to be closely related to any of the other species described here from elsewhere in the tropical American region. However, the shape and particularly the high, domed spire are similar to those of the living West African species *C. tessellata* (Gmelin, 1791) (Abbott, 1968: pl. 3, figs 5–6; Ardevini & Cossignani, 2004: 123, 2 upper right figs, 124, upper left fig.), suggesting the possibility of a phylogenetic relationship between these two species.

***Cassis madagascariensis* Lamarck, 1822**

Pl. 58, Figs 1, 5; Pl. 59, Figs 1, 4

Cassis rotundata Perry, 1811: pl. 33, fig. 1 (*nomen oblitum*).

Cassis madagascariensis Lamarck, 1822: 219; Kiener, 1835b: 7, pl. 2, fig. 2; Deshayes, 1844: 20; Reeve, 1848b: pl. 2, fig. 5; Küster, 1857: 4, pl. 36, figs 1–2; Chenu, 1859: 206, figs 1120–1121; Krebs, 1864: 67; Clench, 1944: 14, pl. 7; Nowell-Usticke, 1959: 57; Richards, 1962: 79, pl. 17, fig. 9; Abbott, 1968: 52, pl. 3, fig. 9; 1974: 161, fig. 1744; Warmke & Abbott, 1962: 98, pl. 1, fig. f; Kaufmann & Götting, 1970: 369, fig. 79; Porter, 1974: 196; H. & E. Vokes, 1983: pl. 10, figs 5–5a; Bandel, 1984: 96, text-fig. 160, pl. 8, fig. 5; Jensen & Harasewych, 1986: 426, fig.; Lipe & Abbott, 1991: 4, illus.; Diaz & Puyana, 1994: 170, fig. 632; Kreipl, 1997: pl. 2, figs 3–3a; Redfern, 2001: 58, pl. 29, fig. 249 (*nomen protectum*).

Cassis cameo Stimpson, 1860a: c.3 (*nomen nudum*); 1860b: 443; Tryon, 1885: 271, pl. 2, fig. 50; Dall, 1889: 134; 1903b: 134; Maury, 1922: 118; Rogers, 1951: 137, pl. 35, fig. 2.

Cassis (Goniogalea) madagascariensis. Mörch, 1877: 37.

Cassis madagascariensis spinella Clench, 1944: 16, pl. 8; H. & E. Vokes, 1983: pl. 10, figs 4-4a.

Cassis aff. *madagascariensis*. Weisbord, 1962: 251, pl. 23, figs 9-10.

Cassis madagascariensis forma *spinella*. Warmke & Abbott, 1962: 99; Kreipl, 1997: pl. 2, fig. 3b.

Remarks.—*Cassis madagascariensis* is the largest living *Cassis* species in the western Atlantic, reaching at least 350 mm H (Abbott, 1968: 52), and is recognizable by (a) its widely flared callus shield that retains its oval shape in heavily calcified adults rather than becoming strongly triangular as in *C. tuberosa*, (b) its plain cream exterior with the spiral and axial sculpture low and not clearly defined, but with obvious, relatively wide spiral cords all over even the largest adults, (c) its flat-sided whorls and prominent shoulder angulation retained at a large size, (d) the three rows of moderately large, compressed nodules (extended in the spiral direction), (e) the black and salmon-pink areas on the callus shield, and (f) having the wide, dark brown to black bars on the inner edge of the outer lip that are present in *C. tuberosa* but absent from *C. flammea*. The form *C. madagascariensis spinella* Clench (1944: 15) is merely based on weakly sculptured specimens of *C. madagascariensis*. Clench (1944) thought that this weakly nodulose form was limited to the Lower Florida Keys, but it is now clear that the two forms are not segregated geographically, and weakly nodulose specimens occur throughout the range of *C. madagascariensis* (as was also concluded by Warmke & Abbott, 1962; Abbott, 1968: 52; and Kreipl, 1997). To judge from other species such as *C. cornuta* (Linnaeus, 1758) (Indo-West Pacific) (Abbott, 1968: 47, caption to pl. 3, fig. 4) and *C. tuberosa*, it seems likely that the form with small nodules around the periphery is female, whereas the form with large nodules is male.

The name *Cassis cameo* was attributed by Dall (1889) to Stimpson's (1860a) list of United States eastern coast shells, where it is a *nomen nudum*. However, as the synonymy by Clench (1944: 14) makes clear, in another almost simultaneous note about a visit to Beaufort, North Carolina, Stimpson (1860b: 443) stated that "The large *Cassis* to which we have applied the name *C. cameo* is identical with the common cameo-shell of the Bahamas, which usually figures in collections under the name *C. madagascariensis*" (*sic*). The name *C. cameo* is available from this reference, and it is clear that Stimpson established it as a replacement name for *C. madagascariensis*, apparently thinking that this name did not apply to the western Atlantic species.

Abbott (1968: 52) pointed out the earlier name *Cassis rotundata* Perry, 1811, and stated that he would apply to the ICZN to have the name declared a *nomen oblitum*, but he never submitted an application. The scientific community has become used to the names of Röding (1798) and Perry (1811), among others, supplanting those proposed by Lamarck (1816,

1822), and it is a pity that Abbott (1968) did not take the step of adopting this name in his very influential monograph. However, because the name *C. rotundata* has never been used as the valid name for a species, Petit (2003: 48) followed the required procedure of ICZN Article 23.9 and declared *C. rotundata* a *nomen oblitum*, and *C. madagascariensis* correspondingly a *nomen protectum*. The only exception of which I am aware to universal usage of the name *C. madagascariensis* for this species is *C. cameo*, which was used for this species by Maury (1922) and Rogers (1951).

Dimensions.—*Cassis madagascariensis* lectotype: H 283 mm; paralectotype: H 201 mm; USNM 877255, unlocalized: H 317, D 225 mm; USNM 124793, "West Indies": H 254, D 187 mm; USNM 818203, Abaco, Bahamas: H 241, D 192 mm; USNM 73332, Dry Tortugas, Florida: H 232, D 171 mm; USNM 653739, *spinella* form, NW of Campeche, Mexico: H 222, D 156 mm (USNM dimensions sent by M. G. Harasewych, pers. comm., 20 May 2008); NMNZ M262287, Nassau, Bahamas: H 134.4, D 108.0 mm (including large dorsal nodule); NMNZ M266752, Haiti: H 137.2, D 96.8 mm; GNS WM18937, Barbados: H 151.3, D 111.3 mm; GNS WM19024, off of St. François, Guadeloupe: H 284, D 213 mm.

Types.—Clench (1944: 15) selected a "type figure," that of Kiener (1835b: pl. 2, fig. 2), for *Cassis madagascariensis*. Because there are two syntypes, both correctly referred to this species, in Lamarck's collection in Geneva, and Clench's (1944) action is not a lectotype selection under the present ICZN Article 74, the specimen figured by Kiener (1835b: pl. 2, fig. 2) is here designated the lectotype of *C. madagascariensis*. The lectotype (MHNG 1100/77; Pl. 58, Fig. 1; Pl. 59, Fig. 4) is the larger of the two syntypes (H 283 mm); the paralectotype (NHMG 1100/78; Pl. 58, Fig. 5; Pl. 59, Fig. 1) is 201 mm H. Clench (1944: 15) stated somewhat equivocally of the type locality: "As the original locality of Madagascar was an error, Beaufort, North Carolina can be accepted on the basis of Stimpson's record" (a reference to Stimpson, 1860b), without using the words "type locality." The type locality is here formally designated as Beaufort, North Carolina. *Cassis madagascariensis spinella*, holotype MCZ 140761 (Clench, 1944: pl. 8), from "Tortugas, Florida." Because the name *C. cameo* was proposed as a replacement name for *C. madagascariensis*, it has the same type material as *C. madagascariensis*.

Material examined.—**Fossils: Venezuela: Late Pliocene:** NMB 17512, Mare Fm, Cabo Blanco, coll. J. & W. Gibson-Smith (1). This species was also reported as a fossil at Cabo Blanco by Weisbord (1962: 251, pl. 23, figs 9-10).

Distribution.—*Cassis madagascariensis* lives at present in the western Atlantic from North Carolina (Clench, 1944; Porter, 1974: 196), USA, to Bermuda and the Caribbean Sea, as far south as the northern coast of Venezuela. There seem to be

no records from Brazil. The only fossil specimen that I have seen from within the study area is from the Mare Fm (Late Pliocene/Pleistocene) at Cabo Blanco, Venezuela. Richards (1962: 79, pl. 17, fig. 9) also recorded Pleistocene fossil specimens from Cape Hatteras, North Carolina. The short time range is presumably accounted for by the evolution of *C. madagascariensis* from *C. floridensis*.

Cassis norai Prati Musetti, 1995
Pl. 55, Figs 4-5

Cassis tuberosa. Cosel, 1982a: 18; 1982b: 54; Guerreiro & Reiner, 2000: 96 (not *Buccinum tuberosum* Linnaeus, 1758).

Cassis norai Prati Musetti, 1995: 45, figs 1-2 (left); Kreipl, 1997: 16, pl. 3, fig. 4.

Cassis tuberosa forma *norai*. Ardovini & Cossignani, 2004: 123, upper left fig.

Remarks.—*Cassis norai* is a distinctive species, resembling *C. tuberosa* in general appearance, including size and coloration, but differing in being markedly taller and narrower in shape, with a taller spire, with much paler and less obvious maculations on the apertural face of the terminal varix, and with more coarsely cancellate sculpture on the last whorl. It also does not develop the heavy, triangular extension of the apertural shield at the top left (in conventional spire-up apertural view) that is so characteristic of *C. tuberosa*. *Cassis norai* resembles *C. flammea* in general appearance also, but differs from *C. flammea* in its larger size, fewer rows of nodules on the last whorl, taller and narrower shape, brighter coloration, and cancellate sculpture. The first apparently authentic record is listed here from Curaçao in the western Atlantic, demonstrating the feasibility of *C. norai* having descended from the Caribbean-Panamic Pliocene fossil species *C. altispira* n. sp.

Dimensions.—Holotype: H 132, D 75 mm; paratype: H 146, D 87 mm; Mindolo, São Vicente, coll. R. von Cosel: H 186.0, D 120.7 mm; GNS WM18926, Mindolo Bay, São Vicente: H 138.0, D 102.3 mm; RMNH 3762, Curaçao: H 163.7, D 103.8 mm.

Types.—*Cassis norai*, holotype “will be deposited in the Museum of Tokyo” (Prati Musetti, 1995, p. 46); paratype in collection of Prati Musetti; both from São Vicente Channel, Cape Verde Islands (not seen).

Other material examined.—**W Atlantic:** Curaçao, 1956, ex C. A. van der Peijl collection (RMNH 3762, 1 specimen, illustrated, Pl. 55, Figs 4-5). **Cape Verde Islands:** R. von Cosel’s material at MNHN: Mindolo, São Vicente Island, from fishermen, collected alive in ca. 15 m (1); Bahia Punta Negra, E coast of Ilha do Sal, coll. R. von Cosel (1); bought from fishermen, Mindolo Bay, São Vicente Island, pres. G. Poppe (GNS WM18926, 2).

Distribution.—*Cassis norai* originally was reported only

from the type locality, and a few more specimens from Sal and São Vicente Islands, Cape Verde Islands, have been seen during this study. Kurt Kreipl (Öhringen, Germany, pers. comm., 2004) has confirmed that at least some records of *C. tuberosa* from the Cape Verde Islands actually refer to that species, so it apparently occurs there sympatrically (although perhaps not syntopically) with *C. norai*. A specimen was illustrated excellently in color by Ardovini & Cossignani (2004: 123, upper left fig.). A Pleistocene fossil record of *C. tuberosa* from the Cape Verde Islands (Garcia-Talavera, 1999: 13) supports this record. To my knowledge, *C. norai* has not been reported previously from elsewhere. A single specimen at RMNH purportedly from Curaçao indicates that this species possibly occurs also in the western Atlantic, where it previously has escaped detection, but this record requires substantiation by more material. I am not aware of fossil specimens.

Cassis sulcifera G. B. Sowerby I, 1850
Pl. 59, Fig. 2; Pl. 60, Figs 1-8

Cassis sulcifera G. B. Sowerby I, 1850: 47, pl. 10, fig. 1; Guppy, 1866: 286; 1876: 525; ?1911: 4 (identity uncertain); Gabb, 1873: 222; Maury, 1917a: 274, pl. 44, figs 1-3; Pilsbry, 1922: 360; Olsson, 1922: 306; ?Woodring, 1928: 304, pl. 19, figs 5-6 (identity uncertain); Rutsch in Stainforth, 1948: 1311; Abbott, 1968: 53, pl. 29 (in part); Vokes, 1990b: pl. 2, figs 1a-c.

NOT *Cassis sulcifera*. Dall, 1916: 508, pl. 86, fig. 4; Abbott, 1968: 53 (= *Cassis flintensis* Mansfield, 1940).

?*Cassidea sulcifera*. Cooke, 1919: 113 (identity uncertain).

Remarks.—*Cassis sulcifera* is common in Dominican Republic Miocene and Early Pliocene rocks, and a range of specimens in different conditions is available for comparison with other species. It is most similar to *C. tuberosa* of the living western Atlantic species, and shares with *C. tuberosa* a low spire, a large, thick, strongly triangular ventral callus shield extending beyond the sides of the rest of the shell in large, heavily callused adults, and teleoconch external sculpture of numerous, sharp-edged, slightly irregular axial ridges, with no spiral sculpture. Most available specimens of *C. sulcifera* are small compared with adult *C. tuberosa* – few *C. sulcifera* are larger than ca. 80 mm H, whereas *C. tuberosa* is one of the largest of living western Atlantic species (exceeded only by *C. madagascariensis*), and large (ca. 250 mm) adults resemble the even larger Indo-West Pacific species *C. cornuta* in overall appearance. The two most obvious differences between *C. sulcifera* and *C. tuberosa*, apart from size, are the fine, regular, close, prominent spiral grooves which, in *C. tuberosa*, cut across the axial ridges, but are virtually absent from *C. sulcifera*, and the very much more extremely developed, widely triangular callus shield of some heavily callused adults of *C. sulcifera*. The recently named species *C. jameshoubrieki* differs from *C.*

sulcifera in its larger size but less strongly developed ventral shield, and possibly is a descendent of *C. sulcifera*, if not simply based on male specimens of *C. floridensis*.

Vokes (1990b) failed to bring out a color pattern on the ventral face of the outer lip of specimens of *Cassis sulcifera* from the Dominican Republic by prolonged treatment with bleach, and concluded that *C. sulcifera* was more closely related to *C. madagascariensis* than to *C. tuberosa*. However, the susceptibility of material from different localities to color enhancement by bleaching is little-understood and seems to be a dubious character for dismissing relationships, in view of the strongly triangular shield of *C. sulcifera*. It should be noted, though, that Vokes (1998: pl. 1, figs 6, 9) did establish a color pattern with bleaching and ultraviolet light for some specimens of *Lyria* (Volutidae) from the Gurabo Fm in the Dominican Republic, lending credence to her claim about *C. sulcifera*. Further study of this character is required; the phylogenetic significance of color bars on the lips of *Cassis* species is also unclear. Of course, it is feasible that *C. delta* and *C. sulcifera* have developed a triangular ventral shield independently (possibly because the shield allows feeding on long-spined echinoids) and are not phylogenetically related to *C. tuberosa*, but in my opinion, the sum of characters of both *C. delta* and *C. sulcifera* is most closely similar to that of *C. tuberosa*.

The species name *Cassis sulcifera* has been used also in the past (Woodring, 1928: 304, pl. 9, figs 5-6) for the *Cassis* species in the Bowden shellbed, Jamaica (Late Pliocene). Although Vokes (1990b) pointed out that the Bowden and Limón records of *Cassis* belong to new species, I noted above (under *C. altispira* n. sp.) that Woodring's (1928: pl. 19, figs 5-6) specimen does resemble *C. sulcifera*, and adults are needed to clarify the identification. The seven specimens from Bowden at NMB (NMB 10635, 2; 10651, 1; 11146, 4) appear to represent two species, because two specimens have very prominent spiral cords (and so tentatively are assigned here to *C. altispira* n. sp.) whereas all of the others lack spiral sculpture altogether. The six specimens without spiral sculpture possibly belong to *C. costulifera* n. sp., but are too small for certain identification. The casts, attaining a larger size than Dominican Republic specimens, reported from Oligocene rocks of Calabazar, Cuba, by Cooke (1919: 113), almost certainly refer to a distinct species.

Dimensions.—Lectotype, BMNH Palaeontology Department, GG20062: H 57.2, D 43.2 mm; largest paralectotype, BMNH Palaeontology Department, GG20061: H 61.8, D 50.5 mm; figured specimen, NMB H 17980, from NMB 16916: H (incomplete) 72.8, D 86.0 mm; figured specimen, NMB H 17982, from NMB 16808: H 63.4, 48.6 mm; figured juvenile specimen, NMB H 17983, from NMB 16869: H 46.0, D 32.6 mm; juvenile specimen illustrated by SEM, NMB H 18016, from NMB 16883, Dominican Republic: H

18.8, D (incomplete) 13.1 mm.

Types.—*Cassis sulcifera*, lectotype (selected here) and six small to moderately large paralectotypes BMNH Palaeontology Department, GG20061-20067, 15 small paralectotypes BMNH Palaeontology Department, GG20070-20077, all labeled "Miocene, Yaque River, St Domingo, Col. T. S. Heneken, ca. 1848." All are conspecific. The second-largest specimen, GG20062, is Sowerby's (1850: pl. 10, fig. 1) figured syntype, with a strongly triangular callus, and is here designated as the lectotype.

Other material examined.—**Fossils: Dominican Republic:**

Late Miocene: Cercado Fm: NMB 15899 (2); 15906 (1); 16835 (6); 16837 (1); 16839 (2); 16842 (4); 17269 (2); TU 1230 (6); 1294 (1); Cercado de Mao [PRI 28766, 1, Maury's (1917a: pl. 18, figs 4-5) illustrated specimen]; Cercado de Mao [PRI 28767, 1, Maury's (1917a: pl. 18, figs 2-3) illustrated specimen]; PRI, Maury's loc. 196, Bluff 3, Cercado de Mao (2); USGS 8522 (1); 8525 (7, USNM 483444); 8526 (1, USNM 483445); 8534 (1, USNM 483447); 8739 (1); 26294 (1); 26298 (1); NMB 16982, Cercado Fm, Río Cana, collection of Bernard Landau (1); TU 1379, Cercado Fm, Río Mao, collection of Bernard Landau (2); NMB 15906, Cercado Fm, Río Gurabo, coll. M. Taviani (Institute of Zoology, University of Bologna, 1); Gurabo Fm: NMB 16910 (2); 16913 (6); 16914 (2); 16916 (4; 1 large illustrated, NMB H 17980; Pl. 60, Figs 1-3); 16918 (1); 16919 (1); 16931 (1); TU 1293 (11, including GNS WM16934, 5); USGS 8737 (1, USNM 483446); PRI loc. 206, bluff 1, Cercado de Mao (2); Bluff 1 of Maury, Río Mao, coll. M. Taviani (Institute of Zoology, University of Bologna, 3); unnamed formation of E. Vokes (1989: 21): NMB 17274 (1); NMB 17275 (5); USGS 26286, Miocene(?), Arroyo Chapadera, A. A. Olsson (1). **Late Miocene/Early Pliocene:** Gurabo Fm: NMB 15871 (1); 15878 (2); 16821 (1); 16833 (2); TU 1225 (3); 1246 (2); 1250 (2, plus GNS WM16929, 6 juveniles); 1277 (9); 1292 (1); 1296 (1); 1297 (1); USGS 8519 (5); 8528 (4); 26275 (5); 26279 (2); PRI loc. 197, zone J, Río Gurabo (2); PRI loc. 198, no data (1); PRI loc. 200, zone D, Río Gurabo (1); loc. 203, zone E, Río Gurabo (2); loc. 207, zone F, Río Gurabo (2); loc. 215, zone C, Río Gurabo (1); NMB, pres. A. A. Olsson, Cercado de Mao, Maury's bluff 1 (1); bluish shale, Yaque River, Sir R. H. Schomburgh, pres. 1852 (1, BMNH Palaeontology Department, G 31025); Miocene, St. Domingo (1, BMNH Palaeontology Department, G 11080); Miocene, St. Domingo, coll. Col. T. S. Heneken, pres. 1853 (5, BMNH Palaeontology Department, G 11107); Miocene, St. Domingo (7, BMNH Palaeontology Department, G 11078). **Early Pliocene:** Gurabo Fm: NMB 15809 (3); 15811 (1); 15814 (2); 15836 (1); 15839 (3); 15842 (2); 15844 (2); 15845 (1); 15846 (3); 15848 (2); 15850 (1); 15858 (1); 15863 (11); 15864 (4); 15865 (2); 15866 (1); 15869 (2);

16808 (1, illustrated, NMB H 17982; Pl. 59, Fig. 2; Pl. 60, Fig. 5); 16817 (2); 16818 (8); 16828 (1); 16862 (1); 16865 (7); 16867 (1); 16868 (2); 16869 (4; 1 illustrated, NMB H 17983; Pl. 60, Figs 4, 6); 16870 (1); 16879 (1); 16883 (1 small, illustrated by SEM, NMB H 18016; Pl. 60, Figs 7-8); TU 1210 (2); 1211 (18, including GNS WM16912, 5); 1215 (many small); 1219 (3); 1227A (GNS WM17920, 1 juvenile); 1278 = NMB 19011 (6); USGS 8516 (1); 8538 (3); 8540 (2); 8545 (3); 8726, upper Gurabo Fm?, S side Río Yaque del Norte, La Canita, 15 km W of Santiago (1); TU 1214, Río Gurabo, collection of Bernard Landau (3); TU 1215, Río Gurabo, Bernard Landau collection (7); float, Río Gurabo, pres. E. Vokes (Institute of Zoology, University of Bologna, 2). **Venezuela: Early Middle Miocene:** NMB 17526, El Porvenir beds, Paraguaná (8 frags); NMB 17527, Buenevara Adentro beds, Paraguaná (7 frags). **Late Miocene:** NMB 17530, Caujarao Fm, Carrizal (7, cf.). The Venezuelan material is referred tentatively, because none of the specimens is complete or well preserved.

Distribution.—*Cassis sulcifera* is recorded here from the Late Miocene to Early Pliocene rocks of the northern Dominican Republic, and tentatively from the Middle and Late Miocene rocks of the Paraguaná Peninsula and Carrizal, Falcón, Venezuela. One specimen illustrated by Woodring (1928: pl. 19, figs 5-6) from Bowden, Jamaica, resembles *C. sulcifera* in a general way, but adults are required before Bowden *Cassis* species can be identified.

***Cassis tuberosa* (Linnaeus, 1758)**

Pl. 61, Figs 4-5

Buccinum tuberosum Linnaeus, 1758: 735; 1767: 1198; Gmelin, 1791: 3473.

Buccinum plicatum Linnaeus, 1758: 735; 1767: 1198.

Buccinum striatum Gmelin, 1791: 3477.

Cassidea tuberosa. Bruguière, 1792a: 436; Deshayes, 1844: 22.

Cassis tuberosa. Lamarck, 1822: 220; Kiener, 1835: 4, pl. 3, fig. 4; Reeve, 1848b: pl. 3, fig. 7; Küster, 1857: 14, pl. 39 (1846), figs 1-2; Chenu, 1859: 206, fig. 1122; Mörch, 1877: 38; Tryon, 1885: 271, pl. 2, fig. 51; Dall, 1889: 134; 1903b: 134; Dall & Simpson, 1901: 418; Maury, 1922: 118; Clench, 1944: 11, pl. 5; Morretes, 1949: 91; Warmke & Abbott, 1962: 98, pl. 1, fig. b; Coomans, 1963: 66, 81; Abbott, 1968: 50, pl. 3, fig. 11, pl. 23; 1974: 161, fig. 1743; Work, 1969: 658; Kaufmann & Götting, 1970: 369, fig. 78; Matthews & Kempf, 1970: 27; Matthews & Coelho, 1972: 2, fig. 1; H. & E. Vokes, 1983: pl. 9, figs 15-15a; Bandel, 1984: 96, pl. 8, figs 4, 7-8; Rios, 1985: 71, pl. 25, fig. 315; 1994: 85, pl. 28, fig. 330; Calvo, 1987: fig. 73 (radula); Diaz & Götting, 1988: 156; Lipe & Abbott, 1991: 4-5, illus.; Diaz & Puyana, 1994: 170, fig. 633; Kreipl, 1997: pl. 4, figs 6-6c; Macsotay & Campos Villaroel, 2001: 62, cover fig.; Redfern, 2001: 58, pl. 29, figs 250A-C.

Cassis labiata Conrad, 1849a: 210 (in part, not lectotype) (junior primary homonym of *C. labiata* Perry, 1811).

Cassis (Goniogalea) tuberosa. Mörch, 1877: 38.

Cassis triangularis Coulon, 1936: 67 (substitute name for *C. tuberosa* Lamarck, 1822, supposedly a junior primary homonym of *C. tuberosa* Linnaeus, 1758).

Remarks.—*Cassis tuberosa* is the medium-sized *Cassis* species of the living western Atlantic fauna, reaching ca. 260-280 mm H, although specimens rarely exceed 220 mm. It is easily distinguished from the other living species by its obvious, finely reticulate spiral and axial sculpture, similar to but a little coarser than that of the Indo-West Pacific type species of the genus, *C. cornuta*, by the few, large, narrow nodes on the dorsum of some specimens (probably male, to judge from *C. cornuta*; Abbott, 1968: pl. 3, figs 3-4), by the dark brown areas of the ventral face of the callus shield, including between the teeth inside the outer lip, as in *C. madagascariensis* and, in particular, by the triangular shape (widest apically) of the callus shield adopted by heavily callused, mature male specimens. Brazilian specimens are illustrated excellently in color on a webpage (<http://www.femorale.com.br/shellphotos>; last accessed 26 April 2006).

Feeding on echinoids by *Cassis tuberosa* has been observed and reported more commonly than that by any other cassid. Foster (1947) reported predation on the sand dollar *Clypeaster rosaceus* (Linnaeus, 1758). Moore (1956) reported it preying upon the regular echinoid *Tripneustes esculentus* (Leske, 1778) in Florida. More surprisingly, Schroeder (1962), Gladfelter (1978), and Snyder & Snyder (1970) reported *C. tuberosa* feeding on the long-spined "needle urchin" *Diadema antillarum* (Philippi, 1845). Cornman (1963) analyzed the toxic saliva used in this type of attack, in which apparently impenetrable spines are anaesthetized. Abbott (1968) reported *C. tuberosa* feeding on *Lytechinus variegatus* (Lamarck, 1816), and Work (1969) observed it feeding on a wide range of echinoids: *Arbacia* sp., *Clypeaster subdepressus* (Gray, 1825), *Echinonius* sp., *Moiria* sp., *Plagiobrissus grandis* (Gmelin, 1788), *Meoma ventricosa* (Lamarck, 1816), and *Mellita quinquiesperforata* (Leske, 1778). Gladfelter (1978) also reported it feeding on *Cassidulus cariboeorum* Lamarck, 1801. McClintock & Marion (1993) observed *C. tuberosa* feeding on the "six-holed sand dollar," *Leodia sexiesperforata* (Leske, 1778), in the Bahamas, and Pequeno & Matthews-Cascon (2001) carried out a laboratory study of predation by juvenile *C. tuberosa* on the "five-holed sand dollar" *M. quinquiesperforata* in northern Brazil. Hughes & Hughes (1981) reported it feeding on *Tripneustes ventricosus* (Lamarck, 1816) and *Echinometra lucunter* (Linnaeus, 1758), and also described general aspects of predation on echinoderms by Cassidae. This list of 15 echinoid species known to be preyed upon by *C. tuberosa* suggests that it eats any echinoids that it encounters.

Dimensions.—Clench (1944: 11) cited the following dimensions of a range of specimens: large, Cat Island, Bahamas:

H 220, D 175 mm; average, Grand Bahama Island: H 178, D 140 mm; small, Little San Salvador Island, Bahamas: H 122, D 101 mm; lectotype of *Buccinum tuberosum*, UUZM 1653: H 154.0, D 124.5 mm (Mats Eriksson, UUZM, pers. comm., 25 August 2008); GNS WM19025, off of St. François, Guadeloupe, 20-25 m: H 228, D 205 mm, H 222, D 191 mm, H 168, D 145 mm.

Types.—According to Dance (1967), an original Linnean specimen of *Cassis tuberosa* (i.e., the most suitable specimen to be the lectotype of *Buccinum tuberosum*) might have been among “large specimens” disposed of before 1967 by the Linnean Society of London. Certainly, none is present in the Linnean Society collection now. Most unusually, Linnaeus (1758: 735) did not cite any illustrations for this species. Any possible syntypes remaining in Uppsala therefore comprise the only material from which a lectotype could be chosen. Wallin (1993: 54) listed two possible syntypes, UUZM 943 and 1653, in the Linnean material at the UUZM, one of them (UUZM 943) identified by the well-known malacologist Nils Odhner as *C. tuberosa*. Olle Israelsson (UUZM) kindly sent me digital images of these two specimens in October 2004. These reveal that UUZM 943 is a specimen of *Echinophoria wyvillei* (Watson, 1886), probably from Japan, whereas UUZM 1653 is a specimen of the species known as *C. tuberosa* to all malacologists after Linnaeus (1758). The specimens are from Queen Ulrica’s collection, and the specimen of *C. tuberosa* is labeled with one of Thunberg’s printed labels (Pl. 61, Figs 4-5). The same reasoning applies here as is followed above for the lectotype designation of *C. flammea*. In view of the lack of evidence to the contrary, specimen UUZM 1653 (Pl. 61, Figs 4-5) is assumed to be a syntype of *B. tuberosum*, and is here designated the lectotype. The type locality was designated by Clench (1944: 12) as “Santo Domingo” [Dominican Republic], citing material at MCZ from Puerto Plata, Santa Bárbara de Samaná, and Jérémie. The type locality is here restricted to Puerto Plata, a large town on the northern coast of the Dominican Republic.

Mörch (1877) cited *Buccinum plicatum* “Linné, 1767, no. 444” as an earlier name for *Cassis madagascariensis*. However, Linnaeus (1758: 735) cited three figures for *B. plicatum*: Buonanni (1681, vol. 3: pl. 161), a poor drawing of *Cypraeacassis testiculus* (Linnaeus, 1758) [note that this figure was also cited by Linnaeus (1758: 736) for *B. flammeum*]; Gualtieri (1742: pl. 40, fig. C), a good drawing that probably represents a juvenile *C. tuberosa*; and DeZallier d’Argenville (1757: pl. 18, fig. D; queried by Linnaeus), a good drawing of *Phalium strigatum* (Gmelin, 1791). It is little wonder that this name largely has been ignored by subsequent authors. Abbott (1968: 94) discussed the several usages of this name for the species now universally known as *P. fimbria* (Gmelin, 1791), resulting from the arguments by Deshayes (1844:

25, footnote), which Abbott (1968: 94) thought “spurious.” Abbott (1968) did not designate type specimens for either *Buccinum plicatum* or *B. fimbria*, although he stated (Abbott, 1968: 94) that “we suggest that Seba, vol. 3, pl. 53, no. 1, serve as the type figure” for *B. fimbria*. To avoid this name threatening any later ones, the specimen of *C. tuberosa* illustrated by Gualtieri (1742: pl. 40, fig. C) is here designated the lectotype of *B. plicatum*. As first reviser, I select *B. tuberosum* as the senior synonym to be used for the species named both *Buccinum tuberosum* and *Buccinum plicatum* by Linnaeus (1758). Unfortunately, the specimens of *Cassis* juveniles illustrated by Gualtieri (1742: pl. 40, figs C-D) could not be recognized when I examined Gualtieri’s collection in January 2000, and apparently are no longer present (at the Museo di Storia Naturale e del Territorio, Università di Pisa, in the Certosa di Calci, outside Pisa), although a larger, adult specimen of *C. tuberosa* is present. I am not aware of any type material for *B. striatum*, but no type designation is made here because of the possibility of syntypes (specimens illustrated by Martini & Chemnitz, in figures cited by Gmelin) remaining in Copenhagen or St. Petersburg.

Conrad (1849a: 211) stated that *Cassis labiata* [validation of a nonbinominal name by “Chemnitz 2” (i.e., Chemnitz, vol. 11 [not vol. 2], 1795): pl. 184, fig. 1790, pl. 185, fig. 1791] is *C. tuberosa* of Linnaeus. Conrad cited six figures (the three listed above for *Buccinum plicatum*, plus Lister, 1685-1697: pl. 1008, fig. 71C; Rumphius, 1705: pl. 23, fig. A; and Petiver, 1713: pl. 2, fig. 10, pl. 7, fig. 10), the Petiver reference not seen by me. Several of these are not illustrations of *C. tuberosa*; the main one cited for *C. labiata* by Conrad (Chemnitz, 1795: pl. 184, fig. 1790, pl. 185, fig. 1791) is an excellent painting of the Miocene-Recent tropical Indo-West Pacific species *C. cornuta*. I here designate the specimen figured by Chemnitz (1795: pl. 184, fig. 1790) as the lectotype of *C. labiata*. This name therefore is a synonym of *C. cornuta*; the specimen could well still be in Chemnitz’s collection at the Zoological Institute, St. Petersburg. *Cassis triangularis* Coulon (1936: 67) was proposed expressly as a substitute name for *C. tuberosa* Lamarck, 1822, on the grounds that it was a junior primary homonym of *C. tuberosa* (Linnaeus, 1758), and because it is a replacement name, it has the same type material as *C. tuberosa*.

Other material examined.—**Fossil: Venezuela: Late Pliocene/Pleistocene:** NMB 17515, Mare Fm, upper shell-bed, Punta Gorda, Cabo Blanco, coll. J. & W. Gibson-Smith (2 large frags, apertural callus shields).

Distribution.—*Cassis tuberosa* lives at present in the western Atlantic from South Carolina, USA, and Bermuda to Brazil (Abbott, 1968), as far south as southern Bahia State and the Abrolhos Islands (Rios, 1994: 85), and in the eastern Atlantic is reported from the Cape Verde Islands (Kreipl, 1997: pl. 4,

fig. 6c). Matthews (1968) recorded juvenile specimens found rarely in the gut of the toadfish or "pacomon," *Amphychthus cryptocentrus*, caught off of Fortaleza, Ceará, Brazil. The only fossil record confirmed in the present report is from the Late Pliocene/Pleistocene Mare Fm upper shellbed at Punta Gorda, Cabo Blanco, Venezuela. However, Rutten (1931: 664) also recorded material of *C. tuberosa* from the Pleistocene of the island of St. Eustatius, citing a thesis by Molengraaff to which I do not have access.

Genus *CYPRACASSIS* Stutchbury, 1837

Cypraecassis Stutchbury, 1837: 214. Type species (by original designation): *Buccinum rufum* Linnaeus, 1758, Recent, Indo-West Pacific.

Levenia Gray, 1847: 137. Type species (by monotypy): *Cassis coarctata* G. B. Sowerby I, 1825, Pleistocene and Recent, eastern Pacific.

Remarks.—*Cypraecassis* is unique among cassids for its combination of the very strongly twisted, dorsally directed anterior siphonal canal in the adult, separated from the wall of the previous whorl only by a narrow slit, otherwise limited to the subfamily Phaliinae, with a disproportionately small (8.2 mm long in a shell 152 mm H; Abbott, 1968: 69), sub-circular operculum with a subcentral nucleus, similar to but much shorter than that of *Cassis*; some adult specimens of *Cypraecassis rufa* (Linnaeus, 1758) lack an operculum. The shell is oblong-oval, thick and heavy, with a thick ventral callus that is adherent rather than forming a free-edged shield as in *Cassis* (except in some large adult specimens of *C. rufa*, in which the callus margin protrudes a little beyond the shell outlines), with a narrow aperture, and numerous fine transverse ridges on both lips, so producing an aperture resembling that of *Cypraea*, and with quite prominent sculpture of rather low, narrow, sharp axial ridges and weak to prominent spiral cords, forming low nodules to quite prominent rounded pustules at the sculptural intersections. The varices are not retained at growth pauses, unlike in *Cassis*. A very small juvenile specimen of *C. rufa* examined at MNHN, from the Marquesas Islands, with only *ca.* 0.6 teleoconch whorls, has not yet developed a twisted anterior siphonal canal (Beu, in prep.). This species undergoes extreme ontogenetic change in canal shape, and commences life with a canal resembling that of species of *Cassis* and *Galeodea*. Again, excellent coverage of the synonymy, range, comparisons, and excellent illustrations are found in the monographs by Clench & Abbott (1943) and Abbott (1968), and need not be repeated here, and excellent colored illustrations by Kreipl (1997) are cited where relevant. The diversity of *Cypraecassis* species (six) in the fauna studied here is unequalled anywhere else.

Abbott (1968) rather tentatively maintained the weak

subgenus *Levenia* Gray, 1847, but I pointed out (Beu, 2005: 36) that *Cypraecassis wilmae* Kreipl & Alf, 2000, is intermediate between *C. coarctata* (G. B. Sowerby I, 1825) and other *Cypraecassis* species, and regarded *Levenia* as a synonym of *Cypraecassis*.

Cypraecassis cantaurana n. sp.

Pl. 63, Figs 3-7; Pl. 64, Figs 4, 9

Cypraecassis tenuis. Beu, 2001: 709, fig. 1.6 (in part).

Description.—Shell moderate-sized for genus, tall and narrow, of parallel-sided to weakly inflated shape, with low spire of weakly concave outline, and large, enveloping last whorl. Protoconch large (H 2.1, D 4.3 mm on paratype, similar but slightly abraded on holotype), tall and narrow for genus, of *ca.* 2.5 whorls (apex slightly abraded in available material). Teleoconch of 3.2 whorls, commencing as slightly inflated (compared with protoconch) almost smooth surface bearing numerous very low, narrow, faint, widely spaced spiral cords; cords increasing in prominence over succeeding whorl to form three prominent, narrow cords, gradually developing low, closely spaced nodules over second teleoconch whorl, becoming increasingly prominent down teleoconch to form three spiral rows of moderately large, narrowly rounded, closely spaced nodules around sutural ramp of last whorl; sutural ramp moderately steeply sloping, weakly concave in larger specimens; surface below ramp bearing 12-14 prominent, spiral rows of small to moderate-sized, narrowly rounded to narrowly axially elongate nodules; 22-30 nodules per row on dorsum of last whorl; most rows subequal in paratype (two widely spaced rows significantly smaller and narrower than others), less consistently even-sized on holotype, on which 2-3 wide rows alternate with one lower, narrower row; basal (anteriormost) spiral cord markedly wider, more prominent, and more sharply defined by undercut edges than all rows above, separated from siphonal fasciole by deep, narrow, parallel-sided groove with evenly concave bottom; basal cord sculptured with 25-30 high, narrow, sharp-crested axial ridges, corresponding to nodules on higher cords. Aperture strongly thickened to form thick, wide callous pad on holotype, thinner and slightly less extensive on paratype; outer lip strongly thickened, forming terminal varix of almost circular cross section, with deeply grooved posterior (abapertural) edge; inner margin bearing 22 prominent, narrow, short transverse ridges on inner edge; outer (left) half of inner lip callus smooth; inner half strongly, prominently, and closely sculptured with 28-32 long, narrow, weakly anastomosing transverse ridges, with interspaces each slightly narrower than one ridge, extending well into aperture, including covering low columellar ridge, extending antero-posteriorly along inner columellar face, producing the most

obviously *Cypraea*-like aperture of any American *Cypraeacassis* species. Anterior siphonal canal deeply and strongly twisted toward dorsum, producing prominent fasciole with posterior (adapical) margin parallel to basal spiral cords of teleoconch exterior; canal deeply notched at posterior edge of tip. Posterior (adapical) end of aperture shallowly notched by narrowly rounded canal, forming weak flexure in spire edge of callus shield, markedly weaker than in *C. tenuis*.

Dimensions.—Holotype: H 57.6, D 37.2 mm; paratype: H 52.4, D 32.2 mm; referred specimen, NMB H 18052, from NMB 17520, upper shellbed, Cantaure Fm: H (incomplete) 65.1, D 50.8 mm; height estimated originally as *ca.* 78 mm.

Types.—Holotype BMNH Palaeontology Department GG22902 (Pl. 63, Figs 5-7), lower (main) shellbed (= NMB 17516), Cantaure Fm (late Early Miocene), near Casa Cantaure, Paraguaná Peninsula, Estado Falcón, Venezuela, collected by Bernard Landau; 1 paratype from the same locality (Pl. 63, Figs 3-4) in the collection of Bernard Landau.

Other material examined.—**Fossils: Venezuela: Late Early Miocene:** Cantaure Fm: NMB 17519, upper shellbed, near Casa Cantaure, Paraguaná Peninsula (1 small); NMB 17520, locality same as last (1 large, incomplete, figured, NMB H 18052; Pl. 64, Figs 4, 9).

Distribution.—*Cypraeacassis cantaurana* n. sp. is known only from the listed material from the Cantaure Fm in northern Venezuela.

Remarks.—The two complete specimens that I have seen of *Cypraeacassis cantaurana* n. sp. differ strongly from all other *Cypraeacassis* specimens examined in this project in their combination of a tall, narrow, parallel-sided shape, not unlike that of *C. testiculus* (Linnaeus, 1758), with complex sculpture of numerous rows of small, rounded nodules, not unlike that of *C. tenuis* (Wood, 1828). The new species reaches a larger size than any American Neogene specimens of *C. testiculus* that I have seen, and differs from *C. testiculus* in its much more coarsely nodulose sculpture. It is also a little taller and narrower than most American specimens of *C. testiculus* that I have seen. It is smaller and narrower than adult specimens of *C. tenuis*, with a well-thickened apertural callous shield at only 58 mm H, and bears more numerous, narrower, and more closely spaced spiral cords and more numerous, more axially elongate nodules than in *C. tenuis*. *Cypraeacassis cantaurana* n. sp. differs from *C. chipolana* Duerr, 2001, and *C. wilmae* in its taller, narrower shape and much more numerous rows of smaller, more closely spaced nodules, and from *C. coarctata* in its more “normal,” out-turned outer lip, its smaller maximum size, and its much more numerous rows of smaller, more raised, more closely spaced nodules. The new species is the second *Cypraeacassis* species recorded from the Cantaure Fm, occurring with a few specimens of *C. testiculus* (see below).

I previously (Beu, 2001: 709, fig. 1.6) identified two in-

complete specimens from the Cantaure Fm as *Cypraeacassis tenuis*. However, the collection of the much more complete type material of *C. cantaurana* n. sp. indicates that the incomplete specimens more likely belong to *C. cantaurana*. At this larger size (larger H 65.1 mm, originally *ca.* 75-80 mm), they display a much more gently rounded shoulder angle and a more steeply inclined, concave, more strongly nodulose sutural ramp than in *C. tenuis*. The sculpture below the periphery is similar in the two species, although the spiral interspaces are narrower and the axial ridges are a little coarser and more prominent in the Cantaure specimens than in *C. tenuis*. The Cantaure specimens are assumed to be large specimens of *C. cantaurana* n. sp. and, as far as I am aware, *C. tenuis* is limited to the Recent fauna of the eastern Pacific, including the Pleistocene and Recent fauna of the Galápagos Islands. However, it seems feasible that *C. cantaurana* was directly ancestral to *C. tenuis*. It is very interesting for biogeography that the Cantaure specimens are distinct from *C. chipolana*, the species in the coeval Chipola Fm. Many tonnoidean species have proven to be common to the Chipola and Cantaure Formations. This case of distinct but closely related species in the two formations, along with that of *Sconsia laevigata* (G. B. Sowerby I, 1850) and *S. paralaevigata* Gardner, 1947, described below, implies some kind of filter barrier to dispersal between Florida and northern Venezuela.

Bunjamin Dharma (Jakarta, pers. comm., February 2002) has a specimen of a tall, narrow, parallel-sided, unnamed species of *Cypraeacassis* with 12-14 rows of low, rounded, closely spaced nodules on the last whorl, from Karas, Rembang, central Java, Indonesia, of Middle Miocene age (Beu, 2005: 38). This specimen strongly resembles *C. cantaurana* n. sp. It appears that biogeographical relationships between Indo-Pacific and Atlantic *Cypraeacassis* species were closer during Miocene time, when the CAI was open, than they have been ever since, and it is certainly clear that the diversity of *Cypraeacassis* has declined since Miocene time.

Etymology.—The species name reflects the type locality.

Cypraeacassis chipolana Duerr, 2001

Pl. 58, Figs 2-3; Pl. 62, Fig. 7

Cypraeacassis tenuis. Beu, 2001: 709, figs 1.1, 2 (in part not *C. tenuis* Wood, 1828).

Cypraeacassis (*Cypraeacassis*) *chipolana* Duerr, 2001: 147, fig. 1.

Remarks.—I included (Beu, 2001) two fragmentary specimens from the Chipola Fm of Florida (late Early Miocene) in *Cypraeacassis tenuis*, the species now inhabiting the eastern Pacific coast of tropical America. This was based partly on the fact that specimens from the coeval Cantaure Fm shellbeds of Paraguaná Peninsula, northern Venezuela, are large and, although incomplete, seemed to be specimens of *C. tenuis*.

Duerr (2001) demonstrated that specimens from the Chipola Fm are consistently much smaller than *C. tenuis*, with a much thicker ventral callus shield, and with sculpture more like that of *C. wilmae* than of *C. tenuis*. The specimens from the Cantare Fm are included above in *C. cantaurana* n. sp. *Cypraecassis chipolana* differs from *C. wilmae* in having (a) one fewer spiral bands of nodules on the last whorl, (b) 10 or 11 nodules per spiral band rather than the 8 or 9 of *C. wilmae*, (c) a thicker, wider outer lip, flared much further outward than in *C. wilmae*, (d) the ventral callus shield expanded much more widely over the siphonal fasciole than in *C. wilmae* to produce a more regularly oval shield, and (e) a deeper posterior apertural canal than in *C. wilmae*. The result is a species that resembles a diminutive version of *C. tenuis* almost as much as it does *C. wilmae*, but differs from *C. tenuis* in its much smaller size, in its much thicker ventral callus shield, and in bearing the prominent groove at the top of the inner margin of the siphonal fasciole that characterizes *C. wilmae*.

The recognition of *Cypraecassis chipolana* and *C. cantaurana* n. sp. complicates the biogeographical history of *Cypraecassis* in the tropical American region and, as suggested by Duerr (2001), indicates that *C. wilmae* probably evolved from *C. chipolana* after constriction or closure of the CAI. This then seems possibly to be one of few tonnoidean examples of a true geminate species pair, possibly resulting from speciation after uplift of the CAI, as is also seen in *Monoplex keenae*/*M. parthenopeus* and *M. macron*/*M. pilearis*. The present distribution of both *C. wilmae* and *C. tenuis* apparently is relict from former wider distributions in tropical America at a time when the CAI was still open, and they seem likely to have come together in recent times from formerly separate areas.

Dimensions.—Holotype: H 57.4, D 36.2 mm (Duerr, 2001); TU 820, Chipola Fm: H (incomplete) 45.9, D (incomplete) 31.0 mm.

Types.—Holotype USNM 517892 (not seen), from TU 950, Chipola Fm (late Early Miocene), Chipola River, W bank ca. 600 m upstream from Farley Creek, Calhoun Co., Florida.

Other material examined.—**Fossils: Florida: Late Early Miocene,** Chipola Fm: TU 820 (= NMB 17597) (1, ventral half of a small specimen, NMB H 17984; Pl. 58, Figs 2-3); 830 (= NMB 17588) (1 frag of dorsum, with prominent sculpture, NMB H 17985; Pl. 62, Fig. 7).

Distribution.—*Cypraecassis chipolana* is recorded only from the Chipola Fm (late Early Miocene) on and near the Chipola River, Florida, USA.

Cypraecassis coarctata (G. B. Sowerby I, 1825)

Pl. 62, Fig. 2; Pl. 63, Figs 1-2

Cassis coarctata G. B. Sowerby I, 1825: 70, appendix: xxi; Wood, 1828: 33, pl. 4, fig. 5; Menke, 1850: 183; Küster, 1857: 30, pl.

48, figs 3-4.

Cassis (Levenia) coarctatus. Chenu, 1859: 208, fig. 1135.

Cassis (Levenia) coarctata. Stearns, 1894: 188; Keen, 1958: 340, fig. 313; Keen, 1971: 501, fig. 947, color pl. 16.

Cypraecassis (Levenia) coarctata. Abbott, 1968: 77, pl. 4, fig. 8, pl. 53; Kreipl, 1997: pl. 7, figs 14-14a; Kaiser, 1997: 32; 2007: 38, pl. 26, fig. 1; Kreipl & Alf, 2000: fig. 4; López de la Fuente & Ramos, 2004: 85.

Cypraecassis coarctata. Cosel, 1984: 219; Finet, 1991: 270; Hickman & Finet, 1999: 69, fig. 59.

Remarks.—*Cypraecassis coarctata* is a highly distinctive species because of the unique inward curve and lack of a flare on the posterior half of the outer lip. Other distinctive characters are the ventral callus being limited to the apertural half of the width of the base, the low, narrow to obsolescent transverse ridges on the inner lip, and the prominent, short, high transverse ridges inside the outer lip. The exterior spiral sculpture is intermediate between those of *C. testiculus* and *C. tenuis*, with 5 or 6 low spiral cords wider than the others and bearing low, wide nodules, separated by several narrow, vaguely defined spiral cords, but the axial costae are very low and narrow, much finer than on any other species of *Cypraecassis*.

Dimensions.—Holotype: H 71.3, D 40.2 mm; Mulegé terrace, Bahia de Santa Inés, W Mexico, collection of Bernard Landau: H 68.6, D 38.7 mm. The maximum recorded height is 85.5 mm (Skoglund, 1992).

Types.—*Cassis coarctata*, holotype BMNH 1967673, illustrated by Abbott (1968: pl. 53) and again here (Pl. 62, Fig. 2). The specimen is without locality; Abbott (1968: 78) designated the type locality as Acapulco, west coast of Mexico.

Other material examined.—Recent material is not listed.

Fossils: Western Mexico: Late Middle Pleistocene (oxygen isotope stage 5e; Emerson *et al.*, 1981): Bahia de Santa Inés, near Mulegé, Baja California Sur, from Mulegé Terrace cover deposit, collection of Bernard Landau (1, illustrated, Pl. 63, Figs 1-2).

Distribution.—*Cypraecassis coarctata* lives now from the Galápagos Islands (Hickman & Finet, 1999) and the Gulf of California to northern Peru (Abbott, 1968), at least as far south as Mancora (Olsson, 1924). Cantera *et al.* (1979) and Cosel (1984) recorded specimens from Gorgona Island, Colombia. Most fossil specimens that have been referred to this species appear actually to be *C. wilmae*; the one fossil specimen of *C. coarctata* that I have seen is illustrated here (Pl. 63, Figs 1-2).

Cypraecassis tenuis (Wood, 1828)

Pl. 58, Fig. 4; Pl. 59, Fig. 3

Cassis tenuis Wood, 1828: 33, pl. 4, fig. 4; Reeve, 1848b: pl. 6, figs 13a-c; Küster, 1857: 25, pl. 45; Pilsbry & Vanatta, 1902: 554.

Cassis massenae Kiener, 1835b: 17, pl. 6, fig. 14.

- Cassis* (*Cassidea*) *tenuis*. Chenu, 1859: 207, fig. 1133.
Cassis (*Cypraecassis*) *tenuis*. Tryon, 1885: 272, pl. 2, fig. 53; Keen, 1958: 340, fig. 312; 1971: 500, fig. 946; Abbott, 1974: 162, pl. 6, fig. 1748.
Cypraecassis (*Cypraecassis*) *tenuis*. Emerson & Old, 1963a: 12, fig. 10; Abbott, 1968: 75, pl. 4, fig. 7; Kreipl, 1997: pl. 6, figs 11-11b; Kaiser, 1997: 32; 2007: 38, pl. 26, figs 2a-b.
 ?*Cypraecassis* cf. *tenuis*. Woodring & Malavassi, 1961: 494, pl. 69, figs 1-2.
Cypraecassis tenuis. Beu, 2001: 709 (in part); Hickman & Finet, 1999: 69, fig. 60.

Remarks.—Typical *Cypraecassis tenuis*, in the Recent fauna of the eastern Pacific, is a relatively elongate species, with a very short spire, a prominent, narrowly rounded shoulder angle, and a very gently sloping, almost flat, weakly sculptured sutural ramp, bearing a few low spiral cords on the posterior surface, and in many specimens, revealing the peripheral nodule row a little above the suture (Kreipl, 1997: pl. 6, figs 11-11b). The sculpture on the last whorl below the periphery, in contrast, is coarse and obvious, with four rows of large, rounded to subrectangular nodules, with a wide, low secondary spiral cord filling most of each spiral interspace between the nodule rows, and a narrow tertiary spiral cord or two in many secondary interspaces. Narrow axial ridges cover much of the surface between nodule rows, but are weak on the posterior (spire) surface. The posterior siphonal notch is particularly deep and obvious for a *Cypraecassis* species, much more obvious than in *C. cantaurana*.

The specimen from the Oligocene Caimito Fm, Gatun Lakes area, Panama, illustrated by Woodring (1959: 198, pl. 26, figs 11, 17), under the name *Semicassis* (*Echinophoria*) *apenes* Woodring, 1959, is more elongate and less strongly shouldered than any species of *Semicassis* or *Echinophoria* of which I am aware. With its several rows of low, rounded nodules, it appears to be a species of *Cypraecassis* similar to *C. tenuis* and *C. cantaurana* n. sp., although the spire is particularly tall and the sutural ramp long and steeply inclined compared with either similar species. Woodring & Malavassi (1961: 494) also referred a moderately large (H 74.7 mm) Miocene internal mold from near Turúcares, Valle Central, Costa Rica, to *C. cf. tenuis*, and the shape and size certainly support such an identification. However, both of these specimens are too poorly preserved to be able to distinguish between *C. tenuis* and *C. cantaurana* with any confidence.

Dimensions.—Moderately large Recent specimen, GNS WM14374, eastern Pacific: H 101.7, D 64.5 mm. Large Recent specimens reach ca. 160 mm H.

Types.—*Cassis tenuis*, no type material known; not at BMNH. *Cassis massenae*, holotype MHNG 1152/37 (Pl. 58, Fig. 4; Pl. 59, Fig. 3), from “les mers de l’Amérique” (but labeled “Galapagos”), a rather small (H 92.5 mm) but normal

specimen of *C. tenuis*. The holotype of *Cassis massenae* is here designated the neotype of *Cassis tenuis*. The type locality is here designated as the Galápagos Islands.

Distribution.—Fossils at least closely related to *Cypraecassis tenuis* are recorded from the Valle Central of Costa Rica (Miocene) and the Caimito Fm (Oligocene) of Panama, although they might well be more closely related to *C. cantaurana* n. sp. than to *C. tenuis*. Garcia-Talavera (1993: 33) recorded Pleistocene fossils from Isla de Santa Fe, Galápagos Islands. In the living fauna, this species is limited to the eastern Pacific, where it ranges from the outer (Pacific) coast of Baja California Peninsula (Chaney, 1996: 30 m on shoal ca. 160 km NW of Bahia Magdalena, 25°43’N, 113°07’W) and from La Paz, Baja California Sur, south to Ecuador. It is also recorded from the Galápagos Islands, Cocos Island, Clarion Island, and the Revillagigedo Islands (Pilsbry & Vanatta, 1902; Finet, 1985; Skoglund, 1992; Chaney, 1996; Hickman & Finet, 1999).

Cypraecassis testiculus (Linnaeus, 1758)

Pl. 62, Figs 4-6, 8-10

- Buccinum testiculus* Linnaeus, 1758: 736; 1767: 1199; Gmelin, 1791: 3474.
Cassidea testiculus. Bruguière, 1792a: 426.
Cassis testiculus. Kiener, 1835b: 20, pl. 4, fig. 7, pl. 9, fig. 17; Reeve, 1848b: pl. 4, fig. 10; Küster, 1857: 37, pl. 51, figs 3-4; Dall & Simpson, 1901: 418; Dall, 1903b: 134; Piele, 1926: 80.
Cassis (*Cassidea*) *testiculus*. Chenu, 1859: 207, fig. 1134; Gregory, 1895: 289.
Cassis (*Cypraecassis*) *testiculus*. Mörch, 1877: 39; Maury, 1917a: 275; 1922: 118; Pilsbry, 1921: 361.
Cypraecassis testiculus. Krebs, 1864: 35; Gabb, 1873: 222; Tryon, 1885: 273, pl. 2, fig. 64, pl. 4, fig. 63; Clench & Abbott, 1943: 1, pl. 1, pl. 2, figs 1-3; Morretes, 1949: 91; Olsson & McGinty, 1958: 15; Nowell-Usticke, 1959: 58; Weisbord, 1962: 252, pl. 23, figs 11-14; Warmke & Abbott, 1962: 99, pl. 3, fig. c; Work, 1969: 659; Kaufmann & Götting, 1970: 369, fig. 80; Andrews, 1971: 103, illus.; 1977: 129, illus.; Matthews & Coelho, 1972: 5, fig. 2; Abbott, 1974: 162, fig. 1747; Princz & Pacheco, 1981: table; Okutani, 1983: 254, illus.; H. & E. Vokes, 1983: 22, pl. 11, fig. 1; Rios, 1985: 72, pl. 26, fig. 316; 1994: 85, pl. 28, fig. 331; Jensen & Harasewych, 1986: 426, illus.; Calvo, 1987: fig. 74 (radula); Diaz & Götting, 1988: 156; Diaz, 1990: 19; Leal, 1991: 107; Lipe & Abbott, 1991: 5-7, illus.; Diaz & Puyana, 1994: 170, fig. 634; Redfern, 2001: 59, pl. 30, figs 251A-B.
Cypraecassis (*Cypraecassis*) *testiculus testiculus*. Abbott, 1968: 72, pl. 4, fig. 9, pl. 48; Kreipl, 1997: pl. 7, figs 12-12b.

Remarks.—*Cypraecassis testiculus* differs from *C. tenuis* in its much smaller size (to ca. 75 mm H, although most fossils are not more than ca. 40 mm), its more rounded oval shape with little sign of a shoulder angulation, its much more dominant axial sculpture, with the narrow axial ridges maintained

across all of the weak spiral cords, and its thicker ventral callus and more prominent transverse ridges on the inner lip. Small specimens (*ca.* 20–40 mm H) have little or no sign of the spiral cords, and the cords develop only gradually on larger specimens. As far as I can see, Late Miocene–Early Pliocene specimens from the Dominican Republic agree with Recent specimens of *C. testiculus testiculus* in all these characters; this was also the opinion of Abbott (1968: 71) and Landau *et al.* (2004). Abbott (1968) recognized a weak geographical subspecies in West Africa, *C. testiculus senegalica* (Gmelin, 1791) (Ardevini & Cossignani, 2004: 123, 2 lower left figs), differing only in some specimens reaching larger size (to *ca.* 100 mm H) and having slightly more prominent, short axial ridges around the shoulder area than are present on *C. testiculus testiculus*. Most of the Dominican Republic fossils are quite small (*ca.* 30–40 mm H) but some reach *ca.* 50 mm, and all agree closely with Recent specimens of comparable size. The protoconch (Pl. 62, Figs 8–9) is large and mammillate, apparently smooth, of *ca.* 3.5 whorls.

A small specimen from the Cantaure Fm (late Early Miocene) at Cantaure, Paraguaná Peninsula, Venezuela, in the collection of Bernard Landau, is similar to most of the western Atlantic fossil material of *Cypraecassis testiculus* in size, shape, most of its sculpture, and in general appearance, but has two rows of small rounded nodules at and just below the periphery. This character is present on specimens in the present-day population of *C. testiculus senegalica* (see Abbott, 1968: 72, pl. 50; Kreipl, 1993: pl. 7, figs 13–13b) from West Africa, and it seems likely that the Cantaure shell is an unusually strongly sculptured specimen of *C. testiculus*. More material is required to evaluate this form. It is much smaller than specimens of *C. cantaurana* from the same formation, but has adult apertural thickening, and so apparently is distinct.

Dimensions.—Linnaeus' syntypes: H 65.1, D 44.4 mm (specimen marked "387"); H 48.8, D 33.6 mm; large Recent specimen, NMB 17686, Bahia Los Totumos, between Caranero and Cabo Codera, Estado Miranda, Venezuela, J. & W. Gibson-Smith collection (1 of 12 in sample): H 67.8, D 47.9 mm; figured specimen, NMB H 17986, from NMB 16828, Dominican Republic: H 34.8, D 24.1 mm; figured specimen, NMB H 17987, from NMB 18585, Dominican Republic: H 45.0, D 30.0 mm; specimen illustrated by SEM, NMB H 17988, locality same as last: H 26.6, D (incomplete) 14.5 mm; Cantaure Fm, Paraguaná Peninsula, collection of Bernard Landau: H 36.7, D 23.2 mm.

Types.—Clench & Abbott (1943: 2) selected as a "type figure" that of Gualtieri (1742: pl. 39, fig. C), one of the two figures cited for this species by Linnaeus (1758). However, the illustrated specimens cited by Linnaeus are merely among the several Linnean syntypes, and Abbott & Clench's selection has little significance in view of the existence of syntypes

in Linnaeus' collection. Abbott (1968: 72) followed Dodge (1956: 182) in stating that the Linnean Society of London houses Linnaeus' "type." Two specimens of the typical western Atlantic form of *Cypraecassis testiculus*, without nodules around the periphery, are present in Linnaeus' collection housed at the Linnean Society of London. The larger bears the number "387" (the number for *Buccinum testiculus* by Linnaeus, 1758: 736) on the upper part of the inner lip, although the smaller is unmarked. The larger, at least, therefore, is a genuine Linnean syntype of *B. testiculus*. Because Linnaeus (1758: 736) also cited the figure by Rumphius (1705: pl. 23, fig. 3) for *B. testiculus*, the two cited figured specimens (those of Rumphius and Gualtieri) constitute further syntypes. The Linnean material at UZM listed by Wallin (1993: 54) includes a further four putative syntypes of *B. testiculus* (UZM 643, 1120, and 1121a–b), one of which (UZM 643) has been identified by the well-known malacologist Nils Odhner as "*Cassis testiculus*." There is therefore a total of eight syntypes of *B. testiculus* and because I am not able to confirm the identity of all of these, the syntype numbered "387" in Linnaeus' collection housed at the Linnean Society of London is here designated the lectotype of *B. testiculus*. Clench & Abbott (1943: 1) correctly pointed out that "Linne's type locality is Jamaica."

Other material examined.—**Fossils: Dominican Republic:**

Late Early Miocene: Baitoa Fm: NMB 17281, Río Yaque del Norte, collection of Bernard Landau (6 good; 2 have unusually prominent spiral cords all over, similar to axial costae).

Late Miocene: Cercado Fm: NMB 16982, Río Cana, collection of Bernard Landau (1); Gurabo Fm: NMB 15888 (1); TU 1298 (GNS WM18859, 1); Bluff 1 of Maury, Río Mao, coll. M. Taviani (Institute of Zoology, University of Bologna, 1); unnamed formation of E. Vokes (1989: 21): NMB 17273 (2). **Late Miocene/Early Pliocene:** Gurabo Fm: NMB 16821 (1); TU 1231 (GNS WM16984, 1); 1293 (GNS WM16932, 1). **Early Pliocene:** Gurabo Fm: NMB 15844 (1); 15846 (1); 15856 (1); 15857 (1); 15858 (1); 16817 (4); 16818 (4); 16824 (1); 16828 (4; 1 illustrated, NMB H 17986; Pl. 62, Figs 6, 10); 16865 (1); TU 1215 = NMB 18581 (4); 1354 = NMB 18585 (7; 2 illustrated, NMB H 17987, H 17988; Pl. 62, Figs 4–5, 8–9); 1449 (GNS WM18860, 1); 1215 = NMB 18581, Gurabo Fm, Río Gurabo, collection of Bernard Landau (3); 1354, Gurabo Fm, Cañada de Zamba, collection of Bernard Landau (8). **Venezuela: Late Early Miocene:** Cantaure Fm: NMB 17519 (1); 17520 (1 large); 17526 (1); lower (main) shellbed (= NMB 17516), near Casa Cantaure, Paraguaná Peninsula, collection of Bernard Landau (1). **Late Miocene:** NMB 17530 (1). **Holocene:** NMB 17565 (3).

Distribution.—*Cypraecassis testiculus* lives now from Beaufort Inlet, North Carolina (Porter, 1974: 197), USA, and Bermuda to Brazil (Abbott, 1968), south to Cabo Frio, Río de Janeiro State, and Trindade Island, Brazil (Rios, 1994:

84). Matthews (1968) recorded specimens found rarely in the gut of the toadfish or "pacomon," *Amphychthus cryptocentrus*, caught off of Fortaleza, Ceará, Brazil. Fossils are recorded here from Miocene and Pliocene rocks of the Dominican Republic and northern Venezuela. Aguayo (1938) recorded Pleistocene fossils from Guantanamo, Cuba, and Gregory (1895) recorded Pleistocene fossils from Barbados. The weakly differentiated subspecies *C. testiculus senegalica* lives now along the West African coast from Sénégal to Angola, and at the Cape Verde Islands, Ascension Island, and St. Helena (Abbott, 1968). Landau *et al.* (2004) pointed out that other, distinct *Cypraecassis* species inhabited Europe and the Mediterranean until Pliocene time, and *C. testiculus* appears to be a geologically recent arrival in the eastern Atlantic from the western Atlantic.

***Cypraecassis wilmae* Kreipl & Alf, 2000**

Pl. 62, Figs 1, 3

Cypraecassis (Levenia) coarctata. Grant & Gale, 1931: 740; Durham, 1950: 116; Emerson & Old, 1963a: 14 (not *C. coarctata* G. B. Sowerby I, 1825).

?*Cypraecassis coarctata*. Schneider, 1999: table 1 (?not *C. coarctata* G. B. Sowerby I, 1825).

Cypraecassis wilmae Kreipl & Alf, 2000: 43, figs 1-3.

Remarks.—Until recently, all authors have confused *Cypraecassis wilmae* with *C. coarctata*, because they have a similar appearance and a similar geographical range. *Cypraecassis wilmae* differs from *C. coarctata* in (a) its shorter and wider shape, (b) its significantly smaller maximum size (40 mm H rather than 90 mm and more), (c) having four rather than five spiral rows of nodules on the last whorl, (d) having only 5-6 nodules per spiral row rather than the 8-9 of *C. coarctata*, (e) having two spiral rows of small gemmae between each pair of major spiral nodule rows, (f) having a relatively thick outer lip only very weakly deflected inward over the upper (posterior) third of its height, rather than a thin-edged lip deflected strongly inward over its upper half to two thirds as in *C. coarctata*, and (g) having a very much more obvious spiral groove at the base of the siphonal fasciole than in *C. coarctata*, visible as a spiral depression on the inner lip.

Dimensions.—Holotype: H 37.2, D 22.5 mm; paratypes, Meeresmuseum Öhringen: H 36.1, D 22.6 mm; H 38.0, D 24.0 mm (Kreipl & Alf, 2000: 43); Mulegé terrace, Bahia de Santa Inés, Baja California Sur, W Mexico, collection of Bernard Landau: H 51.5, D 33.6 mm; figured specimen, NMB H 17989, from NMB 18306, Panama, Pleistocene: H 41.0, D 26.7 mm.

Type material.—*Cypraecassis wilmae*, holotype in Senckenberg Museum, Frankfurt, SMF 320980, from Secas Island, Pacific Panama, dredged in 20-40 m; 2 paratypes, Kurt

Kreipl collection, Meeresmuseum Öhringen, Germany, from Arenas de Quebro, Pacific Panama, dredged in 80 m; 1 paratype, Jens & Christa Hemmen collection, Wiesbaden, same locality as holotype (none seen).

Other material examined.—**Fossils: W Mexico: Late Middle Pleistocene** (oxygen isotope stage 5e; Emerson *et al.*, 1981): Bahia de Santa Inés, near Mulegé, Baja California Sur, from Mulegé Terrace cover deposit, collection of Bernard Landau (1). **Pacific Panama: Pleistocene:** NMB 18306, Armuelles Fm, S of Quebrada Corotú, 3.3 km N of Puerto Limones, Burica Peninsula (3; 1 illustrated, NMB H 17989; Pl. 62, Figs 1, 3). **Ecuador: Pleistocene:** NMB 19149, shell-bed, road cuts on Manta to Montecristi road, 5 km from Manta, Manabi Province (1, abraded and incomplete).

Distribution.—Kreipl & Alf (2000) recorded Recent specimens of *Cypraecassis wilmae* only from eastern Panama. It is likely to occur more widely in the eastern Pacific than these records indicate, probably from West Mexico to at least as far south as Ecuador, and perhaps to northern Peru. All previous records of fossils of *C. coarctata* appear to have been based on *C. wilmae*, although a single authentic fossil specimen of *C. coarctata* is recorded here. Emerson & Old (1963a: 14) listed earlier fossil records by Hanna & Hertlein (1927) from the Pliocene of Monserat Island, Baja California Sur, by Hertlein (1957) from the Pleistocene of Punta Pulpito, by Durham (1950) from the Pleistocene of Coronado Island, by Emerson (1960) from the Pleistocene of Cerralvo Island, and by Grant & Gale (1931) from the Pleistocene of Escondido Bay, Oaxaca, all in western Mexico. Most of these records seem likely to have been based on *C. wilmae*. Schneider (1999) also listed *C. coarctata* from Mulegé Terrace at three localities on the inner coast of Baja California Sur, Mexico, and material sent by Schneider to Bernard Landau consists of both *C. coarctata* and *C. wilmae*. The present records extend the range of fossils south to Panama and Ecuador.

Genus **GALEODEA** Link, 1807

Galeodea Link, 1807: 113. Type species (by monotypy): *Galeodea echinophora* Link, 1807 (= *Buccinum echinophorum* Linnaeus, 1758), Miocene to Recent, southern Europe-Mediterranean.

Morio Montfort, 1810: 479. Type species (by monotypy): *Morio echinophora* Montfort, 1810 (= *Buccinum echinophorum* Linnaeus, 1758).

Cassidaria Lamarck, 1816: 3. Type species (by subsequent designation, Woodward, 1851: 115): *Cassidaria echinophora* Lamarck, 1816 (= *Buccinum echinophorum* Linnaeus, 1758).

Echinora Schumacher, 1817: 75, 249. Type species (by monotypy): *Echinora tuberculosa* Schumacher, 1817 (= *Buccinum echinophorum* Linnaeus, 1758).

Echinophora Latreille, 1925: 194 (error?; emendation of *Echinora* Schumacher, 1817?).

Taieria Finlay & Marwick, 1937: 67. Type species (by original design-

nation): *Taieria allani* Finlay & Marwick, 1937, Paleocene, New Zealand.

Mambrinia Gardner, 1939: 23. Type species (by original designation): *Cassidaria planotecta* Meyer & Aldrich, 1886, Middle Eocene, southeastern USA.

Gomphopages Gardner, 1939: 25. Type species (by original designation): *Galeodea (Gomphopages) turneri* Gardner, 1939, Middle Eocene, Texas, USA.

Caliagaleodea Clark, 1942: 118. Type species (by original designation): *Galeodea (Caliagaleodea) californica* Clark, 1942, Eocene, western USA.

Galeocorys Kuroda & Habe, 1957: 27. Type species (by original designation): *Galeodea leucodoma* Dall, 1907, Recent, northwestern Pacific.

Remarks.—*Galeodea* is a highly speciose, almost cosmopolitan genus (taking the many fossils into account) of cassine cassids recognizable by its sculpture of many fine spiral lirae, strengthened or grouped into wider but low cords in some species, and raised into 3-4 or more spiral rows of narrowly rounded, small to quite large nodules on most species, by its straight to at most lightly twisted siphonal canal, rather than the very strongly twisted, dorsally directed siphonal canal of the superficially similar phaliine genus *Echinophoria* Sacco, 1890 (so that the circular aperture of the canal is directed anteriorly, not dorsally as in *Echinophoria*), and with the outer lip thickened into at least a thin varix, greatly thickened and reflected in many species, but intergrading through to those [such as *G. leucodoma* Dall, 1907 (Kreipl, 1997: pl. 10, figs 23-23a), type species of the synonym *Galeocorys* Kuroda & Habe, 1957] with the lip only slightly flared and not at all reflected back over the whorl surface. Even *G. allani* (Finlay & Marwick, 1937) (Danian, New Zealand; Beu & Maxwell, 1990: pl. 2, figs 1, s; type species of *Taieria* Finlay & Marwick, 1937), without any outer lip thickening, differs so little from *G. echinophora* (Linnaeus, 1758) that it is best regarded as a synonym of *Galeodea* and, indeed, it is not yet clear whether this species might be based merely on immature specimens of a varicate species. Some other early Cenozoic groups are more distinct, however, and seem worthy of subgeneric rank, in particular *G. (Mambrinia)* Gardner (1939: 23). *Galeodea (Mambrinia)* was proposed for a U.S. Gulf Coast Eocene species with a greatly elongated anterior siphonal canal, but I regarded (Beu, 2008) *G. (Gomphopages)* Gardner (1939: 25) as a synonym of *G. (Mambrinia)*. *Pseudogaleodea* Nagao, 1932 [type species *P. tricarinata* Nagao, 1932: 46, pl. 8, figs 1-7; Senonian (Late Cretaceous), Sakhalin and Hokkaido] has a callus layer over the entire exterior surface, masking the suture and finer sculpture, and clearly belongs in the Aporrhaidae (or a closely related stromboidean family) rather than in Cassidae. [The reference of both *Pseudogaleodea* and *Bulbificopsis* Squires & Saul, 2003, to Ficidae by Squires & Saul (2003) is inappropriate because these thick, heavily sculptured shells are unlike the

thin, finely sculptured shells of all true ficids; *Bulbificopsis* appears to me to be a buccinoidean related to the Melonginidae-Busyconidae clade]. Paleocene species of *Galeodea* seem to be the earliest taxa reliably referred to the Cassidae at present.

The one obvious exception to the cosmopolitan (at least, in temperate and tropical seas) distribution of *Galeodea* at present has until very recently been the Americas. The few specimens reported below from the Dominican Republic represent the sole record of the genus from American Neogene to Recent faunas of which I am aware, despite a rich record from Paleogene rocks. Recently, Dominique Lamy (Guadeloupe; pers. comm., 31 May 2007) sent me photographs of a small, very elongate Recent specimen of *Galeodea* closely resembling *G. echinophora*, collected in 500 m off of Martinique, western Atlantic. However, this is so similar to tall, narrow specimens of *G. echinophora* (e.g., Kreipl, 1997: pl. 8, fig. 15a) that it seems likely to be an accidentally dropped Mediterranean specimen, and confirmation of an occurrence of *Galeodea* in the West Indies must await the collection of more material.

***Galeodea* cf. *echinophora* (Linnaeus, 1758)**

Pl. 68, Figs 4, 7

cf. *Buccinum echinophorum* Linnaeus, 1758: 735.

cf. *Galeodea echinophora*. Kreipl, 1997: 24, pl. 8, figs 14-14c; Chirli, 2007: 80, pl. 30, figs 9-16, pl. 31, figs 1-2 (with synonymy); Beu, 2008: 300, figs 1G-H, 6C-D, 11A, C, E, 14G-J, 21B, with synonymy.

Remarks.—Four incomplete specimens are available from the Dominican Republic of a small, generalized *Galeodea*, resembling *G. echinophora* in most characters. The densely spaced fine spiral threads over the entire exterior, the four rows of rather large, narrowly rounded nodules on most specimens, and the well-thickened aperture with a smooth, lightly reflected outer lip all agree with *G. echinophora*. Unfortunately, the anterior end of the last whorl and the siphonal canal are missing from all specimens, so the most useful characters for identification are not available. More complete specimens are required for more detailed comparison with *G. echinophora*, but there seems to be no reason for this species not to be at least closely related to *G. echinophora*, which is very widespread in Miocene to Recent faunas of Europe, and is still common in the Mediterranean Sea. Of course, without the canal, even the identification as *Galeodea* cannot be confirmed with certainty, but the many fine spiral threads leave no real doubt of the generic position. This seems to be the only Neogene and Recent fossil record of *Galeodea* in the tropical American region [apart from the possible specimen of *G. echinophora* mentioned above, and Clench's (1944) incorrect assignment of *Echinophoria coronadoi* (Crosse, 1867) to *Galeodea*].

Galeodea has a very small, cap-shaped protoconch of only

one whorl, *i.e.*, direct development. However, Hughes (1986: 200) revealed that the creeping hatchlings of *G. echinophora* secrete long mucus "drogues" and float away in water currents, explaining the wide dispersal of species in a direct-developing genus.

Dimensions.—NMB H 18005: H (incomplete) 33.7, D 28.9 mm.

Types.—The lectotype and paralectotype (Beu, 2008: figs 14G-J) of *Buccinum echinophorum* are in Linnaeus' collection, housed at the Linnean Society of London, Burlington House.

Other material examined.—**Fossils: Dominican Republic: Middle Miocene:** sta. ES210, Arroyo Najoyo, San Cristobal, Ingenio Nuevo, southern Dominican Republic, coll. C. Sceriel and F. Echavarria, pres. to AGB by E. & H. Vokes (1, incomplete, illustrated, NMB H 18005; Pl. 68, Figs 4, 7). **Late Miocene/Early Pliocene:** "Miocene, Yaque River, St Domingo, coll. Col. T. S. Heneken, c. 1848" (1, BMNH Palaeontology Department, GG20362, rather crushed and incomplete). **Early Pliocene:** TU 1227, Gurabo Fm, Arroyo Zalaya, tributary of Río Yaque del Norte, collection of Bernard Landau (1, spire only).

A similar but juvenile specimen from the eastern Dominican Republic (from an Early Miocene locality for amber near the town of Bayaguana; *ca.* 20 Ma) has been shown to me also by George Poinar (University of Oregon, Corvallis; no. MS 9-49 in his collection). This juvenile specimen is only 23 mm H, and has only a single row of nodules at the periphery, but further rows presumably develop during ontogeny in this species.

Distribution.—*Galeodea echinophora sensu stricto* is restricted at present to the Mediterranean Sea (Beu, 2008), not even extending out into the Iberian Gulf as does *G. rugosa* (Linnaeus, 1767) although, as noted above, a very similar specimen has recently been collected in 500 m off of Martinique, West Indies (likely a dropped shell). However, this species group was widespread in Miocene-Pliocene seas throughout the present area of Europe. It is far from certain that the Dominican Republic Middle Miocene to Early Pliocene records are closely related phylogenetically to *G. echinophora s. s.*, so the significance of these few western Atlantic records of *Galeodea* is unclear, but superficially they seem to represent migration of this species group to the New World.

Genus *SCONSIA* Gray, 1847

Sconsia Gray, 1847: 137. Type species (by original designation): *Cassidaria striata* Lamarck, 1816 [junior secondary homonym of *Sconsia striata* (J. Sowerby, 1812)], = *Sconsia grayi* A. Adams, 1855, Pleistocene and Recent, western Atlantic.

?*Morionassa* Sacco, 1890: 74. Type species (by original designation): *Morionassa amplexens* Sacco, 1890 (aberrant?), Miocene, Italy.

Galeodosconsia Sacco, 1890: 69. Type species (by original designation): *Cassidaria striatula* "Bonelli, 1825" (manuscript name, = *Cassis striatula* Bellardi & Michelotti, 1841, according to Abbott, 1968: 123), Miocene, Europe.

Remarks.—*Sconsia* is one of the major cassid genera in the Cenozoic rocks of tropical America. As the type species, *S. grayi* (A. Adams, 1855) (= *S. striata* Lamarck, 1816, preoccupied), is a relatively uncommon species dredged from offshore in *ca.* 30-200 m in the Caribbean Sea at present, the abundance of *Sconsia* in Cenozoic molluscan faunas apparently reflects the moderately deep offshore deposition sites of the rocks containing those faunas. The genus is immediately recognizable by its elongate, graceful shape with a short spire and a long, gradually tapered last whorl, by its sculpture being almost solely of fine, almost smooth spiral cords, by the presence of varices on the spire in some species, and by the long, drawn out anterior end, merging imperceptibly into a completely untwisted siphonal canal. The protoconch is very small, much the smallest of the cassids studied here, and consists of only one smooth whorl, with an upright, protruding apex, similar to but smaller than that of Recent *Galeodea* species. The operculum and radula were described and illustrated for the first time by Bayer (1971: figs 17A, 20D) and closely resemble those of *Galeodea* in all details. Dall (1909a) pointed out that early Cenozoic species of *Sconsia* and *Galeodea* converge in shell morphology. Also, the genus *Microsconsia* Beu, 2008, resembles *Galeodea* in most characters, including the protoconch, but has fine spiral sculpture resembling that of *Sconsia* and a unique, abbreviated, left-deviated columellar base.

Virtually all material recorded here is from the Atlantic part of the study area and certainly *Sconsia* has been entirely limited to the western Atlantic for much of its history, as it is at present. However, I accepted (Beu, 2005) two Neogene species from Indonesia (*S. pulchra* Pannekoek, 1936; *S. martini* van Regteren Altena, 1942) as typical species of *Sconsia*, and many species occurred in the area now known as Europe during Paleogene and Miocene time. It is of interest for biogeography to note that a few specimens of *S. grayi* are recorded below from two Late Miocene localities in Darien, on the Pacific coast of Panama, and Olsson (1964: 169) recorded *S. grayi* from three localities in the Late Miocene Angostura Fm of Ecuador. They are clearly significant for demonstrating that the Isthmus of Panama had not been uplifted above sea level at the time of their deposition.

Sconsia grayi (A. Adams, 1855)
Pl. 66, Figs 6-7; Pl. 67, Figs 1, 3, 5

Cassidaria striata Lamarck, 1816: pl. 405, figs 2a-b, "Liste des objets": 3; 1822: 216; Kiener, 1835a: 6, pl. 2, fig. 3; Deshayes,

- 1844: 10; Reeve, 1849b: pl. 1, fig. 2; Küster, 1857: 52, pl. 55, figs 1-2 (junior secondary homonym of *Cassis striata* J. Sowerby, 1812, referred to *Sconsia* by Glibert, 1963: 109, and Tracey, 1992: 161).
- Sconsia striata*. Gray, 1847: 137; Clench & Abbott, 1943: 6, pl. 4, figs 1-4; Morretes, 1949: 91; Warmke & Abbott, 1962: 97, pl. 28, fig. g; Bayer, 1971: 138, figs 14, 17A, 20D; Matthews & Coelho, 1972: 13, fig. 8; Abbott, 1974: 160, pl. 6, fig. 1730; Rios, 1985: 73, pl. 26, fig. 320; 1994: 85, pl. 28, fig. 332; Lipe & Abbott, 1991: 8, illus.; Kreipl, 1997: pl. 10, figs 28-28a; Redfern, 2001: 59, pl. 30, fig. 252.
- Sconsia grayi* A. Adams, 1855: 136, pl. 28, fig. 6; Trew, 1992: 34; Beu, 2008: 325, figs 1C-D, 19A-E, G, 20A-K.
- Cassidaria (Sconsia) striata*. Chenu, 1859: 208, fig. 1138; Watson, 1886: 410.
- Cassidaria sublaevigata* Guppy, 1866: 287, pl. 27, fig. 10; 1874: 439; Gabb, 1881: 356.
- Sconsia barbudensis* Higgins & Marrat, 1877: 411, pl. 1, fig. 1; Clench, 1959: 329, pl. 172.
- Sconsia sublaevigata*. Dall, 1903a: 1584; Böse, 1906: 36, pl. 4, figs 9-10; Beu, 2001: 712.
- Leucozonia (Lagena) aff. smaragdula*. Toula, 1909: 699, pl. 25, fig. 9 [not *Leucozonia smaragdula* (Linnaeus, 1758)].
- Sconsia laevigata*. Pilsbry & Brown, 1911: 356; Anderson, 1929: 142; Petuch, 1981: 321 (not *Sconsia laevigata* G. B. Sowerby I, 1850).
- Sconsia laevigata* var. *gabbi* Olsson, 1922: 308, pl. 12, fig. 3.
- Sconsia bocasensis* Olsson, 1922: 309, pl. 12, figs 12-13.
- Sconsia (Sconsia) striata sublaevigata*. Woodring, 1928: 309, pl. 20, figs 3-6.
- ?*Sconsia* cf. *striata*. Rutsch, 1934: 53, pl. 11, fig. 11.
- Sconsia laevigata sublaevigata*. Woodring, 1959: 201, pl. 34, figs 8-9, pl. 35, figs 1-4.
- Sconsia laevigata gabbi*. Olsson, 1964: 169.
- Sconsia lindae* Petuch, 1987: 96, pl. 15, figs 7-8; Robinson, 1991: 305, pl. 13, fig. 14; Diaz & Puyana, 1994: 171, fig. 637; Kreipl, 1997: 30, pl. 10, fig. 26.

Remarks.—*Sconsia grayi* is recognized easily by (a) its graceful, elongate oval shape, (b) its base being drawn out very gradually into a short, completely untwisted siphonal canal, (c) its sculpture of many relatively high, narrow spiral cords with interspaces of varying width, less than or equal in width to one cord, crossed by fine axial ridges in a narrow zone behind the terminal varix, but lacking earlier varices except in a few atypical individuals, and (d) its well-thickened aperture with a thick terminal varix, many short, prominent transverse ridges inside the outer lip, and a thick, nearly smooth inner lip bearing very faint transverse ridges over most of its height and a row of 8-10 shorter and more prominent ones on the base of the columella. The sculpture is the most prominent of all the species considered here.

A problem faced in this study was the scarcity of Recent specimens of *Sconsia grayi* in museum collections, providing a hindrance to both understanding the variation of Recent

species, and comparing them with the fossils. Fortunately, I was able to examine the suite of 124 specimens collected off of the coast of Colombia, southwestern Caribbean Sea, by Rudo von Cosel (MNHN), and now stored at SMF (reviewed and illustrated by Beu, 2008: figs 20A-K). Although three immature specimens were collected from a depth of *ca.* 200 m at *Choco* sta. 621, the others all were collected in *ca.* 30-50 m in 23-m wide Gulf of Mexico semi-balloon shrimp trawls, from localities along the entire Colombian coast; this is precisely the type area of *S. lindae*. The specimens range from coarsely sculptured, moderately short-spined ones of the type usually regarded as “typical” *S. grayi* and even more short-spined specimens with a lightly angled shoulder, through to tall and narrow, tall-spined specimens with relatively weak spiral sculpture, of the type named as the separate “species” *S. lindae* by Petuch (1987: 96, pl. 15, figs 7-8), and through to even more extreme, tall specimens than Petuch’s holotype. There is no geographical or depth control on the occurrence of specimens resembling *S. lindae*; the tall, weakly sculptured specimens were collected from near the center of the Colombian coastline, where they intergrade with shorter and more coarsely sculptured specimens collected on either side. It is therefore clear that the living *S. grayi* population is quite variable in the sort of characters that previously have been used to recognize species, and the fossils need to be reinterpreted with this variation in mind. The three small specimens from *Choco* sta. 200 all are rather more different from “typical” *S. grayi* than any of the others, with a rather more biconic shape than usual, a relatively tall, conic spire, and weaker spiral sculpture than any of the others. They also have a rather more zigzag, axially banded color pattern, not the evenly banded pattern of shallow-water specimens, on which a combination of axial and spiral bands of similar widths produces a vaguely checkerboard pattern of poorly defined squares. The *Choco* specimens more nearly resemble the Pliocene fossils that I initially identified as *S. sublaevigata* than any other Recent material seen, and suggest that along with all of the other complications, a depth control on sculptural prominence needs to be considered when interpreting the fossils.

No one would argue that *Sconsia grayi* intergrades with the Miocene-Early Pliocene *S. laevigata* (G. B. Sowerby I, 1850) (see below), but they are linked through the geological record by an intergrading series of forms, as was pointed out long ago by Gabb (1875; 1881: 357). Several of these forms have received species names, and it is very difficult to tell how many of them should be recognized as species. *Sconsia lindae* was originally identified by Petuch (1981: 321) as *S. laevigata*, but its elongate shape and the presence of fine spiral threads over most of the adult shell show that that is incorrect, and Petuch (1987) later named it as a separate living species. However, the variation shown by both Recent material (discussed

above) and Plio-Pleistocene fossils of *S. grayi* demonstrates that *S. lindae* was based on tall, narrow, weakly sculptured end-members of the *S. grayi* population. Even *S. nephele* Bayer (1971: 139, fig. 15; Sunderland & Sunderland, 1991; Kreipl, 1997: 31) possibly was based on an extreme variant of *S. grayi*, although its weaker sculpture, shorter shape, and unique color pattern of eight spiral bands of alternating lighter and darker square spots (a checkerboard pattern) make it possible that this really is a distinct species. With only the holotype and one other specimen available, it is impossible to judge the status of such forms, and much more material will be needed to solve such questions. It is clear, though, that *S. alexarthuri* Parth (1995: 175, text-fig.; Kreipl, 1997: 30, pl. 10, fig. 25) is a species abundantly distinct from all others in the genus, because its tall spire, narrowly fusiform shape, extremely fine sculpture with an almost smooth last whorl, and almost uniform pale yellowish color are completely unlike the characters of all other Recent species. Indeed, anatomical characters (including the radula) are still required to demonstrate conclusively that this species belongs to *Sconsia*. *Sconsia bocasensis* Olsson (1922: 137) was proposed for coarsely sculptured Pliocene specimens from the Bocas del Toro Basin, Panama, but specimens examined during the present project from the same area are indistinguishable from the Recent *S. grayi*. Olsson (1922) compared his specimens with *S. laevigata* var. *gabbi* Olsson (proposed in the same paper) but, having assumed that they were Miocene in age, did not consider the possibility that they were *S. grayi*. In my opinion, both *S. bocasensis* and *S. laevigata* var. *gabbi* are simply synonyms of *S. grayi*.

The other problem faced in *Sconsia* taxonomy was the status of *S. sublaevigata* (Guppy, 1866), a narrow, slightly more weakly sculptured form in Late Miocene and mid- to Late Pliocene rocks of Atlantic Panama. Initially, some specimens from the Pliocene of Atlantic Panama (Bocas del Toro Basin) were identified as *S. sublaevigata*, whereas other more coarsely sculptured specimens from the same formations were identified as *S. grayi*. From the diversity of Pliocene to Recent species and forms, two conclusions were possible: either *S. sublaevigata* is simply part of the variation of *S. grayi*, or this is not a simple anagenetic ancestor-descendent series, but represents only part of a poorly understood (and poorly represented in the fossil record) plexus of branching lineages. I tried to keep the *S. sublaevigata* and *S. grayi* forms separate in this work, in the hope of being able to use *Sconsia* in biostratigraphy, *i.e.*, that they were segregated chronologically and stratigraphically, but in the end, I have been forced to conclude that this is all one species. For example, most specimens from the Moín Fm (latest Pliocene-Early Pleistocene) at Limón, Costa Rica, are significantly more coarsely sculptured than the Panama Pliocene specimens initially assigned to *S. sublaevigata*, and are assigned here to *S. grayi*. However,

a series of 11 specimens from the Moín Fm at Los Corales, Limón, collected by Bernard Landau, consists of seven specimens of "typical," coarsely spirally sculptured *S. grayi*, and four more weakly sculptured specimens that would have been classified as *S. sublaevigata*. In view of the variation seen in the Recent population and of the intergradation between forms in the Panama area, these are all now considered to be merely part of the normal variation of *S. grayi*. Several specimens in NMB 17635 and one in NMB 18373 have faint but obvious, wavy orange axial color bands, demonstrating that the form identified as *S. sublaevigata* had a similar color pattern to that of Recent specimens of *S. grayi*. In my opinion this is one variable species.

This species has long been known as *Sconsia striata*. However, as Tracey (1992: 162) pointed out, the English Eocene species *Cassis striata* J. Sowerby, 1812, was placed in *Galeodosconsia* by Sacco (1890: 69), and all later authors (*e.g.*, Cossmann, 1903: 133; Dall, 1909a: 66; Wrigley, 1934: 117; Glibert, 1963: 109) have considered *Galeodosconsia* to be a synonym of *Sconsia*. Glibert (1963) and Tracey (1992) took the logical step of referring "*Cassis*" *striata* to *Sconsia*. *Sconsia striata* (J. Sowerby, 1812) is therefore a senior secondary homonym of *S. striata* (Lamarck, 1816), and the latter name must be replaced by the next available synonym. *Sconsia grayi* A. Adams, 1855 was therefore adopted by me (Beu, 2008) as the valid name for the species.

The opportunity is taken to reillustrate (Pl. 67, Fig. 2) the specimen illustrated previously by Rutsch (1934: 53, pl. 11, fig. 11; NMB H 1863) from the Early Pliocene Punta Gavilán Fm at Punta Gavilán, northern Venezuela, under the name *Sconsia cf. striata*. The material is very imperfect, which is hardly surprising because all specimens at this locality are calcite neomorphs. Further collecting has brought very few further specimens to light from this locality. The fine spiral sculpture on this specimen is like that of Panama Pliocene material assigned to *S. grayi*, but the large size and relatively wide, weakly shouldered shape suggest that this form is intermediate between *S. laevigata* and *S. grayi*. Other slightly incomplete to fragmentary specimens from the same locality are present in NMB 17531, collected by W. & J. Gibson-Smith (2), in Kugler & Rutsch's collections (NMB 12040, 2; NMB H 1864/1-2; NMB 12045, 2, including NMB H 1865), and in Bernard Landau's collection (1 in good condition).

Dimensions.—Holotype of *Sconsia grayi*: H 43.0, D 27.8 mm; holotype of *S. barbudensis*: H 67, D 38 mm (Clench, 1959: 330); lectotype of *Cassidaria sublaevigata*: H 41.3, D 26.4 mm; larger paralectotype: H 50.5, D 33.4 mm; figured specimen, NMB H 18010, from NMB 18681, Escudo de Veraguas Island, Bocas del Toro Basin, Atlantic Panama, Pliocene: H 54.3, D 34.5 mm; figured specimens, from NMB 17808, Isla Popa, Bocas del Toro Basin, Atlantic Panama,

Pliocene; NMB H 18014: H 47.3, D 28.5 mm; NMB H 18015: H 49.1, D 34.0 mm.

Types.—*Cassidaria striata*, 2 syntypes MHNG 1100/75/1-2, without locality. The paler syntype, MHNG 1100/75/1, H 51 mm (Beu, 2008: fig. 19D, G), is the specimen illustrated by Kiener (1835a: pl. 2, fig. 3), whereas the smaller, much darker syntype, MHNG 1100/75/2, H 43 mm (Beu, 2008: figs 19B, E), is the specimen illustrated by Lamarck (1816: pl. 405, fig. 2). The paler syntype, MHNG 1100/75/1, is here designated the lectotype of *C. striata*. The two specimens are conspecific, and represent the Caribbean species universally known as *Sconsia striata*. Clench & Abbott (1943: 8) designated the type locality as *Atlantis* sta. 2981A, off of Punta Alegre, Cuba. *Sconsia grayi*, holotype BMNH 1967664 (Beu, 2008: figs 19A, C), without locality. The type locality is here designated as off Punta Alegre, Cuba. *Cassidaria sublaevigata*, lectotype (designated here; figured syntype of Guppy, 1866: pl. 17, fig. 10) BMNH Palaeontology Department 64075, with 2 paralectotypes BMNH Palaeontology Department 64048, all from Bowden shellbed, St. James Parish, Jamaica, Late Pliocene. *Sconsia barbudensis*, holotype at City of Liverpool Public Museum (illustrated by Clench, 1959: pl. 172), from 30 m, off of Barbuda Island, Lesser Antilles (not seen). *Sconsia bocasensis*, holotype PRI 21083, a late Pliocene fossil from Bocas del Toro (= Colon) Island, NE Panama. *Sconsia laevigata* var. *gabbi*, holotype PRI 21074, again a late Pliocene fossil from “Toro Cay” (i.e., Bocas del Toro Island), NE Panama. *Sconsia lindae*, holotype USNM 784457 (not seen), trawled by commercial shrimpers in 35 m, off of Cartagena, Colombia, 1976; 3 paratypes from Gulf of Urabia, Colombia (Petuch, 1987: 96).

Other material examined.—**Recent:** R. von Cosel’s material from the northern coast of Colombia at SMF (48 samples containing 124 specimens) was listed by me (Beu, 2008: 326).

Fossils: Jamaica: Late Pliocene, Bowden: NMB 10635 (1); 10651 (1); 11110 (1). **Atlantic Costa Rica: Late Pliocene-Early Pleistocene,** Moín Fm: NMB 18079 (7); 18084 (4); 18105 (3); 18112 (5); 18113 (6); 18273 (6); 18277 (2); 18278 (6); 18752 (2); TU 1240, Los Corales, Limón, collection of Bernard Landau (11). **Atlantic Panama: Late Miocene:** Chagres Fm: NMB 18764 (6); 18987 (3); 18990 (2); 18991 (1); Gatun Fm: NHMV 1933-18-187, Gatun [1 incomplete specimen identified by Toulou (1909: 699, pl. 25, fig. 9) as “*Leucozonia (Lagena)* sp. aff. *smaragdula* Linné”]; Valiente Fm: NMB 17629 (18); 17824 (19); 18375 (9); 18711 (29); 18769 (4); 18771 (8); Nancy Point Fm: NMB 18727 (2); 18661 (1); 18689 (1); 18710 (6); 18729 (3). **Pliocene:** Escudo de Veraguas Fm: NMB 17621 (1); 17622 (2); 17628 (5); 17833 (1); 17843 (2); 17845 (1); 17847 (1); 17848 (1); 18668 (5); 18669 (1); 18670 (6); 18672 (3); 18677

(2); 18679 (8); 18680 (2); 18681 (15; 1 illustrated, NMB H 18010; Pl. 67, Fig. 1, 3); 18682 (2); 18683 (3); 18684 (2); 18686 (3); Cayo Agua Fm: NMB 17633 (1); 17635 (13; several have faint wavy orange axial color bands); 17808 (22; 2 illustrated, NMB H 18014, H 18015; Pl. 66, Figs 6-7; Pl. 67, Fig. 5); NMB 17812 (3); 17823 (1); 17825 (1); 17828 (3); 17829 (1); 17830 (2); 17904 (1); 18373 (3; one has faint wavy orange axial color bands); 18374 (11); 18377 (2); 18378 (1); 18719 (4); 18722 (17); 18733 (9); 18734 (2); 18736 (2); 18983 (8); 18984 (1); NMB unreg., Water Cay, Panama, pres. A. A. Olsson, ident. as *Sconsia laevigata gabbi* Olsson (2); Shark Hole Point Fm: NMB 17807 (6); 17850 (4); 17855 (1); 18387 (2); 18388 (3); 18705 (23); 18706 (2); 18707 (1); 18723 (4); 18724 (9); 18976 (2); 18977 (1); 18980 (1); 18981 (1). **Pleistocene:** Swan Cay Fm: NMB 18381 (2); 18743 (3). **Panama, Darien: Late Miocene:** NMB 18184, Chucunaque Fm, Río Chucunaque (4); 18510, Tuirá Fm, Río Tuquesa (1).

Distribution.—*Sconsia grayi* lives now throughout the western Atlantic from southern Florida, USA, and the Bahamas (Clench & Abbott, 1943) south to Bahia, Brazil (Rios, 1994: 85). However, it seems to be much more common along the coastline of northern South America than elsewhere. Robinson (1991) recorded many more latest Pliocene-Early Pleistocene specimens in Tulane University collections from the Limón area on the Atlantic coast of Costa Rica that I have not examined (TU 945, 15 specimens; 1239, 19; 1240, 33; 1489, 21; 1495, 18; 1496, 2). Most other fossil records are from either the Bowden Shellbed, Jamaica, or the Bocas del Toro Basin of the Atlantic coast of the Panama Isthmus, but two biogeographically important Late Miocene samples are recorded here from Darien, on the Pacific coast of Panama, representing one of only two occurrences of *Sconsia* in the eastern Pacific of which I am aware. Olsson (1964: 169) also recorded “fragments of a large *Sconsia*,” identified as *S. laevigata gabbi*, from the Late Miocene Angostura Fm at three localities in Ecuador: Telembi, Río Cayapas; Río Onzole (“Picaderos formation”); and Bahia de Carques (“Bahia formation”). His discussion of *Sconsia* characters and how he viewed the taxa suggests that he was describing moderately coarsely sculptured specimens of *S. grayi* similar to those from Darien. The place of *S. grayi* seems to have been occupied in the Pliocene rocks of Florida by *S. hodgii* (Conrad, 1841) (see below), indicating that distinct provinces were occupied by distinct *Sconsia* species during Pliocene time.

Sconsia hodgii (Conrad, 1841)

Cassis hodgii Conrad, 1841: 346, pl. 2, fig. 10.

Galeodia (sic) hodgii. Conrad, 1854: 30; Tuomey & Holmes, 1856: 138, pl. 28, fig. 10; Emmons, 1858: 257, fig. 128; reprint: 166.

Sconsia hodgii. Conrad, 1863: 564; Cossmann, 1903: 133, pl. 6, fig. 3; Woodring, 1928: 310; Mansfield, 1930: 93; Gardner, 1948: 215, pl. 29, fig. 3; Petuch, 1994: 118, pl. 38, figs J-K; Petuch, 1997: 165, fig. 55, fig. J.

Sconsia metae Petuch, 1994: 118, 272, pl. 38, figs L-M.

?*Sconsia sublaevigata*. Petuch, 1994: 118, pl. 38, fig. H [not *S. sublaevigata* Guppy, 1866, = *S. grayi* (A. Adams, 1855)].

Sconsia hodgei (sic). Campbell *et al.*, 1995: 175.

Remarks.—Good illustrations were provided by Gardner (1948: pl. 29, fig. 3; copy of Tuomey & Holmes, 1856: pl. 28, fig. 10) and Petuch (1994: 119, pl. 38, figs J-M). *Sconsia hodgii* is an elongate-oval Pliocene species with a moderately tall spire and fine, even spiral sculpture over the entire exterior. Gardner (1948: 216) noted its distinguishing characters as its heavy (*i.e.*, unusually thick) shell, its stocky outline, its uniform, fine spiral sculpture, its denticulate outer lip, and its closely transversely ridged (“rugose”) inner lip.

Campbell *et al.* (1995: 175) raised the question of the spelling of the specific epithet by using the spelling “*hodgei*.” The species clearly was named by Conrad for J. T. Hodge, the author of the paper Conrad described the fossils within, but Conrad consistently spelled the name “*hodgii*” and evidently intended it that way, *i.e.*, it is not a typographical or similar error. The spelling “*hodgei*” seems to me to be an unjustified emendation.

Sconsia metae Petuch, 1994, supposedly differs from *S. hodgii* in its smaller size (46 mm H rather than 58 mm), its greater inflation, its lower spire, and its proportionally wider and more heavily sculptured inner lip callus (Petuch, 1994: 272). However, the illustrated holotype is little different from most specimens of *S. hodgii*, which is variable in all the characters used to differentiate *S. metae*. *Sconsia metae* seems likely to be a synonym of *S. hodgii*. Petuch (1994: 118, pl. 38, fig. H) also illustrated a short, wide, weakly sculptured specimen with an unusually straight-sided spire outline from Petuch unit 7, APAC pit, Sarasota, Florida (Bermont Fm, early Pleistocene) as *S. sublaevigata*, but it is shown above that *S. sublaevigata* is a synonym of *S. grayi*. The wide specimen illustrated by Petuch is either an unnamed species, or an unusual, wide specimen of *S. hodgii*. Only collection of more material of this form can clarify its relationships.

Dimensions.—Tuomey & Holmes’ (1857: pl. 38, fig. 10) excellent illustration, copied by Gardner (1948: pl. 29, fig. 3), said to be at “natural size”: H 59, D 37 mm. Specimens reach a larger size than this.

Types.—Moore (1962: 64) listed *Cassis hodgii* among the types missing from ANSP; from Duplin Marl (early Late Pliocene; Ward, 1992: fig. 1) at Natural Well, 3 km SW of Magnolia, Duplin Co, North Carolina (Gardner, 1948: 215). Campbell *et al.* (1995: 175) confirmed that this species occurs at Natural Well. *Sconsia metae*, holotype UF 66236 (Petuch,

1994: 272) (not seen), from Petuch unit 10, lower Pinecrest beds (Tamiami Fm, middle Pliocene; Ward, 1992: fig. 1; Vermeij, 2005: 628), Phase 6 pit, Quality Aggregates Inc., Sarasota, Sarasota Co, Florida. I have not seen material of *S. hodgii*.

Distribution.—Gardner (1948: 216) recorded *Sconsia hodgii* from five localities in the Duplin Marl in North and South Carolina, USA, from Jackson Bluff, Leon Co, Florida, and from the upper bed at Alum Bluff, Liberty Co, Florida. Mansfield (1930) recorded it also from the “*Ecphora* zone” and the overlying “*Cancellaria* zone” of the Chotawhatchee Group (Pliocene) in Florida [see Waller (1969: 90-91) and Ward (1992: fig. 1) for an explanation of these “zones” and their stratigraphical relationships; = upper and lower Jackson Bluff Fm, mid-Pliocene]. Petuch (1994: 118) recorded it also from the “Yorktown, Duplin, Rayzor Formations” of the Carolinas, and from Petuch Unit 7, APAC pit, Sarasota, Florida (Tamiami Fm, Pliocene). Petuch (1994: 118) also recorded the apparent synonym *S. metae* from Petuch unit 10 within the same formation. *Sconsia hodgii*, therefore, is widespread stratigraphically and geographically in Pliocene rocks of North Carolina to Florida.

Sconsia laevigata (G. B. Sowerby I, 1850)

Pl. 66, Figs 1-5, 8-10; ?Pl. 67, Fig. 2

Cassidaria laevigata G. B. Sowerby I, 1850: 47, pl. 10, fig. 2; Gabb, 1873: 222; 1875: 361, pl. 24, figs 1-1b; Guppy, 1874: 439; 1876: 525.

Sconsia laevigata. Brown & Pilsbry, 1911: 356 (in part); Maury, 1917a: 275, pl. 19, fig. 2; Pilsbry, 1922: 361; Vokes, 1989: 41, footnote.

Sconsia (*Sconsia*) *laevigata laevigata*. Pflug, 1961: 36, pl. 7, figs 1-8; Jung, 1965: 510, pl. 68, figs 7-8.

Remarks.—*Sconsia laevigata* is a very distinctive species, differing from *S. grayi* in its much wider shape, with a lower spire and a much wider, weakly shouldered last whorl, in retaining low varices all down the spire, in lacking spiral sculpture altogether on the central and peripheral area of large adults, and reduced to fine, low, closely spaced spiral threads on juvenile and half-grown shells, in its more widely flared and thickened outer lip with shorter transverse ridges situated further inside the lip, in the wider, thicker callus area on the base of the lower lip, forming a narrow free margin that extends beyond the margin of the siphonal canal, in having a shorter, wider siphonal canal, and in developing a low, wide swelling, or very low node, on the dorsum of large specimens, so that the whorl becomes weakly shouldered. Pilsbry (1922: 361-362) pointed out that *S. laevigata* is similar to and perhaps descended from *S. lintea* (Conrad, 1848), which occurs in the Vicksburg Oligocene of the southern USA (MacNeil & Dockery, 1984:

109, pl. 17, figs 14, 20, pl. 30, figs 1-3, pl. 50, figs 3-4) but *S. lintea* is a narrower and more coarsely sculptured species than *S. laevigata*. It more nearly resembles the North Carolina-Florida Pliocene species *S. hodgii* than it does *S. laevigata*. Pilsbry (1922) proposed a phylogeny of American *Sconsia* species but, like Woodring's (1959: 201-202) comments, it has little bearing on our present understanding because of the incorrect ages assigned to many of the taxa he compared.

Vokes (1989: 41, footnote) provided a useful observation on relationships in *Sconsia* when she commented that "Although *Sconsia laevigata* has always been considered to be ancestral to the living species *S. striata* (Lamarck, 1816) [*i.e.*, *S. grayi*], the color pattern of *S. laevigata*, as seen under ultraviolet light, is identical to that of *S. nephele*, figured by Bayer, 1971, fig. 15." However, as noted above, the particularly clearly defined checkerboard pattern of *S. nephele* is in my opinion probably merely an extreme version of that of *S. grayi*, and it seems likely that the two names are synonyms. A clearly defined checkerboard pattern on *S. laevigata* demonstrates that this type of "interference pattern" formed by a combination of spiral and axial rows of alternating paler and darker bands, resulting in varying clarity of expression of the checkerboard, has been developed by tropical American *Sconsia* species throughout Neogene time.

Dimensions.—Lectotype: H 33.8, D 21.4 mm; large figured specimen, NMB H 18011, from NMB 17270, Dominican Republic: H 68.9, D 48.4 mm; medium-sized figured specimen, NMB H 18012, from NMB 17276, Dominican Republic: H 47.1, D 33.5 mm; small figured specimen retaining spiral sculpture, NMB H 18013, from NMB 18582 (TU 1227), Dominican Republic: H 35.5, D 21.3 mm; small specimen illustrated by SEM, NMB H 18039, from NMB 15867, Dominican Republic: H 31.1, D 19.0 mm.

Types.—*Cassidaria laevigata*, lectotype BMNH Palaeontology Department, G83945, selected by Pflug (1961: 37, pl. 7, figs 5, 7-8), with 16 paralectotypes, GG20068-20077, from "Miocene, Yaque River, Santo Domingo, coll. Col. T. S. Heneken, c. 1848." The lectotype is an immature specimen retaining spiral threads on the center of the whorls, as are most of the paralectotypes, whereas two of the paralectotypes (GG20068-20069) are larger and smoother, although not extreme adults.

Other material examined.—**Fossils: Dominican Republic: Late Early Miocene:** Baitoa Fm: TU 1226 (1); Arroyo Hondo, Río Yaque del Norte, collection of Bernard Landau (4). **Middle Miocene:** unnamed formation, TU 1249, road cut on road to Bani, southern Dominican Republic (1). **Late Miocene:** Cercado Fm: NMB 15899 (1); 15906 (2); 16801 (1); 16842 (1); Gurabo Fm: NMB 16910 (43); 17266 (2); 17267 (13; 1 illustrated, NMB H 18012; Pl. 66, Figs 1, 3); 17268 (5); USGS 8537 (1); 8702 (6); 8714 (2); Maury's

loc. 206, bluff 1, Cercado de Mao (7); Bluff 1 of Maury, Río Mao, coll. M. Taviani (Institute of Zoology, University of Bologna, 13 small); USGS 26535, Las Cahobas Fm, San Juan region (2); **Late Miocene/Early Pliocene:** Gurabo Fm: NMB 15871 (7); 16809 (2); TU 1206 (7); 1225 (many); 1246 (many); 1250 (several); 1277 (many); 1292 (3); 1293 (many); 1296 (several); USGS 8519 (41); 8527 (2); 8528 (11); 26275 (26); 26277 (3); 26281 (1); 26283 (5); NMB unreg., Dominican Republic, pres. A. A. Olsson, Río Gurabo (3); bluish shale, Yaque River, coll. Sir Robert Schomburgh, pres. 1852 (BMNH Palaeontology Department, G31026, 1; G31024, 1); Miocene, Yaque River, coll. Col. T. S. Heneken, pres. Geological Society, 1911 (BMNH Palaeontology Department, GG20363, 1); Miocene, Santo Domingo (BMNH Palaeontology Department, G11077, 57 small); float, Río Gurabo, pres. E. Vokes (Institute of Zoology, University of Bologna, no. 10125; 2); Miozän, Dominican Republik, Sammlung Weyl, pres. Pflug (SMF, 1). **Early Pliocene:** Gurabo Fm: NMB 15803 (3); 15805 (1); 15807 (2); 15809 (2); 15811 (4); 15813 (2); 15816 (10); 15817 (3); 15821 (1); 15822 (1); 15824 (1); 15833 (6 + frags); 15836 (5); 15842 (11); 15843 (2); 15845 (2); 15846 (3); 15850 (1); 15854 (4); 15855 (1); 15860 (5); 15861 (2); 15862 (2); 15863 (5); 15864 (2); 15865 (7); 15866 (3); 15867 (9; 1 illustrated by SEM, NMB H 18039; Pl. 66, fig. 8, 10); 15868 (1); 15869 (3); 16807 (1); 16810 (3); 16867 (3); 16868 (1); 16869 (2); 16934 (1); 17270 (12; 1 large illustrated, NMB H 18011; Pl. 66, Fig. 2, 4); 17271 (5); TU 1211 (many); 1212 (many); 1213 (several); 1214 (several); 1215 (several); 1219 (many); 1220 (2); 1227A = NMB 18582 (5; 1 small illustrated, NMB H 18013, Pl. 66, Figs 5, 9; GNS WM16921, 1 juvenile); 1248 (1); 1278 (3); USGS 8516 (16); 8538 (1); 8539 (1); 8540 (1); 8541 (1); 8544 (3); 8545 (2); 8546 (1); 8547 (11); 8548 (3); 8549 (5); 8550 (9); 8551 (1); 8726 (1); Los Quemados [PRI 28773, 1, Maury's (1917a: pl. 19, fig. 2) illustrated specimen]; PRI, Maury's loc. 199, zone A, Río Gurabo (2); Maury's loc. 200, zone D, Río Gurabo (5); Maury's loc. 202, zone E, Río Gurabo (4); Maury's loc. 207, zone F, Río Gurabo (6); Maury's loc. 210, zone B, Río Gurabo (3); TU 1214, Río Gurabo, collection of Bernard Landau (5); 1227, Gurabo Fm, Arroyo Zalaya, collection of Bernard Landau (7); Mao Fm: NMB 16122 (2); 16885 (1). **Venezuela: Late Early Miocene,** Cantaure: NMB 12842 (1); 17243 (1, NMB H 13696, specimen illustrated by Jung, 1965: pl. 63, figs 7-8); 17516 (25); 17517 (1); 17519 (4); 17520 (1); Cantaure, collection of Bernard Landau (11; GNS WM17447, 2). **Early Middle Miocene:** NMB 17527, Buenevara Adentro beds (9).

Distribution.—*Sconsia laevigata* is recorded only from the late Early Miocene-Early Pliocene rocks of the Dominican Republic and of the Paraguaná Peninsula, northern Venezuela.

Presumably, though, it originally occurred more widely. As noted under *S. grayi*, the specimen illustrated by Rutsch (1934: 53, pl. 11, fig. 11; NMB H 1863; Pl. 67, Fig. 2) from Punta Gavilán, Venezuela (Early Pliocene), under the name *S. cf. laevigata*, and other material from this locality, is intermediate in shape and sculptural prominence between *S. grayi* and *S. laevigata*.

***Sconsia paralaevigata* Gardner, 1947**

Sconsia paralaevigata Gardner, 1947: 537, pl. 54, fig. 11.

Remarks.—*Sconsia paralaevigata* is a similar species to *S. laevigata* and *S. grayi*, from the Chipola Fm (late Early Miocene) of Florida. Gardner (1947: 537) provided an excellent description. It is shorter and wider than *S. grayi*, with a markedly more inflated last whorl, but with similar sculpture of fine spiral cords and weak axial threads. It is consequently very distinct from *S. laevigata* in its much more obvious sculpture and quite different shape, with a taller spire, a shorter anterior end, a more evenly inflated shape without the low dorsal swelling of *S. laevigata*, and a much less flared outer lip than *S. laevigata*. *Sconsia paralaevigata* seems likely to have been a member of a lineage leading to *S. hodgii*. *Sconsia paralaevigata* is also similar to the earlier species *S. lintea* (Conrad, 1848) (Oligocene; MacNeil & Dockery, 1984: 109, pl. 17, figs 14, 20) and possibly descended from it. They are very similar in size and shape, but *S. lintea* is more finely sculptured than *S. paralaevigata*.

Dimensions.—Holotype: H 36 mm, D 25 mm (Gardner, 1947: 538).

Types.—Holotype USNM 371888, from USGS 2213, Chipola Fm (late Early Miocene), 1.6 km downstream from Baileys ferry, Chipola River, Calhoun Co, Florida (not seen). I have not seen material of *S. paralaevigata*.

Distribution.—Gardner (1947: 538) recorded only one other specimen, from the Chipola Fm, in the Aldrich collection at Johns Hopkins University. To my knowledge, *Sconsia paralaevigata* is limited to the Chipola Fm in Florida, USA.

***Sconsia prolongata* Petuch, 1994**

Sconsia prolongata Petuch, 1994: 118, 272, pl. 38, figs C-D; Petuch, 1997: 205, fig. 75K.

Remarks.—*Sconsia prolongata*, described by Petuch (1994: 272) as the “last fossil *Sconsia* species” in Florida, is taller and narrower and has a much taller spire than all other *Sconsia* species of which I am aware. It is possible that even this form falls within the variation of *S. hodgii*, but it seems likely to be a distinct species. Petuch (1994: 272) differentiated it from *S.*

hodgii as follows: “*Sconsia prolongata* ... is most similar to the older, stratigraphically lower *S. hodgii*, but differs in being a much more slender, elongated, and narrower shell with a far more elongated, protracted spire.” Very few specimens (one?) are known as yet, and this species can only be evaluated when more material is available.

Dimensions.—Holotype, H 66 mm (Petuch, 1994: 272).

Types.—Holotype UF 66235; from Petuch unit 3, “upper Pinecrest beds only” (= Bermont Fm), early Pleistocene, APAC pit, Sarasota, Florida (Petuch, 1994: 272) (not seen). I have not seen material of *Sconsia prolongata*.

Distribution.—Known only from the type material; apparently limited to the Bermont Fm (early Pleistocene).

Subfamily **OOCORYTHINAE** Fischer, 1885

Remarks.—I have previously pointed out (Beu, 2008) that the genera related to *Oocorys* Fischer, 1884 (including *Dalium* Dall, 1889, and *Eucorys* Beu, 2008), differ from *Galeodea* and the other genera of Cassinae in lacking obvious, pigmented eyes, in having a short, wide proboscis rather than the markedly longer and narrower one of all other Cassidae, in having a wide, thin, flattened penis rather than a narrow, cylindrical one, in having a curved to weakly S-shaped osphradium rather than a simple, straight one, and in having an operculum with a spiral section of growth lines near the nucleus, rather than obviously commarginal growth lines throughout growth. I therefore recognized subfamily Oocorythinae for these genera.

Genus **DALIUM** Dall, 1889

Dalium Dall, 1889: 230. Type species (by original designation): *D. solidum* Dall, 1889, deep water, western Atlantic.

Remarks.—*Dalium* is a moderately distinctive genus with few species, identifiable by its tall, conic, almost completely straight-sided spire, by its sculpture of many very low, narrow, closely spaced, flat-topped spiral cords (which also could be described as many narrow, shallow grooves in a smooth surface) and a moderately wide, depressed, concave subsutural band, markedly wider than the similar band present in several species of *Oocorys*, by its simple aperture with an unthickened, unreflected, smooth outer lip and a narrow, thin, smooth inner lip, and by the base drawn out a little but ending in a widely open notch with no real siphonal canal, and the base of the columella curved to the left, appearing slightly abbreviated or “cut away” in conventional view. The familial position was slightly in doubt, despite the close resemblance to *Oocorys* Fischer, 1884, until the radula and operculum were described and illustrated by Bayer (1971: 145-148, figs

20A, 21, 22A), showing that they are closely similar to those of *Oocorys*. Okutani (1983: 268) also illustrated the radula and operculum. It is possible that *Dalium* species differ little enough from *Oocorys* that they should be referred there, *i.e.*, that these generic names are synonyms, but such phylogenetic hypotheses are best answered at present by molecular analysis, and the conservative position of preserving the present classification is adopted here.

The genus *Dalium* appears to contain only the three species *D. solidum* Dall, 1889, *D. dalli* Böse, 1906, and *D. ecuatorianum* Olsson, 1942. It is feasible that these three species constitute a single evolutionary lineage, *D. dalli* representing the ancestor, little-modified from *Oocorys*. *Dalium ecuatorianum* and *D. solidum* are “typical” *Dalium* species in having wide, strap-like spiral cords and an obvious subsutural collar, and the slightly shorter *D. ecuatorianum* might well have been the direct ancestor of the larger and slightly taller *D. solidum*.

Blank (1980: 85, pl. 14, fig. 13) referred a Late Cretaceous species to *Dalium*, *D. cretaceum* Blank, 1980, from the Impen-vyemskaya Subsuite (Maastrichtian) in the Koryak Range, far eastern Russia. The three illustrations show a small (19 mm H), spirally sculptured shell with what appears to be the remnants of a former anterior siphonal canal, now broken off. Blank (1980) described the aperture as “broken.” This species is an exceedingly unlikely addition to an otherwise Neogene and Recent American genus, and appears to belong in the Buccinidae rather than the Cassidae.

***Dalium dalli* Böse, 1906**

Pl. 64, Figs 1-3, 5-6

“*Dalium* (like *solidum*, Dall)”, Dall in Spencer, 1897: 24.

Dalium dalli Böse, 1906: 58, pl. 4, figs 7-8.

?*Dalium* cf. *dalli*. Nielsen, 2003: 92, pl. 16, figs 21-22.

Remarks.—Four samples are available from the Dominican Republic that are assigned to *Dalium dalli*. The shells are relatively small but tall and narrow for the genus, with a relatively tall spire with almost straight outlines. The sculpture consists of a narrow subsutural band of three narrow, closely spaced spiral cords rendered cancellate by fine, close axial lamellae, followed below by a depressed, concave, almost smooth spiral band the same width as the subsutural cancellate band, followed below by many narrow, raised, smooth, round-topped spiral cords with interspaces each narrower than one cord, six cords on spire whorls, and *ca.* 30-32 on the last whorl and base. The base is contracted into a more constricted, short, open siphonal canal than that of the two younger species assigned to *Dalium*. The aperture is moderately thickened, with a narrow, smooth, well-thickened inner lip, and the outer lip is smooth on the interior, and thickened exteriorly into a nar-

row, thin but true varix. One specimen has a varix left at a growth pause approximately one tenth of a whorl behind the terminal varix. These specimens agree in every visible character of the shape, the raised and depressed subsutural bands, and the spiral cords, with the specimens illustrated by Böse (1906: pl. 4, figs 7-8). It is clear that Böse’s specimens also were varicate, because the specimen in his pl. 4, fig. 7, clearly has a varix remaining at a growth pause a short distance before the terminal one, as on one of the Dominican Republic specimens.

Böse (1906) was quite justified in assuming that, because this species has a subsutural cancellate-sculptured band, followed below by a depressed band, it is congeneric with *Dalium solidum*. A few Recent specimens of *D. solidum* have been examined that also have a narrowly varicate outer lip, and the presence of varices in *D. dalli* does not rule out a position in *Dalium*. The one important character that is distinctive is the spiral cords, which are markedly narrower in *D. dalli* than in the two younger species. Taken over all, these characters seem best interpreted as indicating that this is an early species of *Dalium*, perhaps ancestral to the younger species, with spiral sculpture like that of the presumably ancestral genus *Oocorys*.

Böse (1906) pointed out that Dall (list of fossils in Spencer, 1897: 24) had previously recorded a species of *Dalium*, “like *solidum* Dall,” from the 124-km post on the Mexican railway, near Estado Santa Lucretia, at the crossing of the Río Jaltepec, Isthmus of Tehuantepec, 12 km from the type locality of *D. dalli*. He supposed, quite reasonably, that they were conspecific. I do not know the present location of the specimens sent by Spencer to Dall, but more recently collected material from the Río Jaltepec in the USNM (see below) is clearly conspecific.

Sven Nielsen showed me a sample of 16 specimens (at SGO.PI and SMF) from the Ranquil Fm (Oligocene-Early Miocene fossils reworked into Early Pliocene rocks) at Punta El Fraile, west of Arauco, south-central Chile, which appears to belong to a new species of *Dalium* closely resembling *D. dalli* (see Nielsen, 2003: 92, pl. 16, figs 21-22; Finger *et al.*, 2007: fig. 12N). The specimens are indistinguishable from the Dominican Republic material in most characters, but the largest few specimens are slightly larger and more inflated than the largest specimens seen from the Dominican Republic, so at present it is uncertain whether they are conspecific. This record demonstrates that species of *Dalium* had wide distributions during Miocene time, similar to those of *Oocorys* species at present. The specimen illustrated by Finger *et al.* (2007: fig. 12N) is now SGO.PI 6451.

Dimensions.—Figured specimen, NMB H 18007, from TU 1250 (NMB 18558), Río Verde, 10 km N of La Vega, Dominican Republic: H 34.8, D 20.6 mm; figured specimens, TU 1357 (NMB 19017), Río Yaque del Norte, Dominican

Republic: NMB H 18008: H (incomplete) 38.2, D 26.3 mm; NMB H 18009: H (incomplete) 30.6, D 22.9 mm.

Types.—*Dalium dalli*, type material presumably at Instituto Geologico de Mexico, Mexico City (not seen); from km 136, Tehuantepec railway, Division Río Coatzacoalcas, Isthmus of Tehuantepec, Estado Veracruz, Mexico, Middle Miocene. Emily Vokes (formerly of Tulane University, New Orleans; pers. comm., April 2008) provided the information that km 136 is 9 km south of Estancia Santa Lucretia (at km 127), now known as Jesus Carranza, and is Middle Miocene in age (planktic foraminiferal zone N9-12).

Other material examined.—**Fossils: Mexico: Middle Miocene:** USGS 10699, Río Jaltepec, Isthmus of Tehuantepec area (presumably near type locality, and the locality for the specimens listed by Dall (in Spencer, 1897); USNM, 5). **Dominican Republic: Late Miocene/Early Pliocene:** Gurabo Fm, deep-water facies: TU 1250 = NMB 18558, Río Verde (3; one illustrated, NMB H 18007; Pl. 64, Figs 1, 6); TU 1284 = NMB 19013 = ?USGS 8702, S bank Río Yaque del Norte, junction of roads to San José de los Matos and Canela (1); 1357 = NMB 19017, bluff W side Río Yaque del Norte, Bella Vista (3; 2 illustrated, NMB H 18008, H 18009; Pl. 64, Figs 2-3, 5); 1450 = NMB 19022, Arroyo Dicapagua, SW of Santiago de los Caballeros (4); USGS 8702 (= TU 1248) (USNM, 8); “Miocene, Yaque River, St Domingo, coll. Col. T. S. Heneken, c. 1848” (BMNH Palaeontology Department, GG20363, 1 incomplete). **Haiti: Late Miocene:** USGS 18397 (USNM, 1 incomplete).

Distribution.—*Dalium dalli* is recorded only from Middle Miocene to Early Pliocene rocks of the Isthmus of Tehuantepec, Mexico, of Haiti, and of the northern Dominican Republic. This distribution suggests that it must formerly have been widely distributed in the Caribbean region, however, and specimens can be expected in Late Miocene-Early Pliocene rocks of suitable offshore facies throughout the Caribbean. Vokes (in E. & H. Vokes, 1989: 21; Vokes, 1998: 9) commented that Dominican Republic localities near Barranca and Santiago de los Caballeros were deposited in at least 200 m, the deepest water of all Gurabo Fm localities, presumably explaining the occurrence of the deep-water genus *Dalium*. Very similar Oligocene-Early Miocene specimens from Tubul, near Arauco, Chile (on the western coast of South America), probably represent a distinct species. Like many other taxa, *Dalium* apparently had a trans-Isthmian distribution before the uplift of the CAI.

***Dalium ecuadorianum* Olsson, 1942**
Pl. 64, Figs 7-8

Dalium ecuadoriana (sic) Olsson, 1942: 229, pl. 9, figs 2-3.

Dalium ecuadorium (sic). Olsson, 1964: 171, pl. 30, figs 7-7a.

Remarks.—A specimen of *Dalium ecuadorianum* is illustrated here for comparison with the Dominican Republic specimens assigned to *D. dalli*, because it was only by comparison with the Ecuadorian fossils that the taxonomic position was established. *Dalium ecuadorianum* is closely similar to the Recent western Atlantic type species, *D. solidum*, in all characters, differing in having wider grooves between the spiral cords. The subsutural depressed band is significantly wider and more obvious in both *D. ecuadorianum* and *D. solidum* than it is in any *Oocorys* species, and the younger species of *Dalium* differ further from *Oocorys* in their complete lack of any thickening of the outer lip (apart from a few aberrant individuals), despite their thick, solid shells, and their lack of a true, constricted siphonal canal.

Dimensions.—Holotype: H 43, D 20 mm; paratypes: H 39, D 23.5 mm; H 36, D 21 mm (Olsson, 1942: 229); large specimen: H 47, D 30.1 mm (Olsson, 1964: 172); figured specimen, NMB H 17990, from NMB 19019 (TU 1398), Quebrada Camarones, Ecuador: H 38.4, D 23.4 mm.

Types.—*Dalium ecuadorianum*, holotype PRI 4066 (not seen), from Onzole Fm (Pliocene), Punta Gorda, Esmeraldas, northern Ecuador. The holotype designation was made only in the plate caption (Olsson, 1942: 252).

Other material examined.—**Fossils: Ecuador: Early Pliocene,** Onzole Fm: NMB 12818 (1); 12820 (1); 12823 (1); TU 1397 (GNS WM16951, 1 small); NMB 19019 = TU 1398 (1, illustrated, NMB H 17990; Pl. 64, Figs 7-8); TU 1400 (GNS WM16950, 1 incomplete).

Distribution.—*Dalium ecuadorianum* is recorded only from the Onzole Fm (Pliocene) at Punta Gorda and Quebrada Camarones, northern Ecuador. Olsson (1964: 172) stated that it is “not uncommon in the Esmeraldas shales at Punta Gorda and may be considered one of its most characteristic fossils,” reflecting the deep-water deposition site of the Onzole Fm at Punta Gorda.

Genus **OOCORYS** Fischer, 1884

Oocorys Fischer, 1884a: 392. Type species (by monotypy): *O. sulcata* Fischer, 1884, Recent, deep water, Atlantic and Indo-West Pacific Oceans.

Benthodolium Verrill & Smith, 1884: 177. Type species (by monotypy): *B. abyssorum* Verrill & Smith in Verrill, 1884 (= *Oocorys sulcata* Fischer, 1884).

Remarks.—*Oocorys* is the most speciose genus of the deep-water cassids referred to the Oocorythinae; Turner (1948) discussed six species in the western Atlantic, and listed 12 further species from elsewhere in the world, and Quinn (1980) added two further taxa. I revised (Beu, 2008) the Recent species, recognizing only five. The species of *Oocorys* are essentially thin-shelled, generalized cassids adapted to life in the abys-

sal zone and deeper, with sculpture of narrow spiral cords, almost no axial sculpture, a weakly callused aperture, a short, widely open anterior siphonal canal – little more than an anterior notch in the shell margin in several species – and a lightly reflected to moderately well-thickened outer lip. The operculum has an anterior terminal nucleus rather than the subcentral one or, more usually, one with the nucleus near the center of the right edge, present in *Cassis* and *Galeodea*. However, one of the most distinctive characters of the genus is the spiral initial section of the operculum, surrounding the nucleus, although the initially spiral growth changes to more normal commarginal growth as the operculum reaches a larger size. Some species of *Galeodea*, such as *G. maccamleyi* Ponder, 1983, also have a spiral initial segment of growth at a very small size, so this is not a very fundamental distinction from *Galeodea*. I showed (Beu, 2008) that *Oocorys* also differs anatomically from *Galeodea* in lacking obviously pigmented eyes, in its short, triangular penis, rather than the long, narrow one of *Galeodea*, and in having a much shorter and wider proboscis than in *Galeodea*.

Oocorys cf. *clericus* Quinn, 1980
Pl. 65, Figs 1, 3

cf. *Oocorys bartschi clericus* Quinn, 1980: 156, figs 1A, 2C-D, 7;
Diaz & Puyana, 1994: 169, fig. 628.
cf. *Oocorys clericus*. Beu, 2008: 336, figs 4A-B, 9C-E, 22E-F.

Remarks.—A single specimen from the Pliocene of eastern Panama has much of its surface eroded, and the outer lip is incomplete, but it is clear that it represents a species of *Oocorys* similar to *O. clericus*. The shell is relatively wide (height 1.4 times diameter) and the whorls are almost evenly convex, with a slight concavity of outline at a narrow subsutural band. The sculpture consists of many relatively wide, flat-topped, closely spaced spiral cords with interspaces each no more than half the width of one cord. The relatively wide, flat-topped cords with narrow interspaces and the slightly depressed subsutural band are characters shared with *O. clericus*, whereas all other western Atlantic species illustrated by Turner (1948) and Quinn (1980) have narrower spiral cords with relatively wide interspaces, and either no subsutural collar, or a markedly narrower one than that of *O. clericus*. The species will not be identifiable with certainty without more complete material. *Oocorys* species inhabit bathyal depths, and the scarcity of this genus throughout the study area clearly results from the relatively shallow depths of deposition of available fossiliferous rocks.

Dimensions.—H 34.4, D 24.1 mm.

Material examined.—**Fossil:** **Atlantic Panama:** **Early Pliocene:** NMB 17857 = PPP 392, Shark Hole Point Fm, Shark Hole Point, outer of coast Valiente Peninsula (1, illus-

trated, NMB H 18006; Pl. 65, Figs 1, 3).

Subfamily **PHALIINAE** Beu, 1981

Remarks.—The subfamily Phaliinae contains Cassidae that resemble members of subfamily Cassinae in having an oval to subspherical shell with a varicate outer lip, dominantly spiral sculpture, a very short anterior siphonal canal, deeply pigmented eyes, a narrow, cylindrical penis, a relatively long proboscis, and a simply straight osphradium. The most important distinguishing character of the subfamily is the operculum, which resembles that of the bursid genus *Bufonaria*, in being fan-shaped, with the nucleus in the center of the *left* edge, against the columella at the junction of the parietal and columellar sections of the inner lip, with prominent, raised, straight columellar edges and an evenly curved, convex right margin; many species also have prominent ridges on the operculum, radiating from the nucleus. This provides a strong contrast with the evenly oval cassine operculum, with its nucleus near the right edge at a third to half the opercular height, and the similar oocorythine one with a more nearly anterior nucleus and a spiral early area of growth. The members of the subfamily Phaliinae also are united by all having the very strongly twisted, deeply notched, fasciolate, dorsally directed siphonal canal, bent back so far as almost to touch the previous whorl, that is seen only in adult specimens of *Cypraecassis* in the Cassinae. Although the aperture of members of Phaliinae has quite well-thickened lips, with a callus pad on the inner lip of most taxa and with a varicate outer lip, no species in the subfamily produces the very thick, wide, ventral callus shield of *Cassis*. In my opinion, this is a distinct monophyletic group, which has been separate from the Cassinae and Oocorythinae for all of Cenozoic time.

The main genera included in the subfamily are *Casmaria* H. & A. Adams, 1853, *Echinophoria* Sacco, 1890, *Kahua* Marwick, 1928, *Liracassis* Moore, 1963, *Phalium* Link, 1807, and *Semicassis* Mörch, 1853. There has been considerable convergence during the development of descendents of *Echinophoria* through Cenozoic time. Abbott (1968) simplified the situation unrealistically by regarding *Liracassis* as a synonym of *Kahua* (for which he used the later synonym *Mauicassis* Fleming, 1943). There is no doubt that these are separate clades of strongly spirally sculptured Phaliinae that developed independently from *Echinophoria* in the North Pacific (*Liracassis*) and in New Zealand (*Kahua*). They are not particularly close homeomorphs, and no similar shells have been reported from intermediate areas, such as Australia. The widely distributed stem-groups in the subfamily are *Echinophoria* and *Semicassis*, and these are well represented in the Cenozoic fossil record of the tropical American region. Other than the endemic northern Pacific genus *Liracassis*, these

genera are almost entirely limited to the Indo-West Pacific region, although one western Atlantic Recent species and one eastern Pacific Recent species are assigned to *Casmaria*, and species of *Echinophoria* are widespread in the Recent fauna (Beu, 2008).

Abbott (1968) adopted a more conservative classification than that followed here, treating all genera listed here as subgenera of *Phalium*, apart from recognizing the separate genus *Casmaria*. Essentially, what is treated here as subfamily Phaliinae was treated by Abbott (1968) as the genus *Phalium*. In my opinion, this is a group of at least six distinct genera, and even within these, some (such as *Semicassis*) might well be polyphyletic groups of taxa that independently have evolved from *Echinophoria* by loss of the spiral nodule rows. Treating *Kahua* and *Liracassis* as distinct genera removes at least some of the apparent polyphyly from *Semicassis*, but it would not be surprising if there were yet more to be recognized.

Genus *ECHINOPHORIA* Sacco, 1890

Echinophoria Sacco, 1890a: 88 (reprint); 1890a: 195 (*Bollettino*); 1890b: 9; 1890c: 39 (Marshall, 1991). Type species (by subsequent designation, Dall, 1909a: 62): *Cassis intermedia* Brocchi, 1814, Miocene-Pliocene, Italy.

Trachydolium Howe, 1926: 303. Type species (by monotypy): *Galeodea dalli* Dickerson, 1917, Oligocene of Washington, USA (*nomen nudum*).

Euspinacassis Finlay, 1926: 230. Type species (by subsequent designation, Powell, 1928: 631): *E. pollens* Finlay, 1926, Early Miocene, New Zealand [Rutsch (1931) pointed out that this is a synonym of *Echinophoria*].

Shichiheia Hatai & Nisiyama, 1949: 93. Type species (by original designation): *S. etchuensis* Hatai & Nisiyama, 1949, Miocene, Japan.

Bathygalea Woodring & Olsson, 1957: 22. Type species (by original designation): *Cassis coronadoi* Crosse, 1867, Recent, western Atlantic.

Miogalea Woodring & Olsson, 1957: 22. Type species (by original designation): *Cassis (Phalium) dalli* Anderson, 1929 [junior secondary homonym of *Galeodea dalli* Dickerson, 1917, referred to *Phalium (Echinophoria)* by Abbott, 1968] [= *Echinophoria andersoni* (Abbott, 1968) = *Bathygalea (Miogalea) hadra* Woodring & Olsson, 1957], Early Miocene to Recent, Atlantic coast of tropical America.

Mariacassis Petuch, 1988: 17. Type species (by original designation): *Cassis caelatura* Conrad, 1830, Pliocene, St. Marys Fm, Maryland (Petuch, 1988: pl. 2, fig. 13; copy of Martin, 1904: pl. 40, fig. 4).

Remarks.—*Echinophoria* is recognizable by its simple, thin shell with a low spire, an inflated last whorl encompassing most of the previous whorls, sculpture of spiral cords and threads with one or, in most species, several rows of tubercles around the last whorl and one or two on spire whorls, a large aper-

ture with a callus collar formed by the inner lip, free of the shell surface above the neck of the previous whorl, a weakly to very heavily thickened and reflected outer lip varix, no varices remaining on the spire except on occasional aberrant individuals, and a very strongly twisted, dorsally directed siphonal canal forming a prominent fasciole, situated close to the previous whorl. Essentially it resembles *Galeodea* in most characters, but has a very strongly twisted rather than straight or at most weakly twisted siphonal canal. Most species also have less obvious sculpture of fine spiral threads than in *Galeodea*. Also, living species of *Echinophoria* have a fan-shaped phaliine operculum with its nucleus against the left margin of the operculum (Abbott, 1968: pl. 81; Beu, 2008: figs 30I-K), rather than the cassine operculum of *Galeodea*, with its nucleus near the right margin. *Echinophoria* seems likely to have been the stem group of the Phaliinae, evolving from *Galeodea* late in Cretaceous time. Pinna & Spezia (1978: pl. 10, figs 1-1a) illustrated the lectotype of the type species of *Echinophoria*, *Buccinum intermedium* Brocchi, 1814. The generic synonymy follows mine (Beu, 2008: 362-363) in which, e.g., the relatively weakly sculptured species *Mariacassis caelatura* (Conrad, 1830) is considered to be a species of *Echinophoria*.

Echinophoria famulans (Jung, 1971)

Bathygalea (Miogalea) famulans Jung, 1971: 186, pl. 9, figs 1-5.

Echinophoria famulans. Donovan *et al.*, 2003: 262, figs 4c-d.

Remarks.—*Echinophoria famulans* is a distinctive, small (to ca. 40 mm H) but typical *Echinophoria* species, consistently bearing four rows of moderately large, rounded nodules on the last whorl. All specimens examined have a rather poorly preserved exterior surface, because they are preserved as calcite neomorphs like all of the other material from Carriacou that I have seen. Most specimens bear traces of formerly extensive, fine spiral sculpture over most of the teleoconch exterior. As previously noted under *Bursa rugosa* and *Sassia* cf. *apenninica*, the Miocene rocks of Carriacou (Belmont, Kendace, and Grand Bay Formations) are deep-water turbiditic facies (Donovan *et al.*, 2003) that have undergone considerable deformation in a tropical environment, so it is not surprising that the originally aragonitic fossils have been altered to calcite.

Dimensions.—Holotype: H 39.2, D 29.4 mm (Jung, 1971: 186).

Types.—*Bathygalea famulans*, holotype NMB H 15444 (Jung, 1971: pl. 9, figs 1-3), with at least one paratype, NMB H 15445 (Jung, 1971: pl. 9, figs 4-5), from NMB 10710, Grand Bay Fm (Middle Miocene), Grand Bay cliff, Carriacou Island; other specimens (a total of 7) recorded by Jung (1971: 187) from NMB localities 10710, 10716, and 10812, all

Grand Bay Fm, Carriacou.

Other material examined.—**Middle Miocene:** 9 specimens from Grand Bay Fm, Carriacou Island, have been examined: NMB 10710 (4); 10812 (1); 13770 (4) (also listed previously by Jung, 1971). This is one of the more common fossils in the formation, and almost complete specimens are well represented at NMB. Evidently the subspherical shape allows specimens to be extracted more easily than most of the other fossils present. Further specimens were illustrated by Donovan *et al.* (2003: figs 4c-d). A few specimens occur also in the Belmont Fm, Kendace Siltstone Member: NMB 10789 (1); 13759 (1).

Distribution.—*Echinophoria famulans* is recorded only from the Grand Bay and Belmost Formations on Carriacou Island, Grenadine Islands, Caribbean (Middle Miocene; Donovan *et al.*, 2003: 258).

Echinophoria hadra (Woodring & Olsson, 1957)

Pl. 68, Figs 3, 5; Pl. 71, Fig. 4

Cassis (Phalium) dalli Anderson, 1929: 141, pl. 14, figs 10-13 [junior secondary homonym of *Galeodea dalli* Dickerson, 1917, referred to *Phalium (Echinophoria)* by Abbott, 1968: 107].

Bathygalea (Miogalea) dalli. Woodring & Olsson, 1957: 23, pl. 7, figs 1-4, pl. 8, figs 3-4.

Bathygalea (Miogalea) hadra Woodring & Olsson, 1957: 23, pl. 8, figs 1-2; Woodring, 1959: 198, pl. 37, figs 10, 13.

Phalium (Echinophoria) andersoni Abbott, 1968: 107, pl. 89, figs 1-2 [replacement name for *Cassis (Phalium) dalli* Anderson, 1929, preoccupied].

Phalium (Echinophoria) hadrum. Abbott, 1968: 107, pl. 89, figs 3-4.

Echinophoria hadra. Beu, 2008: 371, figs 31G-H.

Remarks.—*Echinophoria hadra* is common in the Chagres Fm (Late Miocene) of the Panama Isthmus. It is easily recognized within the Chagres fauna by being the only *Echinophoria* species present, *i.e.*, the only cassid with sculpture of many fine spiral threads, 1-4 rows of sharp tubercles, and with a strongly twisted siphonal canal. The material available displays a wide range of variation in the number of rows of tubercles. All specimens have one row on the spire whorls, continuing onto the shoulder angle of the last whorl, but the number of rows of tubercles developed on the last whorl below the shoulder angle varies markedly, to having as many as three rows of prominent tubercles below the shoulder row. Most specimens have either one or two rows of tubercles decreasing in prominence down the last whorl, with a further row of weakly developed tubercles below the prominent ones. The variation therefore seems to encompass specimens resembling the type material of *Cassis (Phalium) dalli* Anderson, 1929 (= *P. andersoni* Abbott, 1968), which differs from *E. hadra* only in having one row of tubercles rather than 3-4. Better

knowledge of the variation of the type population of *E. andersoni* is needed before this apparent synonymy is accepted, but the results are not important for this report, because *E. hadra* is an earlier name than *E. andersoni*. The Recent species *E. coronadoi* (Crosse, 1967) (see Beu 2008: 369, figs 31E-F) is considerably larger than *E. hadra* (reaching 120 mm H, compared with *ca.* 60 mm, rarely up to 80 mm, in *E. hadra*) and has a lighter, thinner shell, a taller spire, much thinner inner and outer lips, and a considerably narrower varix. The two species are not particularly similar, and seem unlikely to have an ancestor-descendent relationship.

Echinophoria famulans differs from *E. hadra* in its smaller size (*ca.* 40 mm H, compared with 60 mm and larger for *E. hadra*) and in consistently having four rows of tubercles on the last whorl. Four specimens in the Gibson-Smith collection (NMB 17531) from the Punta Gavilán Fm (Early Pliocene) at Punta Gavilán, northern Venezuela, are quite large (to *ca.* 70 mm H) but agree with *E. hadra* in all significant characters, having two rows and a weak third row of tubercles on the last whorl.

Dimensions.—Figured specimen, NMB H 18018, from NMB 18992, Panama: H 55.0, D 42.9 mm; GNS WM17703, Recent, off of Guiana: H 79.1, D 58.8 mm

Types.—*Cassis (Phalium) dalli* (renamed *Phalium andersoni* by Abbott, 1968: 107), holotype CAS 4649, one paratype CAS 4650, from Las Perdices Fm (Early Miocene), coast 1.6 km W of pier at Puerto Colombia, Departamento de Atlantico, Colombia (Woodring & Olsson, 1957: 23) (not seen). *Bathygalea (Miogalea) hadra*, holotype USNM 562268, with one small damaged specimen, from Chagres Fm (Late Miocene), W Atlantic coast at mouth of Río Indio, Colon, Panama.

Other material examined.—**Recent:** D. Lamy (Guadeloupe, pers. comm., October 2005) sent me photographs of 2 of the 4 known Recent specimens of *Echinophoria hadra* collected off of Suriname and French Guiana, in fishermen's traps in 70-80 m (3 in collection of D. Lamy; GNS WM17703, 1). These specimens have three or four rows of nodules on the last whorl. This species therefore has been added to the Recent tonnoidean fauna of the western Atlantic (Beu, 2008: 371).

Fossils: Atlantic Panama: Late Miocene: Chagres Fm: NMB 18764 (1); 18992 (1, illustrated, NMB H 18018; Pl. 68, Figs 3, 5); 18986 (1); 18988 (8); 18989 (5); 18990 (8); 18991 (12); Valiente Fm: NMB 17824 (1 frag); 18375 (1 frag); Nancy Point Fm: NMB 17859 (1); 18545 (1); 18688 (3); 18690 (3 frags); 18700 (2); 18727 (1 frag); 18768 (1 frag). **Pliocene:** Escudo de Veraguas Fm: NMB 18679 (5 frags); Shark Hole Point Fm: NMB 17854 (4); 17855 (2); 17856 (1); 17857 (1); 18701 (4 frags); 18702 (1); 18703 (2 frags); 18705 (1 frag); 18723 (1 frag); 18726 (1). **Dominican Republic: Early Pliocene:** TU 1227, Arroyo Zalaya, Río Gurabo, deep-

water facies of Gurabo Fm, collection of Bernard Landau (1). **Venezuela: Late Early Miocene**, Cantaure: near Casa Cantaure, Paraguaná Peninsula, N Venezuela (1 incomplete, illustrated, collection of Bernard Landau; Pl. 71, Fig. 4). **Early Pliocene**: NMB 17531, Punta Gavilán Fm, Punta Gavilán, Falcón, coll. J. & W. Gibson-Smith (4).

Distribution.—The range and age accepted for *Echinophoria hadra* obviously depend on whether *E. andersoni* is accepted as a synonym or not. If it is not, *E. hadra* seems to be limited to Late Miocene to Pliocene rocks, at Punta Gavilán in northern Venezuela, and abundant in the Gatun Fm along the Atlantic coast of Panama, as well as living off of the coasts of Suriname and Guiana, northern South America (newly recorded by me; Beu, 2008). However, it seems very likely that *E. andersoni* is a synonym, and that *E. hadra* occurs widely throughout northern South America in Miocene and Pliocene rocks of suitable offshore facies. All fossil records are from the Atlantic part of the study area.

***Echinophoria woodringi* Olsson, 1964**
Pl. 68, Figs 1-2

Echinophoria woodringi Olsson, 1964: 170, pl. 30, figs 8-8a.
Phalium (Echinophoria) woodringi. Abbott, 1968: 108, pl. 90.

Remarks.—*Echinophoria woodringi* is an unusually small member of the genus (most specimens 36-43 mm H), rendered even more distinctive because almost all specimens have only a single peripheral row of small, evenly spaced nodules, very regular in size on different specimens. The low spire and lack of lower nodule rows provide an unusually near-spherical shape. The main surface sculpture consists of regular, fine, even spiral threads and grooves. However, the material newly collected by Naturhistorisches Museum Basel expeditions to Ecuador demonstrates that the number of nodule rows is not completely constant, because one specimen in these collections has no nodules whatsoever on the last whorl, and another has two row of nodules around the periphery. It still remains true, though, that > 95% of specimens have a single row of regular nodules. This species does not closely resemble any other tropical American cassid of which I am aware, and is unlikely to be closely related phylogenetically to either *E. hadra* or *E. famulans*. It is also not closely related phylogenetically to the Recent eastern Pacific species *E. pilsbryi* (Woodring & Olsson, 1957), which is a much more standard, larger *Echinophoria* species with several rows of peripheral nodules (Beu, 2008).

Dimensions.—Holotype: H 36.3, D 29.4 mm; largest paratype (USNM 644059, Punta Gorda): H 49.7, D 37.4 mm (Olsson, 1964: 171); NMB H 18304, from locality NMB 19136: H 40.5, D 31.5 mm; NMB H 18305, from locality NMB 19141: H 44.0, D 34.8 mm.

Types.—*Echinophoria woodringi*, holotype USNM 644057

(Olsson, 1964: pl. 30, figs 8-8a), from Onzole Fm (Early Pliocene), Quebrada Camarones, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town, Ecuador; 1 paratype USNM 644058, from the same locality; 1 paratype USNM 644059, from Punta Gorda, Esmeraldas Province, Ecuador.

Other material examined.—**Fossils: Ecuador: Early Pliocene**, Onzole Fm: NMB 12822 (30); 12824 (12); 12825 (15); 19136 (12, 1 without nodules; 1 illustrated, NMB H 18304, with 1 row of nodules, Pl. 68, Fig. 1); 19137 (1 frag); 19138 (1 juvenile); 19141 (5 small to large; largest has 2 rows of peripheral nodules, illustrated, NMB H 18305, Pl. 68, Fig. 2).

Distribution.—*Echinophoria woodringi* has been recorded only from Pliocene rocks of Ecuador, in the Onzole Fm in the coastal area near Esmeraldas.

Genus **SEMICASSIS** Mörch, 1853

Semicassis Mörch, 1853: 112. Type species (by subsequent designation, Harris, 1897: 198): *Cassis japonica* Reeve, 1848 (= *C. bisulcata* Schubert & Wagner, 1829), Miocene to Recent, Indo-West Pacific.

Faurotis Jousseaume, 1888: 188. Type species (by original designation): *F. faurotis* Jousseaume, 1888, Recent, western Indian Ocean and Red Sea.

Tylocassis Woodring, 1928: 306. Type species (by original designation): *Buccinum inflatum* Shaw, 1811 (= *B. granulatum* Born, 1778), Pleistocene and Recent, western Atlantic.

Xenophalium Iredale, 1927a: 333. Type species (by original designation): *X. hedleyi* Iredale, 1927 (= *Cassidea royana* Iredale, 1914), Recent, northern New Zealand, Kermadec Islands, and south-eastern Australia.

Xenogalea Iredale, 1927a: 339. Type species (by original designation): *Cassis pyrum* Lamarck, 1822, Pleistocene and Recent, New Zealand and southeastern Australia.

Remarks.—The genus *Semicassis* is regarded here as a rather broadly defined, highly speciose group of small to medium-sized Phaliinae with almost entirely spiral sculpture, without regular varices at former growth pauses (although an occasional varix is left before the terminal one in some aberrant individuals), with a thickened and reflected outer lip that can be smooth, denticulate, or ridged internally, and with an inner lip callus forming a free collar over the siphonal fasciole, the collar smooth or bearing nodules, transverse ridges or a combination of both.

Phalium (= *Bezoardica* Schumacher, 1817; = *Bezoardicella* Habe, 1961) is a clearly distinct genus of Phaliinae with prominent axial as well as spiral sculpture, retaining all varices down the entire teleoconch, with a thicker ventral callus extending into a longer free collar in most species than it does in *Semicassis*, and with spines around the anterior end of the

exterior of the outer lip that otherwise, among the genera of Phaliinae, are present only in *Casmaria*. *Phalium* is limited to the Indo-West Pacific province, and seems never to have entered the Atlantic.

Woodring (1928: 306-307) proposed the subgenus *Semicassis* (*Tylocassis*) for tropical American species, and stated that "all the later Tertiary species from eastern America, and ... on the Pacific coast of Mexico and tropical America, represent *Tylocassis*, which differs from *Semicassis* s. s. principally in having wart-like denticles instead of long ridges on the basal part of the inner lip." This character is a very minor one for separating subgenera, and although Abbott (1968: 157) did not synonymize *Tylocassis* with *Semicassis sensu stricto*, he noted of the pustules rather than ridges on the inner lip that "this difference is probably not very significant." This morphological character also is not limited to American species, because it is seen also in the eastern Atlantic-Mediterranean species *S. undulata* (Gmelin, 1791), and combinations of pustules and ridges are seen in some other *Semicassis* species, including the living eastern Atlantic species *S. saburon* (Bruguère, 1792) and in some specimens of *S. pyrum* (Lamarck, 1822) from New Zealand (particularly in specimens from the southernmost part of its range, at Mason Bay, Stewart Island). *Tylocassis* is simply a synonym of *Semicassis*, in my opinion. This also appears to have been the opinion of Wrigley (1934), Emerson & Old (1963a: 16), and Keen (1958, 1971), all of whom included the American species simply in *Semicassis*.

The one taxonomic group that is worthy of recognition as a genus separate from *Semicassis* is *Antecephalum* Iredale (1927a: 350; type species, by original designation, *Cassis semigranosa* Lamarck, 1822, Recent, southeastern Australia). *Antecephalum semigranosum* is a distinctive species with several rows of small, uniform, closely spaced, evenly rounded nodules around the upper third to half of the whorl, at and below the shoulder angle, and with weak axial folds extending for a short distance below the nodules. It and *A. adcocki* (G. B. Sowerby III, 1896) (Abbott, 1968: 147, pl. 134; Kreipl, 1997: pl. 24, fig. 79) from South Australia, with much more prominent axial costae than in *A. semigranosum*, are the living representatives of several lineages of granulose species in the Cenozoic rocks of southern Australia. Although sharing many characters with *Semicassis*, this group has been separated from *Semicassis* for most of Cenozoic time. The third living species of *Antecephalum*, *A. sinuosum* (Verco, 1904: 141, pl. 26, figs 7-10; Abbott, 1968: 148, pl. 135; Kreipl, 1997: pl. 24, figs 81-81a), is a very strange little phaliine, up to only ca. 30 mm H, with an almost completely unthickened outer lip (a very thin, narrow varix is present on a few specimens) that bends in toward the aperture over the adapical half in a similar way to that of *Cypraecassis coarctata* and is sinuous in lateral outline as well, and has external sculpture only of very weak,

narrow spiral grooves. This species seems to have descended from the group of small Australian Miocene species related to *A. sufflatum* (Tenison Woods, 1877). The genus *Antecephalum* is limited to southern Australia.

The taxonomy of *Semicassis* species has troubled zoologists and paleontologists throughout at least the 20th century, and no great advances have been made in recent times to change this picture. Pilsbry & McGinty (1939) expressed a point of view at one end of the spectrum, when they recognised *S. gibba* (Gmelin, 1791), *S. gibba abbreviata* (Lamarck, 1822), *S. gibba inflata* (Shaw, 1811), *S. cicatricosa* (Meuschen, 1781) [Meuschen's names are non-binominal; = *S. cicatricosa* Gmelin, 1791], and *S. cicatricosa peristephes* Pilsbry & McGinty, 1939, all as taxa living in the western Atlantic, although they admitted that "there seem to be also some transitional forms which refuse to be rigidly classified." Clench (1944) took a more middle-of-the-road approach, and recognized only two living western Atlantic species, *Phalium* (*Semicassis*) *granulatum* (Born, 1778) and *P. (S.) cicatricosum* (Gmelin, 1791; attributed to Meuschen, 1787). An approach from the opposite extreme to Pilsbry & McGinty's was taken by Abbott (1968), who recognized only the one subspecies *P. granulatum granulatum* in the western Atlantic, ranking *P. g. centiquadratum* (Valenciennes, 1832), eastern Pacific, and *P. g. undulatum*, eastern Atlantic-Mediterranean, as other geographical subspecies of the one species. Kreipl (1997: pl. 19) followed a similar classification to Abbott's, but recognized forms *peristephes* and *cicatricosa* of *S. g. granulata* in the western Atlantic. Finally, H. & E. Vokes (1983) returned to a subdivision almost as fine as that of Pilsbry & McGinty (1939), recognizing *P. (Tylocassis) cicatricosum*, *P. (T.) inflatum*, and *P. (T.) granulatum* again as full species in the western Atlantic. The apparently distinct geographical ranges accepted by H. & E. Vokes (1983) are based on specimens from Yucatan Peninsula only, and are likely to reflect local ecological conditions rather than the situation in the western Atlantic as a whole. Similar difficulties have been met with in the Indo-West Pacific fauna, in which Abbott (1968) has united into the single species *S. bisulcata* (Schubert & Wagner, 1829) a large number of names that had been proposed for specimens from both the northern and southern Pacific. Similarly, in New Zealand and southeastern Australia, the widespread, abundant species *S. pyrum* (Lamarck, 1822) has received at least 10 synonyms, all based on trivial variants of what is undoubtedly a single species.

A great range of variation in the strength of expression of the spiral cords, in the size of shoulder nodules, and in the number of rows of nodules is demonstrated by specimens in the collections from the Dominican Republic. This makes it clear that a huge range of variation must be allowed in each species of *Semicassis*, and an approach similar to that of Abbott (1968) is followed here. The single species *S. granulata* is rec-

ognized in the living western Atlantic fauna, *S. centiquadrata* is recognized as a further living species in the eastern Pacific fauna, and *S. undulata* is recognized as a further living species in the eastern Atlantic. The occurrence of specimens of *S. granulata* syntopically with *S. undulata* at the Canary Islands and Madeira (Nordsieck & Garcia-Talavera, 1979: 121) makes it clear that these are distinct species, and the eastern Pacific species *S. centiquadrata* in my opinion is just as distinct as these other two. However, it must be recognized from the outset that *Semicassis* remains a taxonomically little-understood genus that lacks "landmark" taxonomic characters (at least, in the protoconch and teleoconch), and so is difficult to use for biostratigraphical and biogeographical research. Study of such taxa by molecular techniques is required to resolve their taxonomy in any final way.

***Semicassis aldrichi* (Dall, 1890)**

Pl. 68, Figs 6, 8

Cassis (*Phalium*) *aldrichi* Dall, 1890: 162; 1893: 263, pl. 21, fig. 2.

Semicassis (*Tylocassis*) *aldrichi*. Gardner, 1947: 536, pl. 54, fig. 6.

Semicassis? (*Tylocassis*?) cf. *aldrichi*. Woodring, 1959: 199.

Phalium (*Tylocassis*) *aldrichi*. Abbott, 1968: 163, pl. 150; Schmelz, 1996: pl. 1, figs 1-5, pl. 2, figs 1-3, pl. 3, figs 2a-b.

Remarks.—*Semicassis aldrichi* was proposed for specimens from the Chipola Fm (late Early Miocene) of Florida. Schmelz (1996) illustrated a range of specimens from this formation, part of a series of 30 specimens that he had available from eight localities, demonstrating that the species is highly variable in shape and in nodule prominence. Almost all specimens have at least one row of nodules on the shoulder angle of spire whorls, and in most specimens the nodules continue prominently onto the last whorl. However, in some specimens the nodules decrease in prominence with growth, so that they have faded out by the last whorl. Several of the illustrated specimens have two or three nodulose cords on the sutural ramp, and two have weak signs of a further elevated cord, similar to the one at the shoulder angle but lacking nodules, at about mid-whorl height. Bernard Landau (pers. comm., December 2005) reported that specimens that he collected at Tenmile and Farley Creeks are larger than any reported by Schmelz (up to H 43.9 mm) and lack the row of nodules at the shoulder, resembling a small specimen of *S. granulata*. They differ from *S. granulata* in their more numerous spiral cords and in the spiral cords being more obviously beaded by the axial growth lines than in *S. granulata*.

Schmelz (1996: 46, pl. 3, fig. 1) proposed the new species *Semicassis murrayi* [originally in *Phalium* (*Tylocassis*)] for a single complete specimen and numerous fragments from the Shoal River Fm (Middle Miocene) in Florida. *Semicassis murrayi* differs from the older species *S. aldrichi* by its larger size,

its more inflated shape, its wider spiral cords, its wider outer lip varix with more prominent internal ridges, particularly toward the adapical end of the aperture, and the lower sides of spire whorls, which are enveloped up to the shoulder angle by the succeeding whorl, rather than exposing a narrow zone of the whorl side. He considered that *S. murrayi* was probably the immediate ancestor of *S. reclusa* (Guppy, 1873) from the Late Miocene-Early Pliocene rocks of the Dominican Republic and the Late Pliocene Bowden shellbed in Jamaica, and distinguished *S. murrayi* from *S. reclusa* by it never having the two or more rows of nodules on the last whorl that are present on many specimens of *S. reclusa*, and by it having a taller protoconch of 3.0 rather than 2.5 whorls. However, such an ancestor-descendent relationship is unlikely, because *S. reclusa* occurs in the late Early Miocene Baitoa Fm of the Dominican Republic (material in the collection of Bernard Landau).

Specimens from the Cantaure Fm (late Early Miocene) of the Paraguaná Peninsula, northern Venezuela, mostly collected by Jack and Win Gibson-Smith, appear to be typical *Semicassis aldrichi*, according to the criteria defined by Schmelz (1996). Most are closely similar to Schmelz's figured Chipola specimens, being moderate-sized, with a subcylindrical last whorl, and one or two rows of small nodules, located at the shoulder angle and on the sutural ramp. A large specimen is illustrated here (Pl. 68, Figs 6, 8) that combines the large shoulder nodules and the exposed edges of spire whorls below the shoulder that are present on extreme specimens of *S. aldrichi* from the Chipola Fm, with a wider shape and the presence of two slightly raised but smooth spiral cords around the mid-whorl. There seems little doubt that the Cantaure Fm specimens are *S. aldrichi*.

Woodring (1959: 199) recorded molds of a *Semicassis* species from the Culebra Fm (Early Miocene) at his localities 110, 111, and 111b (Gaillard Cut, Panama Canal) but was only able to note that "the small size and noded shoulder suggest comparison with" *S. aldrichi*. Such a range extension is quite feasible, but better material is required for the identification to be accepted.

Dimensions.—Figured specimen, NMB H 18019, from NMB 12842, Cantaure Fm, near Casa Cantaure, Paraguaná Peninsula, Venezuela: H 47.1, D 37.9 mm.

Types.—*Cassis* (*Phalium*) *aldrichi*, holotype USNM 112207 (not seen), from Chipola Fm (late Early Miocene), Tenmile Creek, Chipola River, Florida.

Other material examined.—**Fossils: Florida: Late Early Miocene**, Chipola Fm: loc. TU 546, Tenmile Creek, Calhoun Co, collection of Bernard Landau (3); TU 826, Farley Creek, Calhoun Co, collection of Bernard Landau (1). **Venezuela: Late Early Miocene**, Cantaure Fm: NMB 12842 (1, illustrated, NMB H 18019; Pl. 68, Figs 6, 8); 17516 (10); 17519

(1); 17520 (5); Cantaure, collection of Bernard Landau (3).

Distribution.—*Semicassis aldrichi* is recorded only from the Chipola Fm in Florida, USA, and the Cantaure Fm on the Paraguaná Peninsula, northern Venezuela, both late Early Miocene in age. Material recorded tentatively under this name from the Culebra Fm (Early Miocene) of the Panama Canal by Woodring (1959) consists only of molds, and the record requires confirmation from better material.

***Semicassis centiquadrata* (Valenciennes, 1832)**

Pl. 69, Figs 1-2

Cassis centiquadrata Valenciennes, 1832: 310; Mörch, 1860: 84.

Cassis doliata Valenciennes, 1832: 311; Mörch, 1860: 84.

Cassis lactea Kiener, 1835: 35, pl. 16, fig. 35.

Cassis inflata var. β Reeve, 1848b: pl. 9, figs 22a-b.

Cassis inflata var. Menke, 1850: 183.

Cassis abbreviata. Menke, 1850: 183 (not *Cassis abbreviata* Lamarck, 1822).

Phalium (Bezoardica) sulcosum var. *abbreviatum*. Schenck, 1926: 78, pl. 13, figs 2-4 (not *Cassis abbreviata* Lamarck, 1822).

Phalium granulatum abbreviata var. *centiquadrata*. Bayer, 1935: 102, fig. 2.

Semicassis centiquadrata. Pilsbry & Olsson, 1941: 40, pl. 7, figs 3, 6, pl. 8, fig. 2; Emerson & Old, 1963b: 16, figs 14-15; Finet, 1991: 270; Kaiser, 1997: 32; López de la Fuente & Ramos, 2004: 85.

Cassis (Semicassis) centiquadrata. Keen, 1958: 340, fig. 315; 1971: 501, fig. 948.

Phalium (Tylocassis) granulatum centiquadratum. Abbott, 1968: 161, pl. 12, figs 8-10, pl. 149.

?*Cassis (Semicassis) granulatus*. Aguilar, appendix in Seyfried *et al.*, 1985: 64.

Semicassis (Semicassis) granulata centiquadrata. Kreipl, 1997: 54, pl. 19, figs 63-63a.

Remarks.—*Semicassis centiquadrata* is common in collections from Pliocene and Pleistocene rocks of the Pacific coast of Costa Rica and Panama. It is recognizable by the consistently low spire, by almost all specimens having a row of small to quite large nodules at the shoulder angle, all specimens having obvious, wide, flattish spiral cords, and virtually all specimens having a weak spiral sulcus below the row of nodules (or elevated spiral cord, in specimens without nodules) at the shoulder angle. Some specimens have two or more rows of nodules, at and below the shoulder angle. The consistently coarser sculpture indicates that this is a species distinct from *S. granulata*.

Dimensions.—The maximum recorded height is 89.9 mm (Skoglund, 1992); Keen's (1971: fig. 948) figured specimen, CASIZ 170947: H 57.0, D 40.7 mm (R. van Syoc, CASIZ, pers. comm., 2004); probable syntype of *S. centiquadrata*, MNHN: H 64.8, D 50.3 mm.

Types.—Until now, neither *Cassis centiquadrata* nor *C. do-*

liata of Valenciennes (1832) apparently has been represented by type material at MNHN, the only known repository of Valenciennes's types. The type locality is Acapulco, western Mexico. A specimen of *Semicassis centiquadrata* recognized by me in the Valenciennes collection, MNHN, in July 2007 bears a label "*Cassis sulcosa* aff., a figurer, Acapulco," along with another illegible label apparently signed by Valenciennes. It seems likely that this is an authentic Valenciennes syntype, or holotype, of either *C. centiquadrata* or *C. doliata*. The specimen should be considered a "probable syntype" of *C. centiquadrata*. Therefore, no other types are proposed for these names at this time. Abbott (1968: 161) claimed to have examined "Kiener's type" of *Cassis lactea* in MHNG, and gave dimensions of the specimen (H 41.1, D 29.0 mm), but Y. Finet (MHNG, pers. comm., 1998) informed me that this specimen is not recognizable at MHNG. As first reviser, I select the name *C. centiquadrata* as the valid name for the species named both *C. centiquadrata* and *C. doliata* by Valenciennes (1832).

Other material examined.—**Fossils: W Mexico: Late Middle Pleistocene:** (oxygen isotope stage 5e), Mulegé Terrace, Bahía Santa Inés, near Mulegé, Baja California Sur, collection of Bernard Landau (1). **Pacific Costa Rica: Late Miocene,** Punta Judas: NMB 17753 (3); 17754 (4). **Pliocene:** NMB 18294 (4); Charco Azul Fm, Quebrada el Higo, Burica Peninsula, collection of Bernard Landau (6). **Pleistocene:** NMB 17471 (1); 17749 (1); 17771 (1); 18161 (1); 18287 (1). **Pacific Panama: Pleistocene:** NMB 17441 (4; 1 illustrated, NMB H 18076; Pl. 69, Figs 1-2); 17442 (1); 17443 (3); 18061 (1); 18073 (2); 18074 (2); 18076 (8); 18305 (2); 18431 (1); Armuelles Fm, Río Rabo de Puerco, Burica Peninsula, collection of Bernard Landau (4). **Panama, Darien: Late Miocene:** NMB 18504 (1); 18517 (1); 18534 (1); 18540 (1); 18543 (1). **Ecuador: Pliocene:** NMB 19142 (1 frag); 19152 (2 incomplete); 19153 (1 large); 19154 (2 incomplete). **Pleistocene:** NMB 19149 (3 frags).

Distribution.—*Semicassis centiquadrata* lives now from Bahía Magdalena, western coast of Baja California Sur (Emerson & Old, 1963b), to Lobitos, Peru, in the eastern Pacific (Olsson, 1924; Abbott, 1968), including the Galápagos Islands, Cocos Island, Costa Rica (Montoya, 1983, 1984; Skoglund, 1992), and Isla de Gorgona, Colombia (Tomlin, 1923; Cantera *et al.*, 1979; Cosel, 1984; Skoglund, 1992). Fossils have been reported previously from Cerralvo Island, Gulf of California (Pleistocene) by Emerson (1960) and from the Canoa Fm (Pliocene) at Punta Blanca and the Jama Fm (Pliocene) at Puerto Jama, both in Ecuador, by Pilsbry & Olsson (1941). The evenly inflated (rather than shouldered) specimen reported by Olsson (1964: 170, pl. 30, figs 6-6a) under the name "*Semicassis (Tylocassis) granulata* subspecies" from the Onzole Fm (Pliocene) at Punta Gorda, Esmeraldas Province, Ecuador, is possibly a distinct species, which Olsson compared

with *S. granulata* and *S. reclusa*. Fossils are reported here from Late Miocene to Pleistocene rocks along the Pacific coasts of Mexico, Costa Rica, Panama, Darien, and Ecuador, within the present range of the species.

***Semicassis granulata* (Born, 1778)**

Pl. 70, Figs 4, 6; Pl. 71, Figs 2, 5-7, 9-10

Buccinum granulatum Born, 1778: 239; 1780: 248.

Buccinum cicatricosum Gmelin, 1791: 3475.

Buccinum gibbum Gmelin, 1791: 3476.

Buccinum recurvirostrum Gmelin, 1791: 3477; Wood, 1825: 105, pl. 22, fig. 30.

Cassidea granulosa Bruguière, 1792a: 421; ?Gabb, 1881: 356.

Cassis malum Röding, 1798: 31.

Cassis cepa Röding, 1798: 31.

Cassis globulus Röding, 1798: 31.

Buccinum inflatum Shaw, 1811: 959.

Cassis abbreviata Lamarck, 1822: 224; Kiener, 1835: 33, pl. 15, fig. 31; Küster, 1857: 22, pl. 44, figs 3-4, pl. 50, figs 8-9.

Cassis corrugata Swainson, 1822, appendix: 5 (Emerson & Old, 1963b: 16).

Cassis granulosa. Lamarck, 1822: 227; Kiener, 1835: pl. 16, fig. 35.

Cassis laevigata Menke, 1828: 144; 1830: 115 (junior primary homonym of *C. laevigata* Defrance, 1817).

Cassis minuta Menke, 1829: 37.

Cassis tessellata Pfeiffer, 1840: viii (junior secondary homonym of *Buccinum tessellatum* Gmelin, 1791).

Cassis inflata. Reeve, 1848b: pl. 9, fig. 22c; Küster, 1857: 8, 42, pl. 37 (1847), figs 4-5, pl. 42, figs 1-2, pl. 50, figs 5-6, pl. 52, figs 7-8; Dall, 1889: 134; 1903b: 134; Trechman, 1933: 39.

Cassis recurvirostrum. Reeve, 1848b: pl. 7, fig. 16; Küster, 1857: 22, pl. 44, figs 1-2.

Cassis ventricosa Mörch, 1853: 112; 1877: 35.

Cassis (Semicassis) gibba. Krebs, 1864: 34; Mörch, 1877: 36.

Cassis (Semicassis) granulata. Mörch, 1877: 35.

Cassis (Semicassis) abbreviata. Mörch, 1877: 36.

Cassis (Semicassis) cicatricosa. Mörch, 1877: 36.

Cassis (Semicassis) lactea. Mörch, 1877: 37 (not *C. lactea* Kiener, 1835, = *Cassis centiquadrata* Valenciennes, 1832).

Cassis (Semicassis) inflata. Mörch, 1877: 35; Tryon, 1885: 274, pl. 4, fig. 65; Dall & Simpson, 1901: 418; Maury, 1922: 118.

Cassis (Semicassis) undulata. Gregory, 1895: 289 (not *Buccinum undulatum* Gmelin, 1791).

Xenogalea lucrativa Iredale, 1927a: 347, pl. 32, fig. 11; Abbott, 1968: 157, pl. 147.

?*Semicassis (Tylocassis) inflata waltonensis* Mansfield, 1935: 40, pl. 4, figs 5, 9.

Semicassis gibba. Pilsbry & McGinty, 1939: 74, pl. 5, figs 1-3.

Semicassis gibba abbreviata. Pilsbry & McGinty, 1939: 74, pl. 5, fig. 4.

Semicassis cicatricosa. Pilsbry & McGinty, 1939: 75, pl. 5, fig. 6.

Semicassis cicatricosa peristephes Pilsbry & McGinty, 1939: 76, pl. 5, fig. 5.

Phalium (Semicassis) granulatum. Clench, 1944: 6, pl. 1, figs 3-7, pl. 3, figs 1-4; Perry & Schwengel, 1955: 149, pl. 29, fig. 208;

Andrews, 1971: 102, fig.; Redfern, 2001: 59, pl. 30, figs 253A-D.

Phalium (Semicassis) cicatricosum. Clench, 1944: 8, pl. 4, figs 1-5.

Semicassis granulatum (sic). Morretes, 1949: 91.

Semicassis inflata. Morretes, 1949: 91.

Phalium granulatum. Olsson & McGinty, 1958: 15; Warmke & Abbott, 1962: 98, pl. 3, fig. b; Kaufmann & Götting, 1970: 366, fig. 76; Humfrey, 1975: 117, pl. 11, figs 1-1a; Princz & Pacheco, 1981: table; Calvo, 1987: fig. 75 (radula); de Jong & Coomans, 1988: 67; Diaz, 1990: 19; Lipe & Abbott, 1991: 8, illus.; Diaz & Puyana, 1994: 171, fig. 635; Ávila *et al.*, 1998: 499.

Semicassis (Tylocassis) reclusa. Woodring, 1959: 200, pl. 34, figs 1, 4-6 (not *Cassis reclusa* Guppy, 1873).

Semicassis (Tylocassis) granulata. Weaver, 1962: 254, pl. 23, figs 15-18.

Phalium cicatricosum. Warmke & Abbott, 1962: 98, pl. 3, fig. a; Work, 1969: 658; Kaufmann & Götting, 1970: 369, fig. 77; de Jong & Coomans, 1988: 67; Petuch, 1994: pl. 38, fig. F.

Phalium (Tylocassis) granulatum granulatum. Abbott, 1968: 157, pl. 12, figs 1-7, pls 145-147; Matthews & Coelho, 1972: 10, fig. 6; van Regteren Altena, 1975: 6, 35; Andrews, 1977: 128, illus.; Macsotay & Campos Villarroel, 2001: 62.

Phalium (Tylocassis) granulatum. Abbott, 1974: 161, pl. 6, fig. 1737; Rios, 1975: 76, pl. 21, fig. 311; 1985: 73, pl. 26, fig. 321; 1994: 73, pl. 26, fig. 321; Nordsieck & Garcia-Talavera, 1979: 121, pl. 25, fig. 2; H. & E. Vokes, 1983: 22, pl. 10, figs 3-3a.

Phalium (Tylocassis) granulatum forma cicatricosum. Abbott, 1974: 161, pl. 6, fig. 1738.

Phalium (Tylocassis) cicatricosum. H. & E. Vokes, 1983: 22, pl. 9, figs 12-12a.

Phalium (Tylocassis) inflatum. H. & E. Vokes, 1983: 22, pl. 10, figs 2-2a.

Phalium alligator Petuch, 1991: 23, pl. 3, figs 13-14; 1994: pl. 38, figs B, E; 1997: fig. 98.

Phalium granulatum loxahatcheensis Petuch, 1994: 272, pl. 38, fig. A.

Phalium waltonensis. Petuch, 1994: pl. 38, fig. G.

Phalium granulatum. Petuch, 1994: pl. 38, fig. I.

Phalium loxahatcheensis. Petuch, 1997: fig. 107H.

Semicassis (Semicassis) granulata granulata. Kreipl, 1997: 53, pl. 19, figs 62-62e.

Remarks.—The differences pointed out by Abbott (1968: 157) between western Atlantic Recent specimens of *Semicassis granulata* and eastern Atlantic Recent specimens of *S. undulata* indicate that these are two distinct species. *Semicassis undulata* is significantly larger and has *ca.* 17-18 wide, prominent spiral cords on the last whorl, rather than the 20-21 rather narrower ones of *S. granulata*; fine spiral brown lines between the spiral cords and long axial brown flames on *S. undulata* are absent from *S. granulata*; the spire is taller in most specimens of *S. undulata* than in most specimens of *S. granulata*, and the operculum has many prominent, narrow radial ridges on the exterior in *S. undulata*, rather than the few, weak ones or

no radial ridges at all in *S. granulata*. The opercular character seems particularly significant. The coarsely ridged operculum also distinguishes *S. undulata* from the much smaller *S. saburon*, with which *S. undulata* is syntopic, and which has a smooth operculum.

The published debate about the range of variation of the various named forms of *Semicassis granulata* and the correct names to be used for them is summarized above. Specimens from throughout the range of the species display a huge range of sculptural variation, from almost completely smooth to strongly spirally corded, and with or without weak to prominent nodules on the shoulder angle; a few specimens have more than one row of nodules. Some variants seem to be more common in some areas than others, but the full range can be found in large samples, e.g., the large collections from northern Venezuela assembled by Jack and Win Gibson-Smith (listed below). In my opinion, this is one extremely variable species. The several forms named from the Plio-Pleistocene rocks of Florida by Petuch (1991, 1994) are included in the above synonymy because they each are based on a very small part of the range of variation of the Recent western Atlantic population, and in my opinion they are conspecific with *S. granulata*.

Dimensions.—*Semicassis granulata*, Gualtieri collection no. 2231: H 50.8, D 35.3 mm; figured specimens (Pl. 71, Figs 5, 7), GNS WM17118, Recent, fishermen's traps, 250 m, Racket Bank, off of Barthelmy Island, West Indies: H 78.5, D 56.0 mm; H 72.3, D 47.1 mm; GNS WM17704, fish traps, 50-60 m, off of French Guyana: H 57.0, D 44.1 mm.

Types.—Abbott (1968) illustrated the "holotypes" of *Cassis abbreviata* Lamarck, 1822 (Abbott, 1968: pl. 145, upper) and *C. granulosa* Bruguière, 1792 (Abbott, 1968: pl. 145, lower), both of which are at MHNG; *C. abbreviata*: MHNG 1100/64/1 (Pl. 70, Figs 4, 6), without locality, type locality here designated as Barbados; *C. granulosa*: MHNG 1100/6, from "Barbados" (Pl. 71, Figs 2, 6); these are both more strictly syntypes, rendered lectotypes by Abbott's "holotype" statement. However, Abbott made little effort to recognize the type material of the many other names in his synonymy. Most of the other names in fact are no longer associated with particular specimens or collections. Brauer (1878: 44) stated that Born's original specimen was present at NHMV, but (unlike almost all other Born types) was not numbered. However, unfortunately, *Buccinum granulatum* is one of very few of Born's (1778, 1780) names that is *not* now represented by his original specimen at NHMV, and a search in the general collection did not bring the unrecognized original to light (Anita Eschner, NHMV, pers. comm., 14 April 2007). Recognition of the original was not helped by *B. granulatum* not being illustrated by Born. A neotype is required for Born's name. Born (1780: 248), under *B. granulatum*, cited illustrations

by Rumphius (1705: 25, fig. C), Petiver (1713: pl. 9, fig. 6), Gualtieri (1742: pl. 20, fig. E), and Martini (1773: pl. 32, figs 344-345). The specimen from Gualtieri's (1742) collection referred to by Born is probably present in Gualtieri's collection at the Museo di Storia Naturale e del Territorio, Università di Pisa, in the Certosa di Calci, outside Pisa; there are no *Semicassis* specimens on Gualtieri's pl. 20, and the reference by Born (1778, 1780) to Gualtieri's pl. 20, fig. E, evidently is an error for pl. 40, fig. E. A large (H 77.0, D 52.3 mm; Gualtieri collection no. 2229), weakly colored specimen of *Semicassis granulata* is segregated as a figured specimen. It does not obviously match any of Gualtieri's (1742) figures, and is not identified with a particular figure by an inscription on the shell, but is probably the specimen in Gualtieri's pl. 40, fig. E. However, the association with Gualtieri's (1742: pl. 40, fig. E) illustration is uncertain, and in my opinion this is not a suitable specimen for use as a neotype. The lectotype of *Cassidea granulosa* Bruguière, MHNG 1101/6 (Pl. 71, Figs 2, 6; see below), from "Barbados," West Indies, is here designated the neotype of *B. granulatum*, of *B. gibbum* and *B. recurvirostrum* of Gmelin, 1791, of *Cassis cepa*, *C. malum*, and *C. globulus* of Röding, 1798, of *B. inflatum* Shaw, 1811, of *C. minuta* Menke, 1828, and of *C. laevigata* Menke, 1829. The name *B. cicatricosum* Gmelin, 1791, deliberately has been left out of this list, as some studies have concluded that it is a species distinct from *S. granulata*, and Ardovalini & Cossignani (2004: 124, lower right fig.) illustrated a specimen of this form from the Canary Islands, suggesting that it might well be a distinct species. The specimen figured by Pilsbry & McGinty (1939: pl. 5, fig. 6) as *Phalium cicatricosum*, ANSP 149945, from Georgetown, Grand Cayman Island, is here designated the neotype of *B. cicatricosum*. The specimen was collected by H. A. Pilsbry on 16 April 1929, during the Pinchot Expedition (P. Callomon, ANSP, pers. comm., December 2004).

Cassidea granulosa, apparent lectotype MHNG 1101/6 (Pl. 71, Figs 2, 6), labeled "Barbados." This specimen is from Lamarck's collection, and is one of nine specimens of *Cassis granulosa* "Lamarck" that were present in Lamarck's collection, according to Rosalie de Lamarck's annotations in Lamarck's copy of *Animaux sans Vertèbres* (Y. Finet, MHNG, pers. comm., 1998). Because it is marked with the number "20" inside the aperture, and *C. granulosa* is *Cassis* species no. 20 in *Animaux sans Vertèbres*, there is no doubt that it is an original Lamarck syntype. What is in some doubt is whether Bruguière (1792a) used material that is now in Lamarck's collection. However, as noted above under "Type material of early-named species," none of Bruguière's material remains at MNHN, and the few original Bruguière specimens known are now in Lamarck's collection, so it is reasonable to assume that Bruguière *did* use the material now in Lamarck's collection, and Bruguière's material could all have been acquired by

Lamarck. This specimen is therefore accepted as the lectotype of *Cassidea granulosa*.

Emerson & Old (1963b: 16) pointed out the name *Cassis corrugata* Swainson (1822, appendix: 5), based on a specimen supposedly from "Gallipagos," and so possibly an earlier name for *C. centiquadrata*. However, they noted that because no type material is known for this name (presumably having been sold in the sale for which the Bligh catalog was prepared), and much of the Bligh collection material is known to be wrongly localized, the application of the name *C. corrugata* is unknown. They treated it as a *species inquirendum*. Because this name has never been used as a valid name for a species, and all authors since Bayer (1935) have used the name *C. centiquadrata* Valenciennes, 1832, as the valid name for the eastern Pacific species, *C. corrugata* Swainson could possibly qualify as a *nomen oblitum* under ICZN Article 23.9. However, I do not know of enough usages of *Semicassis centiquadrata* during the last 50 years to satisfy the requirements of this Article. To remove the possibility of the name *C. corrugata* threatening the stability of the long-accepted name *S. centiquadrata*, the lectotype of *Cassidea granulosa*, MHNG 1101/6, is here also designated the neotype of *Cassis corrugata*.

Two syntypes are present at MHNG of *Cassis abbreviata* Lamarck, 1822, and although Abbott (1968: 159) stated that specimen MHNG 1100/94/1 is the "holotype," this does not constitute a lectotype designation under ICZN Article 74.6, because it cannot be said to have won "acceptance," no one having discussed Lamarck's types since. This specimen, MHNG 1100/94/1 (Pl. 70, Figs 4, 6), is therefore here designated the lectotype of *C. abbreviata*, with one paralectotype, MHNG 1100/94/2 (Pl. 71, Figs 9-10), both labeled "Portugal?" The type locality is designated here as Barbados. Rosalie de Lamarck's annotations on Lamarck's copy of *Animaux sans Vertèbres* indicate that Lamarck owned two specimens (Y. Finet, MHNG, pers. comm., 1998), and the dimensions are similar to those cited by Lamarck; MHNG 1100/94/1 is 44.5 mm H, and MHNG 1100/94/2 is 28.3 mm H. *Cassis tessellata* Pfeiffer (1840: viii) is based on the validation of the non-binominal name *Buccinum cassideum tessellatum* Chemnitz (1795: 76, pl. 186, figs 1792-1793); these are good dorsal and ventral views of a specimen of *S. granulata*. A type is not designated here, because possible type material (*i.e.*, the specimen illustrated by Chemnitz) could be at either ZMC or, more probably, the Zoological Institute, Russian Academy of Sciences, St. Petersburg. *Xenogalea lucrativa*, holotype AMS C.53267, from "northern Australia," ex W. H. Hargreaves collection, pres. 1877. Abbott (1968: 157) suggested that Iredale's holotype is a mislocalized West Indian specimen of *S. granulata*, and examination of the specimen confirmed that this is likely; it has a weakly granulate inner lip, five rows of red-brown maculations on the last whorl, and

a subsutural row of large, darker, vaguely defined maculations, as in many specimens of the *cicatricosa* form. *Semicassis cicatricosa peristephes*, holotype ANSP 173344, from Peanut Island, Lake Worth, Florida (Pilsbry & McGinty, 1939: 76). *Semicassis (Tylocassis) inflata waltonensis*, holotype USNM 373150, from the Pliocene "Arca zone" [see Waller (1969: 90-91) and Zullo (1992: fig. 1) for explanations of these "zones" and their stratigraphical relationships], Jackson Bluff Fm, Choctawhatchee Group, Vaughan Creek, Walton Co, Florida. *Phalium alligator*, holotype at Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, CM 35678, and one paratype in Petuch's collection, from Caloosahatchee Fm (latest Pliocene), canal dredging along Miami Canal, 16 km S of Lake Harbor, Palm Beach Co, Florida (neither seen). *Phalium granulatum loxahatcheensis*, holotype UF 66234, from "Griffin Pit fauna," Palm Beach Rock pit, Loxahatchee area, along State Road 80, W of West Palm Beach, Florida (not seen).

Other material examined.—**Fossils: Florida: latest Pliocene:** Upper Caloosahatchee Fm, Griffin Bros pit, Holey Land Area, Palm Beach/Broward Co line, collection of Bernard Landau (4 large; type locality of *S. alligator*). **Pleistocene:** Bermont Fm, N New River Canal, 20 km S of South Bay, Palm Beach Co, Florida, collection of Bernard Landau (3); Bermont Fm, Palm Beach Rock pit, 3 km W of Loxahatchee, Palm Beach Co, collection of Bernard Landau (11 large; type locality of *S. granulata loxahatcheensis*). **Atlantic Costa Rica: Latest Pliocene-Early Pleistocene,** Moín Fm: NMB 18112 (1); 18113 (2); TU 1240, Los Corales, Limón, collection of Bernard Landau (4); Rte. 32, 3 km W of Puerto Limón, coll. J. A. Todd, February 1998 (BMNH Palaeontology Department, 1). Robinson (1991) also recorded 9 specimens from Limón in the Tulane University collections that I have not examined. **Atlantic Panama: Miocene:** Gatun Fm: NMB 18322 (1; widely spaced spiral cords); lower Gatun Fm, bed 1 of Todd, quarry floor, Los Lomos Suites, Cativa, Colon, coll. J. Todd, July 1999 (BMNH Palaeontology Department, GG22587, 1, coarse spiral cords, but no nodules; *S. reclusa*?); Valiente Fm: NMB 17629 (1). **Pliocene:** Cayo Agua Fm: NMB 17822 (1); 17830 (1); 17904 (1); 18373 (2); 18733 (2); Escudo de Veraguas Fm: NMB 17845 (1); Shark Hole Point Fm: NMB 17850 (1); 17854 (4); 18705 (1); 18706 (1). **Venezuela: Late Pliocene,** Mare Fm: NMB 17512 (42); 17513 (2); 17515 (1). **Pleistocene:** NMB 17541 (1).

Distribution.—*Semicassis granulata* lives now from North Carolina, USA, and Bermuda to Brazil (Abbott, 1968: 157) and to the coast of Uruguay, Martin Vaz Island, and all seamounts off of the Brazilian coast (Rios, 1994: 86). It is also recorded from the Canary Islands and Madeira in the eastern Atlantic (Nordsieck & Garcia-Talavera, 1979: 121; Kreipl, 1997: 53) and from the Azores (Ávila *et al.*, 1998); it is sympatric with *S. undulata* at all of these central and

eastern Atlantic localities. Fossils are reported here from Late Pliocene-Pleistocene and possibly Late Miocene rocks of the Atlantic coasts of Florida, Costa Rica, Panama, and northern Venezuela. Robinson (1991) recorded several specimens from the Late Pliocene-Early Pleistocene Moín Fm at Limón, Costa Rica (TU 954, 3 specimens; 956, 5 specimens; 1490, 1 specimen). Richards (1962: 79, pl. 17, fig. 10) also recorded Pleistocene fossil specimens from Cape Hatteras, North Carolina, and Gregory (1895: 189, table) recorded Pleistocene fossils from Barbados. The separation of *S. centiquadrata* and *S. granulata* seems to have taken place well before the closure of the Isthmus of Panama.

***Semicassis reclusa* (Guppy, 1873)**

Pl. 69, Figs 3-10; Pl. 70, Figs 1-3, 5, 7-10

Cassis monilifera Guppy, 1866: 287, pl. 17, fig. 8; 1874: 439; 1876: 525; Pilsbry & Brown, 1917: 34 (junior primary homonym of *Cassis monilifer* [sic] G. B. Sowerby I, 1846).

Cassis reclusa Guppy, 1873: 84 (reprint, Harris, 1921: 68); 1874: 434.

Cassidea granulosa. Gabb, 1873: 222 (not *Cassidea granulosa* Bruguière, 1792).

Dolium? (*Endolium* [sic]) sp. indet. Toulou, 1909: 698.

Phalium moniliferum. Maury, 1917a: 110, pl. 44, figs 4-5, pl. 45, fig. 1; Olsson, 1922: 135, pl. 15, fig. 11.

Cassis inflata monilifera. Pilsbry, 1922: 361.

Semicassis (*Tylocassis*) *reclusa*. Woodring, 1928: 307, pl. 19, figs 7-9, pl. 20, figs 1-2; Woodring, 1959: 200.

Cassis (*Phalium*) *moniliferum*. Anderson, 1929: 142.

Phalium (*Tylocassis*) *granulatum reclusum*. Abbott, 1968: 163.

Phalium (*Tylocassis*) *reclusa* (sic). Schmelz, 1996: pl. 3, figs 3-4.

Remarks.—The name *Cassis monilifer* of G. B. Sowerby I (1846) was misspelled; the “-ifer” ending is masculine, and the gender of *Cassis* is feminine. This name is a senior primary homonym of that proposed by Guppy (1866: 287). The next available name for the Caribbean species discussed here is *C. reclusa* Guppy, 1873.

Semicassis reclusa is abundant at many Dominican Republic Late Miocene-Early Pliocene localities. Most specimens are small, and have two or three rows of small nodules around and below the shoulder angle, and have weak axial ridges lower on the last whorl. These are much more coarsely sculptured than all but a very few Late Pliocene-Recent specimens of *S. granulata*, and in my opinion, this is a species distinct from *S. granulata*. A few specimens from the Dominican Republic have smoother spiral cords and only one weak row of nodules at the shoulder (Pl. 70, Figs 1-2) and these more nearly resemble *S. granulata*. The range of variation in even one small sample can be large, and there is no doubt that this is all one variable species. What is less certain, however, is the relationship of the Dominican Republic specimens to

the specimens from the Late Pliocene Bowden Shellbed in Jamaica, which is important because Bowden is the type locality of both *Cassis monilifera* Guppy and *C. reclusa*. Six small specimens from Bowden (NMB 10651 and 11146) all have one row of nodules at the shoulder, coarse on some specimens and, although the nodules are very weak on the holotype of *C. reclusa* (Woodring, 1928: pl. 20, figs 1-2), they are more prominent on spire whorls even on this specimen, and Woodring (1928: 307-308) commented on the large range of variation of the Bowden specimens that he observed. The ranges of variation of the Bowden and Dominican Republic specimens overlap greatly, and they seem to represent a single species. Specimens from the Gatun Fm (Late Miocene) of Panama discussed and illustrated by Woodring (1959: 200, pl. 34, figs 1, 4-6) all have only one row of shoulder nodules, at the most, and are more like the Recent *S. granulata* than the earlier *S. reclusa*. However, species boundaries are obscure, and whether Panama Late Miocene-Pliocene specimens should be referred to *S. reclusa* or *S. granulata* is unclear. The taxonomic interpretation of the variable populations of *Semicassis* in the Miocene to Recent faunas of the western Atlantic is complex, and the present treatment undoubtedly is not the last word on the subject, but it seems to be pragmatic to subdivide available collections in the traditional way.

Abbott (1968: 163) synonymized with *Semicassis reclusa* several other nominal taxa based on Miocene or Early Pliocene specimens from Florida or the tropical American region. These are *Phalium paraense* Maury, 1924, from the Pirabas Fm (late Early Miocene) of Bahia Pirabas, Paraná, Brazil; *P. (Tylocassis) sulcosa* var. *senni* Rutsch, 1934, Punta Gavilán Fm (Early Pliocene), Venezuela; *Semicassis (Tylocassis) inflata waltonensis* (Mansfield, 1935), Choctawhatchee Group, Pliocene, Vaughan Creek, Walton Co, Florida; and *S. (T.) maleaformis* H. Vokes, 1938, Springvale Fm (Early Pliocene; Donovan, 1994), Springvale Quarry, Trinidad. *Semicassis inflata waltonensis* is synonymized above with *S. granulata*. All of the other named taxa synonymized with *S. reclusa* by Abbott require more careful study before either synonymy with or separation from *S. reclusa* is accepted; most appear to be distinct species. *Semicassis senni* is discussed below; I have seen no further material from Springvale, and Maury's material from the Pirabas Fm is too poorly preserved for adequate study.

Dimensions.—Figured specimen, NMB H 18024, from NMB 18559 (TU 1363), Dominican Republic: H 44.7, D 29.9 mm; figured specimen, NMB H 18020, from NMB 16913, Dominican Republic: H 36.4, D 26.1 mm; 3 figured specimens, NMB H 18021-18023, from NMB 15905, Dominican Republic: H 32.3, D 23.5 mm; H 31.3, D 22.9 mm; H 26.9, D 19.0 mm; 2 specimens illustrated by SEM, NMB H 18040 and 18041, from NMB 15907, Dominican Republic: H 7.03, D 4.45 mm; H 6.61, D (incomplete) 4.51

mm.

Types.—*Cassis monilifera*, lectotype designated here, Guppy's (1866: pl. 17, fig. 8) figured syntype, BMNH Palaeontology Department, 64074; 1 unfigured paralectotype, BMNH Palaeontology Department, 64036, both from Bowden shellbed (Late Pliocene), Jamaica; 2 paralectotypes USNM 115504, from Bowden, Jamaica, too small for certain identification; so the best of the syntypes is here designated the lectotype. *Cassis reclusa*, holotype USNM 115505, from Bowden shellbed (Late Pliocene), Jamaica.

Other material examined.—**Fossils: Jamaica: Late Pliocene,** Bowden: NMB 10635 (5), 11146 (1). **Dominican Republic: Late Early Miocene:** Baitoa Fm: NMB 17286 (1); TU 1363 = NMB 18559 (1, illustrated, NMB H 18024; Pl. 69, Figs 8, 10). **Late Miocene:** Cercado Fm: NMB 15896 (1); 15897 (1); 15899 (7); 15900 (8); 15903 (390, mostly juvenile); 15904 (173, mostly juvenile); 15905 (11; 3 illustrated, NMB H 18021-18023; Pl. 69, Figs 3-7, 9); 15906 (124, mostly juvenile); 15907 (341, mostly juvenile; 2 illustrated by SEM, NMB H 18040 and 18041; Pl. 70, Figs 3, 5, 7-10); 15909 (9); 15910 (104, mostly juvenile); 15911 (3); 15912 (3); 15913 (1); 15914 (5); 15915 (8); 15917 (1); 16835 (2); 16837 (1); 16839 (4); 16853 (2); 16855 (2); 16857 (3); 17269 (3); TU 1230 (GNS WM16900, 41); 1294 (1); USGS 8521 (1; USNM 483451); 8525 (2, USNM 483449); 8534 (1; USNM 483450); Cercado de Mao (PRI 28772, 1, specimen illustrated by Maury, 1917a: pl. 19, fig. 1); Cercado Fm, Río Cana, collection of Bernard Landau (13); Gurabo Fm: NMB 15888 (1); 16910 (2); 16912 (1); 16913 (3, one illustrated, NMB H 18020; Pl. 70, Figs 1-2); 16914 (1); 16915 (3); 16917 (1); 16918 (2); 16919 (1); 16922 (1); 16923 (1); 16932 (1); TU 1410 (GNS WM18862, 1); NMB 15882, Río Gurabo, collection of Bernard Landau (10); Bluff 1 of Maury, Río Mao, coll. M. Taviani (Institute of Zoology, University of Bologna; 2). **Late Miocene/Early Pliocene:** Gurabo fm: NMB 15873 (2); 15878 (5); 16820 (1); 16821 (5); TU 1231 (GNS WM16923, 2); 1250 (GNS WM16930, 21 small); 1277 (2); 1293 (GNS WM16935, 12); 1297 (3); USGS 8519 (4); "Caimito" (PRI 28768, 1, specimen illustrated by Maury, 1917a: pl. 18, figs 4-5); PRI, Maury's loc. 196, zone A, Río Gurabo (1); PRI, Maury's loc. 197, zone B, Río Cana (2); PRI, Maury's loc. 204, zone G, Río Gurabo (1). **Early Pliocene:** Gurabo Fm: NMB 15842 (1); 15846 (1); 15858 (1); 15864 (1); 15867 (1); 16814 (1); 16818 (8); 16825 (1); 16828 (5); 16869 (1); 16870 (1); 16934 (1); TU 1219 (2); 1278 (2, including GNS WM18861, 1); 1215, Gurabo Fm, Río Gurabo, collection of Bernard Landau (6); TU 1219, Cañada de Zamba, collection of Bernard Landau (4); NMB 15906, Río Gurabo, Gurabo Fm, coll. M. Taviani (Institute of Zoology, University of Bologna; 5). **Venezuela: Late Miocene:** NMB 17530, Caujarao Fm, Carrizal (8).

Distribution.—*Semicassis reclusa* is recorded from Late Miocene and Pliocene rocks of Jamaica (Bowden shellbed, type locality), the Dominican Republic, and Venezuela. It probably occurred throughout tropical America region during Miocene-Pliocene time.

***Semicassis senni* (Rutsch, 1934)**

Pl. 71, Figs 1, 3

Phalium (*Tylocassis*) *sulcosum senni* Rutsch, 1934: 55, pl. 3, figs 1-2.

Remarks.—The holotype of *Semicassis senni* and material collected subsequently from the type locality are all large, tall-spined, unusually elongate specimens with wide, almost smooth spiral cords separated by very narrow grooves and bearing few nodules. The interior of the outer lip also is unusually coarsely ridged, and the wide, strongly thickened inner lip collar bears very coarse nodules and transverse ridges. Rutsch (1934) seems to have been correct to compare it most closely with the similar eastern Atlantic-Mediterranean species *S. undulata* (Gmelin, 1791), but the latter reaches a considerably larger size and has a taller spire and higher and narrower spiral cords (*i.e.*, deeper and wider grooves between the cords) than *S. senni*. However, the preservation as distorted calcite neomorphs makes *S. senni* difficult to compare with other material. *Semicassis senni* tentatively is accepted as a distinct species, but this conclusion requires confirmation from more material.

Dimensions.—Holotype: H 62, D 38 mm (Rutsch, 1934: 56).

Types.—Holotype NMB H 1866 (Pl. 71, Figs 1, 3), from NMB 1769, Punta Gavilán Fm (Early Pliocene) at Punta Gavilán, N Venezuela.

Other material examined.—NMB 17531, Punta Gavilán, Early Pliocene, coll. J. & W. Gibson-Smith (6); locality same as last, collection of Bernard Landau (1).

Distribution.—Recorded only from the Punta Gavilán Fm (Early Pliocene) at Punta Gavilán, northeastern Venezuela.

Family **TONNIDAE** Suter, 1913 (1825)

Conserved under ICZN Article 49.2.

Remarks.—The family Tonnidae contains those Tonnoidea that (a) lack an operculum in large specimens of the benthic adult stage (although those that have been investigated have one in the veliger larval stage, and it has now been observed to be present in some small benthic specimens up to 20 mm H; see below), (b) have a thin, very inflated, subspherical shell with a low spire and very capacious last whorl, (c) have sculpture almost entirely of spiral cords that are low, wide and closely spaced in most taxa, (d) have a thin, or reflected and thickened, or exceedingly prominently varicose outer lip but no va-

rices remaining at growth pauses before the terminal one in all but a few abnormal specimens, (e) have a thin, uncalled or heavily callused and nodulose inner lip, (f) have a completely straight to weakly twisted, very short siphonal canal, and (g) have a radula in which the central teeth have large, basal, ventrally directed, pointed processes ("hooks") for interlocking the whole row of central teeth, because the adult feeds by ingesting entire, large holothurians and the radula is used to pull a holothurian into the lumen of the proboscis. Members of the Tonnidae apparently are limited to soft substrata, and so evidently live far enough from the habitats of shell-peeling calappid crabs to be able to dispense with the episodic growth that is so characteristic of the Bursidae, Personidae, Ranellidae, and (at least most) Cassidae.

The genera included in the family are *Eudolium* Dall, 1889, *Malea* Valenciennes, 1832, and *Tonna* Brunnich, 1772. The fauna of the study area includes one fossil *Eudolium* species and two living ones. The living ones [*E. crosseanum* (Monterosato, 1869) and *E. bairdii* (Verrill & Smith in Verrill, 1881)] have been revised excellently by Marshall (1992), have no fossil record in the study area, and will not be mentioned further here. The fauna also includes fossil records of the two living western Atlantic *Tonna* species, revised by Turner (1948) and Vos (2007), and a diverse, complex record of *Malea* species in Miocene and Pliocene rocks throughout the region.

Post-metamorphic operculum.—It has been accepted for many years that benthic, metamorphosed specimens of all Tonnidae lack an operculum, and this still seems to be the case for large adults. However, I have observed an operculum up to 3.3 mm H in three specimens of small, post-metamorphic, benthic tonnids, with shells up to 19 mm H (*Tonna zonata* (Green, 1830), Expedition *Taiwan* 2002, shrimp trawler *Cheng Meng Fa*, off of SW coast of Taiwan: sta. CP167, 100 m, 1 specimen, shell 16.5 mm H; *T. zonata*, sta. CP168, 53 m, 1 specimen, shell 19.4 mm H; *Eudolium bairdii*, Expedition *Norfolk* 1, Norfolk Ridge, S New Caledonia: sta. DW1692, Sponge Bank, 507-967 m, 1 specimen, shell 19.1 mm H; all MNHN). It appears that the operculum is lost early in benthic life, rather than at metamorphosis, in at least some specimens of Tonnidae. The operculum of each of these specimens is subtriangular, with an anterior and a posterior shallow groove radiating from the mid-right lateral nucleus, producing slight indentations at the anterior and posterior ends of the left margin. It is almost identical to the less obviously triangular larval operculum (Warén & Bouchet, 1990: figs 61-62), but with all three margins straighter. It is also very little larger than the larval operculum reported by Warén & Bouchet (1990; 3.1 mm H), indicating little post-metamorphic growth of the operculum. The opercular shape is not unlike the more strongly triangular one of the bathyal Antarctic ranellid *Obscuranella papyrodes* Kantor & Harasewych, 2000,

making the operculum of the latter species appear much less unusual than it seemed at first. The presence or absence of an operculum in benthic Tonnidae requires further study.

Genus *EUDOLIUM* Dall, 1889

Doliopsis Monterosato, 1872: 49. Type species (by monotypy): *Dolium crosseanum* Monterosato, 1869, Recent, Mediterranean and eastern and western Atlantic (junior homonym of *Doliopsis* Vogt, 1852, and of *Doliopsis* Conrad, 1865).

Eudolium Dall, 1889: 20, 232. Replacement name for *Doliopsis* Monterosato, 1872, preoccupied.

Galeodolium Sacco, 1891: 4. Type species (by subsequent designation, Cossmann, 1903: 139): *Cassidaria mutica* Michelotti, 1861, Oligocene, Italy.

Tuberculodolium Sacco, 1891: 9. Type species (by subsequent designation, Cossmann, 1903: 139): *Eudolium antiquum* Sacco, 1891, Oligocene, Italy. The holotype of *E. antiquum* was figured by Ferrero-Mortara *et al.* (1984: pl. 3, fig. 5). It was said to be "taller and narrower than *Eudolium* species" by Bouchet & Warén (1993: 797), but in my opinion it is a poorly preserved *Eudolium* specimen with the outer lip broken back.

Remarks.—*Eudolium* includes the relatively small *Tonna*-like shells with narrow spiral cords separated by several series of secondary and tertiary spiral ridges and threads, and with a relatively thick, reflected and, in some species, toothed and ridged outer lip. In my opinion, the subdivisions *Galeodolium* and *Tuberculodolium*, proposed by Sacco (1891), are based on trivial specific characters. This was also the opinion of Marshall (1992). I questioned (Beu, 2005) the significance of the distinction between *Eudolium* and *Tonna*, because these supposed genera intergrade in most characters, and juvenile specimens of *T. galea*, the type species of *Tonna*, have identical sculpture to that of adult specimens of *Eudolium* (Pl. 76, Fig. 5). I recently repeated these qualms about the status of *Eudolium* (Beu in Vos, 2007: 11-12). However, I tentatively maintain the traditional two genera here, because the relationship requires further study, and should only be changed after molecular analysis.

Eudolium subfasciatum Sacco, 1890

Pl. 71, Figs 8, 11

Eudolium subfasciatum Sacco, 1890a: 201 (*nomen nudum*); Sacco, 1890b: 22, with varieties *supratuberculifera*, *unituberculifera*, *percostata*, and 9 unnamed varieties; Ferrero Mortara *et al.*, 1984: 21, pl. 3, figs 4a-b.

Eudolium (*Galeodolium*) *subfasciatum*. Sacco, 1891: 6, pl. 1, fig. 4, with varieties *subtuberculata*: 7, pl. 1, fig. 5; *magnovoidea*: 7, *trilatetuberculata*: 7; *conica*: 7; *supratuberculifera*: 8, pl. 1, fig. 6; *oblongata*: 8; *pantanensis*: 8; *unituberculifera*: 8, pl. 1, fig. 7; *percostata*: 8, pl. 1, fig. 8; *crassilabiata*: 9; *tuberculifera*: 9; and *inflata*: 9; Vokes, 1986: 178, text-figs 1-3; J. Gibson-Smith & W.

Gibson-Smith, 1988: 119, text-fig. 1; Vokes, 1997: 212.

Remarks.—*Eudolium* specimens from the late Early Miocene Chipola Fm of Florida (Vokes, 1986) and the coeval Cantaure Fm of the Paraguaná Peninsula, northern Venezuela (J. & W. Gibson-Smith, 1988), were referred to *E. subfasciatum* Sacco, 1890, by these authors, and comparisons of specimens with the illustrations by Sacco (1891: pl. 1, figs 4-8) and the illustration of a syntype by Ferrero Mortara *et al.* (1984: pl. 3, figs 4a-b) show clearly that American specimens are indeed conspecific with the Italian Miocene specimens described and illustrated by Sacco. However, the relationships of *E. subfasciatum* to other European nominal species of *Eudolium* are beyond the scope of this report, and require further research (B. Landau & M. Harzhauser, pers. comm., June 2009). Important diagnostic characters are (a) the strongly reflected outer lip forming a wide varix with a concave abapertural face and a flat, strongly radially ribbed adapertural face, (b) the 15 or more groups of prominent ridges on the inner edge of the outer lip, (c) the uppermost one subdivided into three ridges and most of the others into two ridges (some of the lowest ones are only weakly subdivided in some specimens), (d) the coarsely ridged inner lip, particularly over the lower columellar area where it is raised into a free collar over the neck of the preceding whorl, and (e) the long, gradually tapered neck of the last whorl, merging gradually into a relatively long (for the genus), open, straight siphonal canal. Although the canal is straight, the weakly convex to almost straight lower part of the outer lip and the lower part of the columellar and left edge of the canal being inclined slightly to the left give the anterior part of the shell an unusual, distinctive inclination to the left at the end of a very extended outer lip, which continues unbent down the right edge of the siphonal canal. This same shape is shown clearly in Sacco's (1891: pl. 1, figs 5a-b, 7a-b) illustrations of his varieties *subtuberculata* and *unituberculifera* in particular. Most specimens are relatively small for the genus (to ca. 40 mm H), but one specimen collected by Bernard Landau is much larger (H 58.5 mm).

In view of the almost worldwide range of the living species *Eudolium bairdii* (Verrill & Smith, 1881) (Marshall, 1992; Vos, 2007), it is not surprising to find that the one species of *Eudolium* recorded from Miocene rocks of the tropical American region is conspecific with an Italian Miocene species. The only other record of Neogene fossil species in the Americas of which I am aware that is assigned to *Eudolium* is by Petuch (1988a: 71, pl. 1, figs 4-5; 1994: pl. 35, figs C-D; 1997: figs 39B, cover fig.), who reported the unusually tall-spined species *E. marylandicum* Petuch, 1988, from the Late Miocene (Tortonian) St. Marys Fm of Maryland and Eastover Fm of Virginia, and noted that impressions of this or a very similar species have been collected from the Ochopee

Limestone (Pliocene) along the Tamiami Trail, Florida. Obviously, it is desirable to check whether this species also has been named earlier in Europe, in view of the worldwide ranges that are normal for *Eudolium* species, but the tall spire appears to be a unique character of *E. marylandicum*. Petuch (2004: pl. 34, figs A-B) illustrated this species again (with a rather lower spire) from the Windmill Point Member of St. Marys Fm, Chancellor's Point, Maryland. Beside these, the Oligocene species referred to *Galeodaria* by MacNeil & Dockery (1984: pl. 4, figs 1-2, pl. 17, figs 1-4, pl. 49, figs 9-13; but not the type species of *Galeodaria* Conrad, 1865, which is a species of *Galeodea*) in my opinion are further species of *Eudolium*.

Dimensions.—Cantaure, Venezuela, largest seen, collection of Bernard Landau: H 58.5, D 46.0 mm; figured specimen, NMB H 18025, from NMB 17516, lower shellbed, Cantaure Fm, Paraguaná Peninsula, Venezuela: H 30.8, D 23.1 mm.

Types.—Ferrero Mortara *et al.* (1984: 21-22) reported that syntypes of *Eudolium subfasciatum* and of most of Sacco's varieties are housed at the Museo Regionale di Scienze Naturali, in Turin, with catalog numbers BS.027.01.004-009, 011-014 (not seen).

Other material examined.—**Fossils: Florida: Late Early Miocene:** Vokes (1986: 179) listed material of *Eudolium subfasciatum* from the following Chipola Fm localities in Florida, USA, all on Tenmile Creek, between Florida Highway 70 and the base of the formation (listed from W to E): TU 70 (2); 655 (4); 456 (2); 546 (5); 998 (2); 951 (4); 830 (8). **Venezuela: Late Early Miocene:** NMB 17521, La Candelaria beds (3); 12842, Cantaure (1); 17516, Cantaure (14; 1 illustrated, NMB H 18025; Pl. 71, Figs 8, 11); 17519, Cantaure (1); Cantaure, collection of Bernard Landau (3).

Distribution.—*Eudolium subfasciatum* is recorded widely in the Turin Hills, Italy (Tortonian, Late Miocene), from Grund, Vienna Basin, Austria (Badenian, Middle Miocene) (Sacco, 1891; Vokes, 1986), and from the Chipola Fm, Florida, USA, and the Cantaure Fm, Venezuela, in the tropical American region. All localities are Miocene in age, and the two tropical American ones are both late Early Miocene. Specimens from Korytnica, Poland (Miocene) illustrated by Baluk (1995: 201, pl. 16, figs 9-10) as *Cassidaria cingulifera* Hoernes & Auinger, 1884, belong to a different group of *Eudolium* species, more nearly related to *E. stephaniophorum* (Fontannes, 1879) and the Recent species *E. bairdii* (Verrill & Smith in Verrill, 1881), than to *E. subfasciatum*.

Genus *MALEA* Valenciennes, 1832

Malea Valenciennes, 1832: 324. Type species (by subsequent designation, Herrmannsen, 1847: 13): *M. latilabris* Valenciennes, 1832 (= *Cassis ringens* Swainson, 1822), Pliocene to Recent,

eastern Pacific.

Quimalea Iredale, 1929a: 345. Type species (by original designation): *Buccinum pomum* Linnaeus, 1758, Recent, Indo-West Pacific and (rarely) northeastern Brazil.

Remarks.—*Malea* is a distinctive genus of Tonnidae with a wide, flat-faced terminal varix formed by a deep infolding of the outer lip, which remains visible as a deep furrow on the exterior of the shell just behind the last varix, and is followed by a major reflection of the lip back out over the inward fold, and is then thickened and ridged, so that it is relatively thin for such a huge, wide varix (40 mm or more wide on a large specimen of *M. ringens* Swainson, 1822), but bears prominent, narrow radial ridges across the whole width of the terminal face of the varix, forming denticles along both the inner and outer margins of the flange. The inner lip also is greatly thickened, forming a wide callus pad on the inner lip that is represented only by a thin smear in *Tonna* and *Eudolium*, and a knob bearing several prominent transverse ridges is formed on both the center of the lower columella and on the base of the inner lip, leaving a deep, narrow columellar embayment between the two knobs. The number and prominence of the ridges on the upper columellar knob are species characters and, e.g., the European Neogene fossil species *M. orbiculata* (Brocchi, 1814) has only a single, narrow central columellar ridge (Sacco, 1904: pl. 22, figs 6-10; Cavallo & Repetto, 1992: 71, fig. 132; immature holotype illustrated by Pinna & Spezia, 1978: pl. 11, figs 1-1a; Solsona, 1999: figs 6-7; Landau *et al.*, 2004: pl. 1, fig. 2; Chirli, 2007: 74, pl. 28, figs 7-12; specimen examined at GNS). The exterior is sculptured only with simple spiral cords, and the width and spacing of the cords and the overall shell shape are the main characters distinguishing the tropical American Neogene and living species.

Only two species of *Malea* occur in the world living fauna, much the larger being the eastern Pacific type species, *M. ringens* (Swainson, 1822), which reaches 270 mm H (Keen, 1971: 499; Vos, 2007: 30). The much smaller species, *M. pomum* (Linnaeus, 1758), is common throughout the tropical Indo-West Pacific, and is very similar in size, sculpture, and apertural armature to the abundant tropical American Miocene and Pliocene species *M. camura* Guppy, 1866. Relatively recently, a supposed third species has been discovered in Brazil, and is said to be limited to the Fernando de Noronha Islands and Atol das Rocas: *M. noronhensis* Kempf & Matthews (1969: 57, figs 1-5; Abbott & Dance, 1982: 119, top left fig.; Rios, 1990; 1994: 84, pl. 28, fig. 328; Vos, 2007: pl. 5, figs 1a-3b). *Malea noronhensis* (paratype examined at MNHN) is very closely similar indeed to *M. pomum*, differing only in its paler coloration and, because all of the type material consists of faded and abraded beach specimens, clearly is a synonym of *M. pomum* (see Beu, 2005: 114; Vos,

2007: 29). Several fresher specimens were illustrated excellently in color by Vos (2007: pl. 5), as well as on a webpage (<http://www.femorale.com.br/shell/photos>, last accessed 28 April 2006) showing that the peach-pink exterior, maculated with white, also is identical to that of Pacific specimens. The fauna of the tropical American region during the Neogene displays much the greatest diversity of *Malea* species ever recorded (six named species and a further two unnamed ones are described here, not including *M. springi* Petuch, 1989, in the Florida Plio-Pleistocene), and the taxonomy of this complex interplay of forms at various ages remains poorly understood. Clearly, considering its formerly wide distribution and taxonomic diversity in the tropical American region before the uplift of the CAI, and the subsequent reduction to the one common eastern Pacific species and one common Indo-West Pacific species that straggles to eastern Brazil, *Malea* is an interesting subject for biogeographical study, and deserves to be analyzed very critically. However, *Malea* in this region is another taxonomically “difficult” group, almost as perplexing as *Semicassis* and, again, the version provided here is unlikely to be the final word on the subject.

***Malea camura* Guppy, 1866**

Pl. 72, Figs 1-4, 6

Malea camura Guppy, 1866: 287, pl. 17, fig. 9; 1874: 439; 1876: 525; Maury, 1917a: 276, pl. 45, fig. 3; 1920: 59; 1925: 218, pl. 36, fig. 7; Jones, 1918: 741; ?Cooke, 1919: 561 (identity uncertain); Hubbard, 1921: 148; Pilsbry, 1922: 363; Woodring, 1928: 311, pl. 20, figs 7-8 (in part); Vokes, 1938: 24; Pflug, 1961: 42, pl. 10, figs 3, 6 (“holotype”).

Malea ringens. Gabb, 1873: 223 (in part not *Cassis ringens* Swainson, 1822).

Malea elliptica. Olsson, 1922: 311, pl. 15, fig. 2 (not *Malea elliptica* Pilsbry & Johnson, 1917).

Remarks.—The name *Malea camura* has been used very widely throughout the Caribbean region for Miocene and Pliocene *Malea* specimens, and the fact that at least three species occur together in the Dominican Republic faunas demonstrates that a little more rigor is desirable in the use of this species name. It is not possible now to confirm or deny the identity of all the many usages of this species name, but I have tried to make the synonymy reasonably rigorous.

It is particularly unfortunate, in such a taxonomically difficult genus, that the lectotype designated here (Pflug, 1961: pl. 10, figs 3, 6; as “holotype”) of *Malea camura*, from the Late Pliocene Bowden shellbed, Jamaica, is a very incomplete specimen that is difficult to compare with the abundant, excellently preserved Dominican Republic specimens. The specimen from the Bowden shellbed illustrated by Woodring (1928: pl. 20, figs 7-8) and five small specimens from the same locality

at NMB are all too small to compare with specimens from other localities with any confidence that similarities or differences would persist in adults, and no larger specimens are available from Bowden. In fact, the available Bowden specimens are a little more elongate and have slightly narrower spiral cords than the usual Dominican Republic specimens assigned to *M. camura*, and so resemble Dominican Republic specimens of *M. elliptica* as much as the usual interpretation of *M. camura*. However, Dominican Republic shells are highly variable in shape and sculpture, and the only possible course of action at present seems to be to continue the traditional usage of the name *M. camura* as the shorter and wider of the common Dominican Republic species, and *M. elliptica* as the taller and narrower species. It would not be surprising if in fact all of the Dominican Republic species are distinct from *M. camura*; Bowden material is simply not adult enough for satisfactory comparison. A small selection of specimens from one sample (NMB 16913; 3 of 50 specimens in the sample) is illustrated (Pl. 72, Figs 2-4, 6) to show the range of variation in shape of specimens attributed to *M. camura* in the Dominican Republic; the narrowest matches the Bowden specimens closely, whereas the widest is significantly wider than any specimens seen from Bowden.

The species here interpreted, in the traditional way, as *Malea camura* is small relative to *M. ringens* (H up to ca. 70 mm), with a much lower spire than *M. elliptica*, with wide but fairly high spiral cords with rounded, rather vaguely defined edges. Most specimens have relatively wide spiral interspaces, but each interspace is only about a quarter to a third of the width of one cord. The terminal varix is very thick for its width, in comparison with that of *M. ringens*, inclined forward in the apertural plane, and significantly wider in the center of the lower half of its height than higher up; it also is straight in lateral view. The thick, smooth, inner lip callus pad rides up almost to the shoulder angle on large specimens, and the columellar knobs are large at all sizes, and each bear two or, in a few specimens, one or three transverse ridges. The lower columellar area, near the lower columellar knob, bears a few coarse, smooth, irregular transverse ridges. Most specimens assigned here have even spiral cords all over, whereas a few have narrower and more sharply defined spiral cords in a narrow subsutural zone than lower down, defining a much clearer sutural ramp than on most specimens (these probably should be referred to *M. goliath* Pilsbry & Johnson, 1917; see below). The spiral cords are wide, low, and rounded in cross-section, and the overall appearance of the shell and the style of spiral sculpture closely resemble those of the smaller living species *M. pomum* (= *M. noronhensis*). The great similarity of *M. camura* to this living species as well as to the other, coeval Caribbean fossil species demonstrates that the "subgenus" *Malea* (*Quimalea*) Iredale, 1929, is of no significance.

Dimensions.—Lectotype: H 26.9 (very incomplete), D 21.7 mm; large figured specimen, NMB H 18026, from NMB 16919, Dominican Republic: H 71.2, D 54.2 mm; 3 small figured specimens, NMB H 18027-18029, from NMB 16913, Dominican Republic: H 44.9, D 32.3 mm; H 40.2, D 30.1 mm; H 38.8, D 32.2 mm.

Types.—*Malea camura*, lectotype (designated here) BMNH Palaeontology Department 64076 (Pflug, 1961: pl. 10, figs 3, 6; as "holotype"), an incomplete specimen from the Bowden shellbed, Jamaica, Late Pliocene, "pres. Lucas Barrett, 1862"; 1 paralectotype USNM 115507, "Haiti, Guppy," a small specimen apparently referable to *M. elliptica* rather than to *M. camura*. Two other very small specimens, each less than 20 mm H (BMNH Palaeontology Department 64035) from Bowden, Jamaica, also were available to Guppy (also labelled "pres. Lucas Barrett, 1862") and so all four specimens are considered to be syntypes. Pflug's (1961) statement that his figured specimen (BMNH Palaeontology Department 64076) is the "holotype" does not constitute an inadvertent designation of this specimen as the lectotype, because Pflug obviously was not intending to differentiate it from the other syntypes (and might not have been aware of them), and the designation has not become "generally accepted" (ICZN Code Article 74.6), so this specimen, BMNH Palaeontology Department 64076 (Pflug, 1961: pl. 10, figs 3, 6), is here designated as the lectotype of *M. camura*.

Other material examined.—**Fossils: Jamaica: Late Pliocene:** Bowden: C. T. Trechman collection (BMNH Palaeontology Department GG3896, 1); NMB 10635 (2); 10651 (1); 11110 (1); 11146 (1); 10831 (1); USGS 23476 (1); USNM, main Bowden collection (14). **Dominican Republic: Late Miocene:** Cercado Fm: NMB 16839 (1 + frags); 16842 (1); 16857 (9 frags); 17269 (11); TU 1230 (5, including GNS WM16901, 1); 1294 (20+, including GNS WM16936, 5); USGS 8525 (25); 8526 (1); 26273 (2); 26279 (6); 26280 (5); 26292 (1); PRI, Maury's loc. 196, bluff 3, Cercado de Mao (9); Dominican Republic collection presented to NMB by A. A. Olsson, 1930, bluff 3, Cercado de Mao (2); Gurabo Fm: NMB 15885 (1); 15887 (1); 15888 (1); 16910 (2, narrow spiral cords); 16912 (4); 16913 (55; 3 illustrated, NMB H 18027-18029; Pl. 72, Figs 2-4, 6); 16914 (2); 16916 (11); 16917 (1); 16918 (6); 16919 (3; 1 illustrated, NMB H 18026; Pl. 72, Fig. 1); 16923 (2); 16924 (11); 16927 (12); 16928 (20); 16931 (3); TU 1298 (1); 1379, Gurabo Fm, Río Mao, collection of Bernard Landau (6); Bluff 1 of Maury, Río Mao, coll. M. Taviani (Institute of Zoology, University of Bologna, 1); unnamed formation of E. Vokes (1989: 21): NMB 17278 (1). **Late Miocene/Early Pliocene:** Gurabo Fm: NMB 16820 (1); TU 1205 (1); 1206 (1); 1231 (GNS WM18858, 1 small); 1246 (1); 1277 (2); 1293 (1); 1295 (1); USGS 8527 (1); 26274 (1). Miocene, St. Domingo (BMNH

Palaeontology Department G 11079, 2); Miocene, 13.5–14.8 km from Santiago on San José de los Matos Road, pres. H. D. Pflug (BMNH Palaeontology Department GG 20293, 1).

Early Pliocene: Gurabo Fm: NMB 15807 (2); 15859 (1); 15860 (2); 15863 (3); 16828 (5 + frags); 16864 (1); 16865 (1); 16866 (1); 16879 (1); TU 1210 (1); 1215 = NMB 18581 (2; smaller one probably *M. elliptica*); 1219 (6); 1278 (1); 1354 (7); USGS 8516 (1); Los Quemados (PRI 28774, 1; specimen illustrated by Maury, 1917a: pl. 19, fig. 3); USGS 8726, upper Gurabo Fm(?), S side Río Yaque del Norte, La Canita (1); Mao Fm: USGS 8555 (1). **Venezuela: Late Early Miocene:** NMB 17521, La Candelaria beds (3 small). **Late Miocene:** NMB 17530, Caujarao Fm, Carrizal (2).

Distribution.—Material assigned to *Malea camura*, as defined here, is limited to the Bowden shellbed, Jamaica (Late Pliocene), to the Late Miocene–Early Pliocene rocks of the Dominican Republic (where it is abundant), and to a few Miocene localities in Venezuela. As noted by Woodring (1959: 209), literature records based on molds and impressions from Cuba, Puerto Rico, Trinidad, and Peru need confirmation from better material. It seems likely that at least the Peruvian material (recorded by Spieker, 1922) should be referred to *M. ringens*. The mold of the interior reported as *M. camura* from near Havana, Cuba (supposedly Oligocene), by Cooke (1919: 114) could refer to any of numerous *Malea* species.

Malea densecostata (Rutsch, 1934)

Pl. 74, Figs 4, 8

Tonna (Malea) ringens densecostata Rutsch, 1934: 60, pl. 3, figs 6–7. NOT *Malea densecostata*. Olsson & Petit, 1964: 554, pl. 79, fig. 5; Petuch, 1989: fig. 4; 1992: 108, fig. 3M (= *Malea mareana* Weisbord, 1962).

NOT *Malea* cf. *densecostata*. Petuch, 1994: pl. 35, fig. G (= *Malea mareana* Weisbord, 1962).

Remarks.—The holotype of *Malea densecostata* is illustrated for comparison with the other taxa reviewed here. It has many similar, very narrow, closely spaced, low, weakly convex to almost flat spiral cords, not matched by those of material that I have seen from any other locality. Many specimens are present in the Punta Gavilán Fm collections, all consistent in the diagnostic narrow, closely spaced spiral cords. Most specimens seem also to be very short-spined and subspherical in shape, but the preservation as calcite neomorphs, most quite distorted, makes shape comparison difficult.

Dimensions.—Holotype: H 76.3, D 58.2 mm.

Types.—*Tonna (Malea) ringens densecostata*, holotype NMB H 1873 (Pl. 74, Figs 4, 8), 2 paratypes NMB H 1871/1–2, all from NMB 12045, Punta Gavilán Fm (Early Pliocene), Punta Gavilán, Falcón, N Venezuela.

Other material examined.—**Fossils: Venezuela: Early Plio-**

cene: All material from Punta Gavilán Fm: NMB 12040 (2, NMB H 1875/1–2, identified by Rutsch as *T. (M.)* cf. *densecostata*); 12043 (1); 12045 (2, beside types); 12865 (7); 13892 (2); 17531 (18); collection of Bernard Landau (3).

Distribution.—I have seen specimens of *Malea densecostata* only from the type formation, from localities near Punta Gavilán, northern Venezuela. This suggests that the Punta Gavilán fauna occupied a basin isolated in the eastern Caribbean during Early Pliocene time, and offers a useful comment on the possible rapid speciation and restricted ranges of *Malea* species.

Malea elliptica Pilsbry & Johnson, 1917

Pl. 72, Figs 5, 7–9; Pl. 74, Figs 1–3, 6

Malea elliptica Pilsbry & Johnson, 1917: 169; Pilsbry, 1922: 363, pl. 29, fig. 3.

?*Malea* cf. *elliptica*. Trechman, 1934: 486, pl. 25, fig. 11.

?*Malea camura* var. *elliptica*. Maury, 1925: 218.

NOT *Malea*? cf. *elliptica*. Woodring, 1959: 209, pl. 31, figs 2, 5 (apparently an unnamed, still taller species).

Remarks.—*Malea elliptica* seems to be a species distinct from *M. camura*, although apparently occurring only in the Dominican Republic. Specimens are markedly less common than *M. camura*. They differ from the latter in (a) the more elongate shape, (b) the much taller spire, so that the inner lip callus pad ascends only to approximately the upper third of the last whorl, (c) the spiral cords being lower, wider, more closely spaced, with a flatter crest and with more clearly defined edges, and with a single very narrow intermediate thread in some or all interspaces in a few specimens, (d) the terminal varix being more even in width over its full height, flatter than in *M. camura*, and curving forward a little toward the posterior (adapical) end of the aperture rather than straight as in *M. camura*, (e) the knobs on the inner lip being markedly narrower in most specimens and bearing only one or, in a few specimens, two narrow transverse ridges, rather than the two or three on the much more prominent knobs of *M. camura*, and (f) the lower columellar area bearing many, very irregular, anastomosing bumps and ridges, rather than the rather simple, elongate ridges of *M. camura*.

Dimensions.—Holotype: H 53.5, D 34.7 mm (Pilsbry & Johnson, 1911: 170); 2 figured specimens, NMB H 18032–18033, from NMB 17283, Baitoa Fm (late Early Miocene), Río Yaque del Norte, Dominican Republic: H 76.4, D 51.7 mm; H 60.4, D 42.5 mm; medium-sized figured specimen, NMB H 18030, from NMB 15909, Dominican Republic: H 43.9, D 29.2 mm; small figured specimen, NMB H 18031, from NMB 16842, Dominican Republic: H 32.7, D 20.9 mm.

Types.—*Malea elliptica*, holotype ANSP.IP 2590 (Pl. 74,

Figs 2, 6), from the Dominican Republic (otherwise unlocalized), *ex* Gabb collection.

Other material examined.—**Fossils: Dominican Republic:**

Late Early Miocene: Baitoa Fm: NMB 17282 (1); 17283 (2, illustrated, NMB H 18032-18033; Pl. 72, Figs 7, 9); 17281, Río Yaque del Norte, collection of Bernard Landau (2); TU 1364, Arroyo Hondo, Baitoa, Río Yaque del Norte, coll. M. Taviani (Institute of Zoology, University of Bologna, 3). **Late Miocene:** Cercado Fm: NMB 15909 (1, illustrated, NMB H 18030; Pl. 74, Figs 1, 3); 16835 (2); 16842 (1, illustrated, NMB H 18031; Pl. 72, Figs 5, 8); 16852 (1); USGS 8525 (8, + juveniles); 8526 (1, USNM 483445); 26273 (7 juveniles); 26280 (1); PRI, Maury's loc. 196, bluff 3, Cercado de Mao (18); Gurabo Fm: USGS 8733 (1); PRI, Maury's loc. 198, bluff 2, Cercado de Mao (2); NMB 16982, Río Cana, collection of Bernard Landau (2). **Late Miocene/Early Pliocene:** Gurabo Fm: NMB 15880 (1); TU 1231 (1); 1297 = NMB 19162 (2); USGS 8519 (2); PRI, Maury's loc. 204, zone G, Río Gurabo (2); PRI, Maury's loc. 207, zone F, Río Gurabo (4; 1 with very narrow spiral cords); PRI, Maury's loc. 205, Guayabin-Mao road (1 frag); Miocene, Yaque River, St. Domingo, Col. T. S. Heneken (BMNH Palaeontology Department GG 20432-7, 6 + one unregistered). **Early Pliocene:** Gurabo Fm: NMB 16817 (2); TU 1278 = NMB 19011 (1); 1354 (GNS WM16942, 7 small); USGS 8538 (3); 8544 (1); TU 1215, Gurabo Fm, Río Gurabo, collection of Bernard Landau (2); 1354, Gurabo Fm, Cañada de Zamba, collection of Bernard Landau (2).

Distribution.—Apart from three records, I am aware of *Malea elliptica* only from the Late Early Miocene-Early Pliocene rocks of the Dominican Republic (although there are few specimens from confirmed Pliocene rocks, and this species alone occurs in the late Early Miocene Baitoa Fm), where it occurs in Late Miocene rocks with but is less common than *M. camura*. One of the exceptions is the specimen from the Late Miocene of Tobago recorded by Trechman (1934: 486, pl. 25, fig. 11), which is certainly taller and narrower than *M. camura*, but is too incomplete for certain identification. A specimen from the Gatun Fm of Panama, recorded by Woodring (1959: 209, pl. 31, figs 2, 5), is much narrower still than any specimens of *M. elliptica* that I have seen, and appears to be the single specimen that I know of representing yet another species. The third record is from the Miocene of Trinidad by Maury (1925: 218), but again this is an incomplete, not certainly identified specimen.

Malea goliath Pilsbry & Johnson, 1917
Pl. 73, Figs 1-4; Pl. 75, Figs 1-2, 5

Malea goliath Pilsbry & Johnson, 1917: 170; Pilsbry, 1922: 363, pl. 29, figs 1, 9.

Remarks.—*Malea goliath* is used here in the original sense of Pilsbry & Johnson (1917), for a very large species (for fossil *Malea* specimens, at least, up to *ca.* 170 mm H), with very wide, flat-topped spiral cords separated only by very narrow grooves, with only low, wide knobs on the central and basal columella, bearing 3-4 of the same prominent, wide transverse ridges as all the rest of the inner lip, and with a relatively wide, flat-faced, strongly ridged outer lip, separated from the rest of the shell surface by a deep inward fold in the shell wall as in *M. ringens*, rather than the rather shallower and narrower groove seen in *M. camura*, *M. elliptica*, and *M. densecostata*. Woodring (1928: 312) speculated that *M. goliath* might have been based on adult specimens of *M. camura*, but three specimens collected in one sample from the Early Pliocene rocks of Cayo Agua, Bocas del Toro Basin, Atlantic Panama, by Antoine Heitz (NMB) demonstrate that the species characters hold true at other localities and *M. goliath* is not limited to the Dominican Republic. It is therefore probable that this is a distinct, if rare, species. The spiral sculpture of low, wide bands is in fact much more like that of *M. elliptica* than of *M. camura*. *Malea camura* seems to be adult at *ca.* 70-80 mm H, and the shape, the sculpture of high but widely separated spiral cords, and the relatively narrow outer lip indicate that it is closely related to the small living species *M. pomum* rather than to *M. goliath* and *M. ringens*.

Six small specimens (*i.e.*, approximately the size of normal adult *Malea camura*) from the Gurabo Fm (Late Miocene) in the Río Gurabo, Dominican Republic, collected by Bernard Landau, are most unusually wide, and tentatively are assigned to *M. goliath*. Their subspherical shape is markedly wider than that of any specimens assigned here to either *M. camura* or *M. elliptica*. They have sculpture of low, wide, closely spaced, strap-like spiral cords, of which two or three cords are much narrower than the others on the sutural ramp, and they have a low, wide, mid-columellar knob, bearing three ridges on some specimens and four on the others. The basal columellar knob bears two or three prominent, narrow ridges, the neighboring area of the inner lip is coarsely rugose, with several short, irregular, anastomosing transverse ridges, and the thick, smooth callus pad stops well below the shoulder, despite the low, wide shape of the shells. Several incomplete specimens in PRI loc. 196, Maury's (1917a) collection from "bluff 3, Cercado de Mao," Dominican Republic, are conspecific with these more complete specimens. These specimens indicate that (a) several other, incomplete specimens in the NMB and TU collections are probably conspecific, as shown by their low spires and the narrow cords on the sutural ramp, and (b) there are three possible scenarios for the interpretation of *M. goliath*.

The interpretation adopted here is that the wide specimens collected by Bernard Landau are referable to *Malea goliath*, as are the large specimens from NMB 18374, Cayo Agua,

Panama. This is then a relatively long-ranging, widespread, variable species. The relatively small specimens from the Dominican Republic have the apertural face of the terminal varix sloping inward toward the aperture [as was pointed out by Pilsbry (1922: 363) for *M. camura*], whereas the Panama specimens have a flat apertural face, as in Recent specimens and in the other fossil specimens assigned here to *M. ringens*. The second possible interpretation is, therefore, that all of the Dominican Republic large and small specimens belong to *M. goliath*, and that the Panama specimens are an unusually coarsely sculptured form of *M. ringens*. The third possible and quite likely interpretation is that the largest specimens from both the Dominican Republic and Panama are the real *M. goliath*, and the smaller, subspherical specimens collected by Bernard Landau represent yet another, unnamed species. The material available at present is insufficient to distinguish between these three possibilities, and so the simplest of them is adopted.

Dimensions.—Holotype: H 129, D 107 mm (Pilsbry & Johnson, 1911: 170); 2 figured specimens, NMB H 18034-18035, from NMB 18374, Cayo Agua, Bocas del Toro Basin, Panama, Early Pliocene: H 102.6, D 82.2 mm; H 171, D 145 mm.

Types.—*Malea goliath*, holotype ANSP.IP 2592, from the Dominican Republic, not otherwise localized, ex Gabb collection.

Other material examined.—**Fossils: Atlantic Panama: Pliocene:** Cayo Agua Fm: NMB 18374, E side Punta Norte, Cayo Agua (3, 1 very large, others medium; 2 illustrated, NMB H 18034-18035; Pl. 73, Figs 1-4); 18733, 1 km SE of Punta de Tiburón, Cayo Agua (1 moderate-sized, with wide, flat cords and narrow interspaces). **Dominican Republic: Late Early Miocene:** Baitoa Fm: NMB 17281 (1). **Late Miocene/Early Pliocene:** Gurabo Fm: NMB 15870 (3 frags); 15871 (2). **Early Pliocene:** Gurabo Fm: NMB 15865 (4); 16808 (3 frags); PRI, Maury's collection from "zone J, Río Gurabo" (1 large frag, 107.6 mm x 88.4 mm, from a shell originally ca. 130 mm H, but apparently *not* the one mentioned by Maury (1917a: 277) from "Zone I, Río Cana at Caimito," which she stated was 110 mm in diameter); TU 1215, Gurabo Fm, Río Gurabo, collection of Bernard Landau (6, 1 illustrated, Pl. 75, Figs 1-2, 5).

Distribution.—*Malea goliath* is recorded only as relatively few specimens from the Dominican Republic (late Early Miocene to Early Pliocene) and four specimens from Cayo Agua, Atlantic Panama (Pliocene).

Malea mareana Weisbord, 1962

?*Dolium galea*. Tuomey & Holmes, 1856 (in 1855-1857): 139 (in part; not pl. 28, fig. 11).

Malea ringens mareana Weisbord, 1962: 272, pl. 24, figs 1-2.

Malea densecostata. Olsson & Petit, 1964: 554, pl. 79, fig. 5; Petuch, 1989: fig. 4; 1992: 108, fig. 3M (not *M. ringens densecostata* Rutsch, 1934).

Malea cf. *densecostata*. Petuch, 1994: pl. 35, fig. G (not *M. ringens densecostata* Rutsch, 1934).

?*Malea* cf. *densecostata*. Campbell & Campbell, 1995: 82, pl. 4, figs 5-6.

Remarks.—Very few specimens are known so far that seem to belong in *Malea mareana*. The holotype is most unusual in having low, regularly alternating wide and narrow cords over the upper half of the last whorl and on the spire, with only very narrow grooves between the cords. Unfortunately, the very extensive collections from the Mare Fm at Cabo Blanco made by Win & Jack Gibson-Smith contain only one fragment attributed to *M. mareana*, and do not help knowledge of the species. This apparently is a rare species.

The specimen from the Pinecrest Fm (middle Pliocene) at Indian Prairie Levee, Florida, illustrated by Olsson & Petit (1964: 554, pl. 79, figs 5-5a; repeated by Petuch, 1989: fig. 4; 1994: pl. 35, fig. G) and a juvenile specimen from Bird Road, Miami, illustrated by Petuch (1992: 108, fig. 3M) agree with the spiral sculpture of *Malea mareana*, are similar in age, and seems to be conspecific with *M. mareana*. Certainly, they are not *M. densecostata*, which differs strongly in having uniform, low, narrow, closely spaced spiral cords. *Malea springi* and what is apparently *M. mareana* in the late Pliocene and early Pleistocene of Florida demonstrate that *Malea* was still surprisingly diverse in the Atlantic well after the traditional time of closure of the Panama seaway. I am grateful to Lyle Campbell and Dick Petit (pers. comm., 11 September 2008) for pointing out that Campbell & Campbell (1996: 82) discussed several internal molds of *Malea* from the Goose Creek Limestone (Early Pliocene) of South Carolina. They illustrated one in the Charleston Museum from Fetteressa (locality details by Campbell & Campbell, 1996, Appendix 1: 91, loc. 14) and listed "a small population of internal molds" from the Mason Dixon pit, near Conway, South Carolina (Campbell & Campbell, 1996, Appendix 1: 94, loc. 69). They followed Olsson & Petit (1964) and Petuch (1994) in identifying the molds as *M. cf. densecostata* but, like Florida material, in my opinion they are more likely to be related to *M. mareana*. Only better knowledge of the exterior sculpture will help identification of the elongate-oval Goose Creek Limestone specimens. Campbell & Campbell (1996: 82) pointed out that this is probably the same taxon as that recorded by Tuomey & Holmes (1856 in 1855-1857: 139) as "*Dolium galea*," from "the marl of Goose Creek" at "Smiths," although they suggested that the specimen illustrated by Tuomey & Holmes (1856 in 1855-1857: pl. 28, fig. 11) is actually an internal mold of a species of *Ficus*.

Dimensions.—Holotype: H 46.5, D 36.2 mm.

Types.—*Malea ringens mareana*, holotype PRI 26184, from Weisbord's loc. I258a, W bank Quebrada Mare Abajo, Lower Mare Fm (Late Pliocene), Cabo Blanco, Venezuela.

Other material examined.—**Fossils: Venezuela: Late Pliocene:** NMB 17512, Mare Fm, type locality, Cabo Blanco, Venezuela, coll. J. & W. Gibson-Smith (1 frag).

Distribution.—*Malea mareana* is recorded only from the type locality, Mare Fm (Late Pliocene) at Cabo Blanco, northern Venezuela, but as noted above, records of *M. densecostata* from the Late Pliocene-Early Pleistocene of Florida, USA, are based upon specimens of *M. mareana*. Little is known of the time and geographical range of this species.

***Malea ringens* (Swainson, 1822)**

Pl. 74, Figs 5, 7; Pl. 75, Figs 3, 4

Cassis ringens Swainson, 1822, appendix: 4; 1840: 35; G. B. Sowerby I, 1825, appendix: 21.

Dolium dentatum Barnes, 1824: 135, pl. 9, fig. 3; Menke, 1850: 182; Winckworth & Tomlin, 1933: 209; Bayer, 1937: 30.

Dolium personatum Menke, 1828: 35; 1830: 62; 1846: 138.

Buccinum ringens. Wood, 1828: 11, pl. 4, fig. 1.

Malea latilabris Valenciennes, 1832: 325; Chenu, 1859: 211, fig. 1147.

Malea crassilabris Valenciennes, 1832: 327.

Dolium latilabre. Kiener, 1835: 14, pl. 4, fig. 7.

Dolium plicosum Menke, 1846: 138 (in synonymy of *Malea crassilabris* Valenciennes); 1850: 182 (in synonymy of *D. crassilabre* "Menke", i.e., Valenciennes).

Dolium ringens. Reeve, 1848c: pl. 4, fig. 5; Küster, 1857: 76, pl. 64, fig. 1; Tryon, 1885: 265, pl. 4, fig. 27.

Malea ringens. Conrad, 1857: 72, pl. 5, fig. 22; Chenu, 1859: 211, fig. 1148; Dall, 1909a: 227; Hanna, 1926: 450; Anderson, 1929: 140; Grant & Gale, 1931: 741; Jordan, 1936: 114; Pilsbry & Olsson, 1941: 41; 1964: 167, pl. 31, fig. 1; Turner, 1948: 176, pl. 80; Durham, 1950: 116, pl. 34, fig. 1; Keen, 1958: 338, fig. 311; 1971: 499, fig. 942; Emerson & Old, 1963b: 12, fig. 9; Cosel, 1984: 219; Finet, 1991: 270; Kaiser, 1997: 32; 2007: 38; Hickman & Finet, 1999: 68, fig. 58; Beu, 2001: 712; López de la Fuente & Ramos, 2004: 84; Vos, 2007: 30, text-figs 8-9, pl. 6, figs 1a-3b.

Dolium (Malea) dentatum. Mörch, 1860: 83; Kobelt, 1875: 265.

Dolium (Malea) ringens. Mörch, 1860: 83; Kobelt, 1875: 266; Stearns, 1894: 189.

?*Malea* sp. Nelson, 1870: 196.

Dolium (Malea) sp. Toulou, 1911: 500, pl. 30, fig. 7.

Malea camura. Brown & Pilsbry, 1911: 356; Woodring, 1959: 208, pl. 33, figs 1-4; Aguilar, appendix in Seyfried *et al.*, 1985: 64 (not *M. camura* Guppy, 1866).

Dolium (Malea) camura. Spieker, 1922: 52 (not *M. camura* Guppy, 1866).

Tonna (Malea) ringens. Kiliyas, 1962: 17, fig. 14.

?*Malea elliptica*. Aguilar & Denyer, 1994: 63, pl. 1, fig. 10 (not *M. elliptica* Pilsbry & Johnson, 1917).

Remarks.—*Malea ringens* is much the largest of *Malea* species, reaching 270 mm H (Vos, 2007: 30) but most of the fossil specimens are much smaller than this, reaching *ca.* 100 mm at the most. The species is recognized easily by its (a) low spire, (b) subspherical last whorl, (c) high, widely spaced, but rather vaguely defined spiral cords, with rounded edges merging gradually into the concave interspaces that each are approximately the same width as one cord, or only a little narrower, (d) wide, almost completely smooth inner lip callus pad, which is raised into a thin, wide collar over the neck of the previous whorl on large specimens, (e) the mid-columellar knob being low and bearing only two or, in a few specimens, three prominent transverse ridges, (f) the basal columellar knob being considerably more prominent than the upper one and bearing at least three very prominent transverse ridges, and (g) the outer lip being very strongly bent inward to form the terminal varix, then bent back out again to produce an enormous, wide, flat, strongly transversely ridged adapertural variceal face, up to 40 mm wide or more in large specimens. Fossils are abundant in the Pliocene rocks of both Atlantic and Pacific Panama, but although it has been reported quite widely from a variety of other localities, it is difficult to judge from literature records whether the species was correctly identified.

Dimensions.—Figured specimen, NMB H 18036, from NMB 18306, Panama, Pleistocene: H 70.1, D 57.3 mm; lectotype of *Cassis ringens*: H 52.2, D 39.2 mm; holotype of *Malea crassilabris*: H 54.2, D 42.7 mm; holotype of *M. latilabris*: H 136, D 101 mm; apparent syntype of *Dolium plicosum*: H 50.5, D 40.0 mm. Vos (2007: 30) stated that the world record height is 270 mm

Types.—*Cassis ringens*, "probable syntype" BMNH 1837.12.1.2718 (Pl. 75, Figs 3-4), a small specimen from the Bligh collection (Bligh sale catalog lot no. 393) and the Broderip collection, without locality; the type locality is here designated as Acapulco, Mexico. In the absence of any other type material, and because the appendix to the Bligh catalog describing new species was prepared by Swainson, this specimen is accepted as a syntype and is designated here as the lectotype of *Cassis ringens*. *Dolium dentatum* Barnes, 1824, location of any original material not known to me; Green (1830: 131) pointed out of *D. dentatum* that "Mr. Swainson, of London, seems first to have noticed it under the name of *D. ringens*." Dance (1966: 294) recorded that Menke's material was "purchased by M. J. Landauer and dispersed," but part of Menke's collection recently was acquired by SMF, within the H. G. Bronn collection (of Recent shells; most or all of Bronn's fossils were acquired by Louis Agassiz and are at the Department of Geology, Museum of Comparative Zoology, Harvard University), and some *Tonna* types are present, including 2

syntypes of *Tonna costata* (Menke, 1828) (= *T. allium* Dillwyn, 1817) (SMF 314411/2, with two localities: "Cape of Good Hope, F. Krauss, 1840" and "Java, ex Winter, 1836"). One specimen is labelled *D. plicosum*, "Peru, identified and written by the author, 1851"; this specimen from Bronn's collection is a small specimen of *M. ringens*, and is assumed to be the remaining syntype of *D. plicosum*. However, no type material is present of *D. personatum*. *Malea crassilabris*, holotype MNHN, from "Acapulco," a typical small specimen of *M. ringens* with the spire apex missing. A moderately large specimen (H 136, D 101 mm) with a wide adult outer lip was recognized by me in the Valenciennes collection, MNHN, during July 2007, still attached to a thin wooden tablet, bearing the label on the back "Dolium no. 12. Cervantes, Acapulco écrit par Bonpland 1801. *Malea latilabris* Val. Recueil v. 6. zool. II page," and a second label reading "*Buccinum ringens* British Museum Woods [illegible] suppl." This specimen is apparently the holotype of *M. latilabris*.

Other material examined.—**Fossils: California: Pliocene:** Latrania Fm (Demere & Rugh, 2006; formerly Imperial Fm), loc. 19, Alverson Canyon, Coyote Mountains, Imperial Co, C. H. Sternberg collection (BMNH Palaeontology Department G37701-2, 2 poor molds). **Western Mexico: Late Middle Pleistocene:** uplifted terrace, oxygen isotope stage 5e, Bahia de Santa Inés, near Mulegé, Baja California Sur, collection of Bernard Landau (1 large). **Pacific Costa Rica: Late Miocene:** NMB 17760, Punta Judas (1 large, cf.). **Pliocene:** NMB 18035 (1); 18042 (2). **Pleistocene:** NMB 17746 (2); 17799 (2, cf.); Charco Azul Group, Armuelles Fm, Quebrada el Higo, Burica Peninsula, collection of Bernard Landau (2); Montezuma Fm, Playa Cocalito, Nicoya Peninsula, collection of Bernard Landau (1). **Atlantic Panama: Miocene:** Gatun Fm: NMB 17637 (12); 17643 (10); 17644 (5); 17649 (3, cf.); 17868 (4); 17871 (5, cf.); 18261 (3); 18322 (12); 18325 (5); 18391 (1); 18662 (3); 18667 (1); "in some shelly beds on the eastern side of the Isthmus of Panama, about 2½ miles [4 km] from the shores of Navy Bay, ... about 15 feet [5 m] above the Atlantic, in a cutting of the Panama Railway," coll. J. T. Green, pres. G. H. Saunders (BMNH Palaeontology Department, GG5408, 1); lower Gatun Fm (Middle Miocene), bed 1 of Todd, quarry floor, Los Lomos Suites, Cativa, Colon (BMNH Palaeontology Department, GG22610-22613, 22617-22619; 7); lower Gatun Fm (Middle Miocene), bed 2 of Todd, quarry floor, Los Lomos Suites, Cativa, Colon (BMNH Palaeontology Department, GG22620-1, 2 poor); lower Gatun Fm (Middle Miocene), bed 3 of Todd, quarry floor, Los Lomos Suites, Cativa, Colon (BMNH Palaeontology Department, GG22622, 1 poor); lower Gatun Fm (Middle Miocene), bed 6 of Todd, quarry floor, Los Lomos Suites, Cativa, Colon (BMNH Palaeontology Department, GG 22614-22616, 3); lower Gatun Fm (Middle Miocene), beds 3-5 of

Gale & Todd, "Sand Dollar Hill," Sabanita, Colon (BMNH Palaeontology Department, GG 22623, 1 poor); lower Gatun Fm (Middle Miocene), beds 2-15 undivided, *ex situ*, "Sand Dollar Hill," Sabanita, Colon (BMNH Palaeontology Department, GG22625-6, 2 poor); stratigraphically lower than last (BMNH Palaeontology Department, GG22624, 1 poor); Gatun, Panama-Kanal (NHMV 1933/18/210-211, the 2 specimens reported by Toulou, 1911: pl. 30, fig. 7); Gatun Fm (Late Miocene), TU 961, Cativa, Colon, collection of Bernard Landau (2); Valiente Fm: NMB 18375 (1); 18711 (1). **Pliocene:** Escudo de Veraguas Fm: NMB 17622 (1); Cayo Agua Fm: NMB 17831 (5); 17862 (1); 17904 (2); 18373 (4); 18377 (1); 18378 (1); 18380 (1); 18719 (2); 18721 (1); 18730 (2); 18731 (1); 18736 (1); Shark Hole Point Fm: NMB 18387 (1); 18716 (1); 18976 (1). **Pacific Panama: Pleistocene:** NMB 17442 (1); 18066 (3, cf.); 18306 (1; illustrated, NMB H 18036; Pl. 75, Figs 5, 7). **Panama, Darien: Late Miocene:** NMB 18495 (1); 18501 (18); 18504 (2); 18516 (1); 18517 (5); 18522 (1); 18526 (1); 18527 (3); 18533 (1); 18534 (5); 18535 (2); 18657 (1). **Ecuador: Late Miocene:** NMB 19078 (3 incomplete); 19125 (5 poor); 19126 (2 poor). **Pliocene:** NMB 19146 (1 large apertural frag); 19153 (1 good). Olsson (1964: 167) also illustrated a specimen from the Onzole Fm (Pliocene) at Punta Gorda, Esmeraldas Province. **Pleistocene:** 10 m above sea, Punta Santa Elena, "associated with *Megatherium*" (BMNH Palaeontology Department G20542, 2 outer lip frags).

In addition, Emerson & Old (1963b) pointed out that *Malea ringens* has been recorded from the following localities: Latrania Fm (Demere & Rugh, 2006; formerly Imperial Fm) (Late Miocene/Early Pliocene), Coyote Mountain, Imperial Co, California (Hanna, 1926; Powell, 1988: table; "occurs rather abundantly" in Latrania (= Imperial) Fm, especially near Alverson Canyon; Grant & Gale, 1931: 741), Pliocene, Arroyo de Gua, near Loreto, E side of Baja California Sur (Durham, 1950), Pleistocene, Bahia Magdalena, W coast of Baja California Sur (Jordan, 1936), Pleistocene, Carmen Island, off the Gulf coast of Baja California Sur (Durham, 1950), and Colotepec Fm (Pleistocene), 16 km W of mouth of Río Colotepec, E coast of Oaxaca, Mexico (Palmer & Hertlein, 1936: 68). Garcia-Talavera (1993: 12, 33) recorded fossil specimens from the Holocene Brattle locality, Puerto Villamil, Isabela Island, and from Pleistocene localities on Santa Fe Island, in the Galápagos Islands. Other fossil specimens have been recorded from the Pliocene of NW Ecuador by Olsson (1964: 167, pl. 31, fig. 1), and probably the specimens from the Pliocene of the Río Banáño, Atlantic Costa Rica, from Bocas del Toro Basin, and from Red Cliff Creek, recorded by Olsson (1922: 139, pl. 12, fig. 2) are all *M. ringens*, because the illustrated specimen identified as *M. elliptica* is much too short and wide to be that species. Also, specimens from the

Gatun Fm (Late Miocene-Early Pliocene) of Panama identified by Woodring (1959) as *M. camura* clearly are *M. ringens*, as was also realized by Olsson (1964: 167).

A record from the latest Pliocene-Early Pleistocene (2.1–1.5 Ma) of Limón, Atlantic Costa Rica, as *Malea elliptica*, by Aguilar & Denyer (1994: 63, pl. 1, fig. 10), represents the one record of *Malea* of which I am aware from Limón. It is much shorter and wider than *M. elliptica* and much more nearly resembles *M. ringens*, but the single incomplete specimen is not certainly identifiable. Whichever species this represents, it is a biogeographically important record.

Distribution.—*Malea ringens* lives now from Puerto Penasco, Gulf of California, Mexico, south to Paita, Peru (Keen, 1971), and south to Isla Lobos de Afuera, Peru (Peña, 1970; Skoglund, 1992) including the Galápagos Islands (Finet, 1985; Hickman & Finet, 1999), Clipperton Island (Kaiser, 2007), and Isla Gorgona, Colombia (Cantera *et al.*, 1979; Cosel, 1984; Skoglund, 1992). Colored illustrations, including a large Galápagos specimen, are provided on a web page (<http://www.femorale.com.br/shellphotos>, last accessed 28 April 2006). Late Miocene to Pleistocene fossils are recorded as far north as Coyote Mountain, Imperial Co, California, USA, throughout the Gulf of California, Pacific coastal Costa Rica, and Panama, in Darien and as far south as the Onzole Fm in northwestern Ecuador. Most interestingly for Panamic biogeography, specimens of *M. ringens* are abundant also in Pliocene rocks in the Atlantic coastal area of Panama, and a single specimen is recorded from the Pliocene-Pleistocene boundary interval at Limón, Atlantic Costa Rica.

Malea springi Petuch, 1989

Malea springi Petuch, 1989: 94, figs 1–2; 1994: 112, pl. 35, figs A–B, F; 2004: pl. 81, fig. G.

Malea petiti. Petuch, 2004: pl. 87, fig. A [not *M. petiti* Petuch, 1989, = *Tonna galea* (Linnaeus, 1758)].

Remarks.—The large, unusually finely sculptured species *Malea springi* is very distinctive. It reaches a large size, but has a markedly narrower terminal varix than *M. ringens* at the same size. Most specimens are a little taller and narrower in shape than *M. ringens*, and the anterior siphonal canal is a little longer and more obvious than in most other *Malea* species. The most distinctive character is its fine sculpture of many low, narrow, closely spaced spiral cords, 26 on the last whorl of the holotype, separated only by narrow grooves, or by a single narrow secondary cord over the upper part of the last whorl and on the sutural ramp of the spire whorls. The inner lip callus is thick, and spreads well to the left of the aperture on some specimens (Petuch, 1994: pl. 35, fig. F). The upper callus nodule on the inner lip is large, and bears 3 or 4 prominent transverse ridges,

whereas the lower nodule protrudes well into the aperture but is weakly ridged; the resulting columellar embayment is deep and U-shaped. The spire is a little taller than on most other *Malea* species, so that the top of the aperture rides up only to the base of the rounded shoulder of the previous whorl, and 7–9 narrow spiral cords are revealed on spire whorls.

Dimensions.—Holotype: H 189, D 130 mm; paratypes: H 178, 170, and 156 mm (Petit, 1989: 94).

Types.—Holotype UF 21455, from uppermost Caloosahatchee Fm (Ayers Landing Member?), latest Pliocene or, possibly, earliest Pleistocene, dredged from 20 m depth in Miami Canal, due W of Talisman Sugar Refinery, 10 km N of Broward-Palm Beach Levee, SW Palm Beach Co, Florida; 3 paratypes from same locality, one ANSP.IP 1133, one Spring collection, one Petuch collection (Petuch, 1989: 94) (none seen). I have not seen material of *Malea springi*.

Distribution.—Petuch (1994: 112, pl. 35, fig. F) later illustrated a further good specimen of *Malea springi* from what is apparently the type locality, “Miami Canal dig, Lake Harbor, Palm Beach Co,” Florida. Further specimens of what seems to be typical *M. springi* were also illustrated by Petuch as both *M. springi* (Petuch, 2004: pl. 81, fig. G; Fort Denaud Member of Caloosahatchee Fm, latest Pliocene) and *M. petiti* (Petuch, 2004: pl. 87, fig. A; Holey Land Member of Bermont Fm, early Pleistocene). *Malea springi* therefore seems to occur in late Pliocene-Early Pleistocene formations of southern Florida, but its range is poorly known as yet [Caloosahatchee Fm is latest Pliocene according to Zullo (1992: fig. 1) and Vermeij (2005: 628), but Early Pleistocene according to Ward (1992: fig. 1); Bermont Fm is accepted as Early Pleistocene; Vermeij, 2005: 628]. A Pleistocene occurrence of *Malea* in Florida helps the concept of faunal connections through the CAI remaining open until Early Pleistocene time, although of course *M. springi* belongs to a clade distinct from that of the eastern Pacific species *M. ringens*.

Malea n. sp. A

Pl. 77, Figs 3–4

Remarks.—A single small *Malea* specimen from the Cantaure Fm in northern Venezuela is the sole record from this locality, and one of the earliest records from tropical America, although the few specimens of *M. elliptica* that I have seen from the Baitoa Fm (late Early Miocene) in the Dominican Republic are coeval. The Cantaure specimen is remarkable for its adult appearance, with a strongly callused aperture, at a very small size. It is also unique among the *Malea* material examined here in having one or two obvious but narrow spiral threads in each primary spiral interspace, in having many low, narrow, sharply defined, rather widely spaced axial ridges over the entire teleoconch surface (as in *Eudolium*, Marshall 1992;

as in *Tonna galea*, Pl. 76, Fig. 5) and in having a well-defined parietal ridge, very prominent over the uppermost (most posterior) spiral cords on the inner lip callus pad, and visible as an angling ridge on the next three cords below that. From a single specimen, it is impossible to tell whether this is an aberrant individual of a species resembling *M. camura* or, as seems more likely, it represents an unnamed species. More, larger specimens are required to determine the status of this specimen, but *Malea* is obviously rare at Cantaure because there are no specimens in the large Gibson-Smith collection from there.

Dimensions.—H 36.8, D 26.7 mm.

Material examined.—**Fossils: Late Early Miocene:** Cantaure: Lower (main) shellbed (= NMB 17016), near Casa Cantaure, Paraguaná Peninsula, Estado Falcón, N Venezuela, collection of Bernard Landau (1 small; Pl. 77, Figs 3-4).

Malea n. sp. B
Pl. 77, Fig. 2

Remarks.—Three specimens from the Cubagua Fm on Cubagua Island represent another unnamed species of *Malea*. Again, they are the only specimens that I have examined from this locality and formation in all collections. The smallest, complete specimen (illustrated here) has an obviously immature appearance, with a very weakly callused aperture and, in particular, a narrowly out-turned, only weakly ridged outer lip, and only a little callus on the inner lip and columella. A low, smooth callous pad is present on the outer (left) part of the inner lip above the unusually deep columellar embayment, and about 10 high transverse ridges are present on the inner lip in the embayment and on the upper (posterior) part of the anterior siphonal canal, but the transverse ridges are not elevated on raised callous pads. It is also unique among *Malea* material that I have examined in its very wide, subspherical shape, with a wide, strongly convex last whorl and a low spire, even more extremely near-spherical than Recent juvenile material of *M. ringens*. The spiral sculpture is also unique, with numerous narrow, rather weakly defined spiral cords with convex crests separated by interspaces, each only a little narrower than one cord. On the uncorroded areas on the base and behind the outer lip, the spiral cords are seen to be sharply defined, with slightly flatter crests and low but more clearly vertical sides than on the corroded areas of the shell. The numerous narrow cords are similar to those of *M. densecostata* from the nearby Pliocene Punta Gavilán Fm in mainland northern Venezuela, but the cords are lower, wider, and much more closely spaced and the teleoconch is markedly taller and narrower in *M. densecostata* than in the smallest Cubagua specimen. By this size, juvenile specimens of *M. ringens* have already developed the deep outer lip fold that permits growth of the wide ventral

plate of the outer lip in adults, whereas the Cubagua specimen has only a narrowly thickened aperture. It also has some similarity to the poorly known *M. goliath*, and to the Florida Pleistocene species *M. springi*. *Malea springi* is similar in its relatively narrow outer lip and numerous, narrow spiral cords, but again is significantly taller and narrower than the smallest Cubagua specimen. The two larger specimens show that this species is still more nearly similar to *M. springi* than the low-spined juvenile would suggest, because they are still taller-spined than *M. springi*, and have a very similar, relatively narrow outer lip and similar relatively narrow, *i.e.*, sharply defined, well-raised callous areas on the inner lip, but differ from *M. springi* in their fewer, much more widely spaced spiral cords. There is little doubt that the Cubagua *Malea* is an unnamed species closely related phylogenetically to *M. springi*.

Dimensions.—Smallest, complete specimen: H 48.9, D 39.5 mm.

Material examined.—**Fossils: Early Pliocene:** Cerro Negro Member, Cugabua Fm, Cañon de las Calderas, Cubagua Island, collection of Bernard Landau (1 complete juvenile, Pl. 77, Fig. 2, and 2 incomplete large shells).

Genus *TONNA* Brönnich, 1772

Tonna Brönnich, 1772: 248. No included species. Type species (by subsequent designation, Suter, 1913: 314, and ICZN Opinion 237, 1954: 347): *Buccinum galea* Linnaeus, 1758, Late Miocene to Recent, Mediterranean and E & W Atlantic (*Tonna* was placed on the Official List of Generic Names in Zoology in ICZN Opinion 237, 1954).

Cadus Röding, 1798: 150. Type species (by subsequent designation, Woodring, 1959: 310): *Buccinum perdx* Linnaeus, 1758, Recent, Indo-West Pacific.

Dolium Lamarck, 1801: 79. Type species (by monotypy): *Buccinum galea* Linnaeus, 1758.

Cadium Link, 1807: 113. Type species (by subsequent designation, Woodring, 1928: 310): *Cadium perdx* Link, 1807 (= *Buccinum perdx* Linnaeus, 1758).

Perdx Montfort, 1810: 447. Type species (by original designation): *P. reticulatus* Montfort, 1810 (= *Buccinum perdx* Linnaeus, 1758) (junior homonym of *Perdx* Brisson, 1760).

Macgillivrayia Forbes, 1852a: 77; 1852b: 383, pl. 3, figs 8a-d. Type species (by monotypy): *M. pelagica* Forbes, 1852 (as *Macgillivrayia* in Forbes, 1852b; = *Tonna* sp., planktotrophic larva).

Galea Mörch, 1853: 110 (in synonymy of *Dolium* Lamarck, 1801).

Simplidolium Sacco, 1891: 237. Type species (by monotypy): *Pyrula fasciata* Borson, 1821, Miocene and Pliocene, Italy. The lectotype of *P. fasciata* (Pavia, 1976: text-fig. 1, pl. 1, figs 9a-b) was considered by Bouchet & Warén (1993: 797) to be “a young *Tonna*”; in my opinion, it is a juvenile specimen of the sole Mediterranean species, *T. galea* (see also Landau *et al.*, 2004: 38-39).

Foratidolium Rovereto, 1899: 107. Replacement name for *Perdx* Montfort, 1810, not of Brisson, 1760.

Parvitonna Iredale, 1931: 216. Type species (by original designation, Iredale, 1931: 232): *P. perselecta* Iredale, 1931 (= *Tonna cumingii* Reeve, 1849, according to Winckworth & Tomlin, 1933: 211; Vos, 2007: 79), western Pacific.

Remarks.—*Tonna* has the simplest shell of the Tonnidae, with the aperture so little callused or armored in most species that the base of the inner lip coils around onto the siphonal fasciole to produce a deep, narrow false umbilicus, and in most species the outer lip remains unthickened even at an enormous size, although in some species the lip is narrowly but definitely reflected and a narrow, weakly to quite prominently dentate thickening on the interior of the outer lip produces a definite terminal varix (e.g., *Tonna sulcosa* (Born, 1778); Vos, 2007: pl. 15; *T. tessellata* (Lamarck, 1816); Vos, 2007: pl. 12). The thin, spirally folded shell is surprisingly strong for its size and thickness, because it is strengthened by the folds. The inner lip is a thin, smooth glaze in all species, although forming a narrow free collar over the neck of the previous whorl in a few species. The sculpture is entirely of low, wide spiral cords, with essentially no axial sculpture, apart from very fine, closely spaced ridges. The relatively enormous protoconch, ca. 4.5–6 mm in diameter, is low-turbiniiform in shape, glassy, and semitransparent in fresh Recent material but opaque in fossils, and remaining intact on most quite large fossil specimens. The larval shell is large enough that several workers over the years have regarded it as a separate genus quite unrelated to *Tonna*, and Forbes (1852a, b) provided it with its own generic name, *Macgillivraya*. *Tonna* is of very low diversity in the Atlantic, and only the two living Atlantic species recorded by Turner (1948) occur as fossils in the study area. *Tonna* also has a very poor fossil record in general, with no pre-Miocene records to my knowledge, and so it is somewhat surprising to find that both Atlantic species have a record from Miocene time onward, although both are very uncommon fossils in the study area. I agree with Winckworth & Tomlin (1933), Turner (1948), and Vos (2007) that *Cadus* Röding, 1798, and *Parvitonna* Iredale, 1931, are synonyms of *Tonna*.

All *Tonna* and *Eudolium* species feed by ingesting entire, large holothurians (Mifsud, 1974; Kropp, 1982; Hughes, 1985; Morton, 1991; Marshall, 1992; Beu, 1998a: 803; Vos, 2007), pulling them into the lumen of the large, unusually wide proboscis with the hooked jaws and strongly interlocked rows of radular teeth, and digesting them whole. This presumably accounts for the very widely inflated shells of members of these genera. The feeding habits of Recent *Malea* species have not been described to my knowledge. Petuch (2004: 236) claimed that *Malea* species prey upon cidaroid echinoids, but it seems likely that this is an assumption based on the predation of echinoids by *Cassis*, and that *Malea* also ingests entire holothurians. The anatomy of the digestive system of the Mediterranean-Atlantic species *T. galea* was described

by Weber (1927), and more recently Simone (1995) has described the anatomy of both of the Atlantic species of *Tonna* in some detail. These therefore are unusually well known for tonnoideans. Excellent colored illustrations of both Atlantic species are provided on a webpage (<http://www.femorale.com.br/shellphotos>, last accessed 28 April 2006).

Tonna galea (Linnaeus, 1758)

Pl. 76, Figs 3–7; Pl. 77, Fig. 1

- Buccinum galea* Linnaeus, 1758: 734; 1767: 1197; Born, 1778: 228; Bruguière, 1789: 255; Gmelin, 1791: 3469; Dillwyn, 1817: 582.
- Buccinum olearium* Linnaeus, 1758: 734; 1767: 1196; Wood, 1825: pl. 22, fig. 1; Beu, 2005: 120.
- Cadus galea*. Röding, 1798: 150.
- Cadium galea*. Link, 1807: 114.
- Pyrula fasciata* Borson, 1821: 321, pl. 1, fig. 20; Pavia, 1976: text-fig. 1, pl. 1, figs 9a–b.
- Dolium galea*. Lamarck, 1822: 259; Risso, 1826b: 180; Kiener, 1835c: 7, pl. 2, fig. 2; Potiez & Michaud, 1838: 401; Deshayes, 1844: 139; Reeve, 1848c: pl. 1, fig. 1; Küster, 1857: 64, pl. 57, fig. 1; H. & A. Adams, 1858: 196; Chenu, 1859: 210, fig. 1144; Hanley, 1860: 487; Kobelt, 1875: 263; Tryon, 1885: 261, pl. 1, fig. 3; Dall, 1903b: 134.
- Dolium tenue* Menke, 1830: 143.
- Dolium sagrae* d'Orbigny, 1841a: 34, pl. 3, figs 4–5.
- Dolium crenulatum* Philippi, 1846: 148; 1849: *Dolium* pl. 1, fig. 1.
- Morio fasciata*. d'Orbigny, 1852: 177.
- Dolium antillarum* Mörch, 1877: 41.
- Dolium antillarum* var. *brasiliiana* (sic) Mörch, 1877: 42 (homonym of *D. perdix* var. *brasiliiana* Mörch, 1877: 43).
- Dolium galea*, with vars. *epidermata*, *spirintrorsum*, and *tardina* Gregorio, 1884: 114–115.
- Eudolium* (*Simplicodolium*) *fasciatum*. Sacco, 1891: 13, pl. 1, figs 19–22.
- Dolium* cf. *galea*. Böse, 1906: 87.
- Tonna galea*. Maury, 1922: 119; Winckworth & Tomlin, 1933: 210; Turner, 1948: 173, pl. 75, fig. 4, pl. 78, figs 1–2; Morretes, 1949: 93; Abbott, 1954: 199, pl. 23, fig. f; 1974: 168, fig. 1785; Perry & Schwengel, 1955: 150; Woodring, 1959: 210; Warmke & Abbott, 1961: 104; Weisbord, 1962: 274, pl. 24, figs 3–4; Kaufmann & Görting, 1970: 372, fig. 90; Andrews, 1971: 107, illus.; 1977: 129, illus.; Malatesta, 1974: 250; Humfrey, 1975: 130, pl. 11, fig. 5; van Regteren Altena, 1975: 39, pl. 6, fig. 10; Nordsieck & Garcia-Talavera, 1979: 122, pl. 26, fig. 6; Abbott & Dance, 1982: 118; Okutani, 1983: 265, illus.; H. & E. Vokes, 1983: 23, pl. 12, fig. 1; Bandel, 1984: 102, fig. 159, pl. 10, fig. 5; Bernard, 1984: 58, fig. 89; Rios, 1985: 70, pl. 25, fig. 312; 1994: 83, pl. 28, fig. 326; Matthews *et al.*, 1987: 31, figs 1–5; Calvo, 1987: fig. 71 (radula); de Jong & Coomans, 1988: 71; Diaz, 1990: 19; Lipe & Abbott, 1991: 8, illus.; Barash & Danin, 1992: 116; Diaz & Puyana, 1994: 168, fig. 625; Cachia *et al.*, 1996: 109, pl. 10, fig. 6; Giannuzzi-Savelli *et al.*, 1997: 204, figs 832–834; Guerreiro & Reiner, 2000: 91; Tolman, 2001: 7, 8,

illus.; Ardovini & Cossignani, 2004: 121, lower right fig., 122, upper left fig.; Vos, 2007: 62, text-figs 13-14, pls 21-27.

Tonna galea brasiliiana. Turner, 1948: 176, pl. 79, figs 1-2; Abbott, 1954: 199; 1974: 168; Kiliyas, 1962: 41, fig. 31b; Tolman, 2001: 8.

Tonna galea galea. Kiliyas, 1962: 36, fig. 31a; Macsotay & Campos Villaroel, 2001: 71, pl. 5, figs 1, 6.

Dolium (Dolium) galea. Priolo, 1964: 537 (with long synonymy).

Eudolium (Eudolium) fasciatum. Caprotti, 1970: 174, pl. 6, fig. 11.

Tonna (Tonna) galea. Rios, 1975: 74, pl. 20, fig. 301.

Malea petiti Petuch, 1989: 94, fig. 3; 1994: pl. 35, fig. E.

Eudolium fasciatum. Solsona, 1999: 73, figs 2-3, 16D-E; Chirli, 2007: 73, pl. 28, figs 1-6 (in part).

Tonna galea abbotti Macsotay & Campos Villaroel, 2001: 71, pl. 13, fig. 12.

Remarks.—*Tonna galea* is easily distinguished from *T. pennata* (Mörch, 1853) by its much larger size, its much more nearly spherical shape, with a shorter spire and much shorter and wider last whorl, and by its narrower and much more prominent spiral cords, with at least one narrow secondary spiral cord in each interspace; secondary cords are not present on *T. pennata*. As noted by Turner (1948), *T. pennata* is closely similar to the Indo-West Pacific elongate living species *T. per-dix* (Linnaeus, 1758), whereas *T. galea* is much more similar to the western Pacific species *T. zonata* (Green, 1830). The European literature on *T. galea* is very extensive, and Priolo (1964) provided a useful list of further synonyms. Pavia (1976: text-fig. 1) provided an excellent illustration (enlarged eight times) of the apical area of the lectotype of *Pyrula fasciata* (a juvenile specimen of *T. galea*), showing the protoconch (lacking the periostracum, obviously, in this fossil specimen) and early teleoconch whorls. The distinctive, narrow, well-raised, obvious axial ridges on early whorls of *Tonna* species (as on adult whorls of *Eudolium* species) are shown clearly in this illustration, as are the complex orders of spiral sculpture. The juvenile sculpture of *T. galea* is also shown here (Pl. 76, Figs 3-5, 7). Vos (2007) recently discussed and richly illustrated both *T. galea* and *T. pennata*.

Turner (1948) treated *Tonna galea brasiliiana* as a valid subspecies of *T. galea* limited to Brazil. However, Matthews *et al.* (1987: 35-37, fig. 5) demonstrated that both the normal and *brasiliiana* forms occur in Brazil, and that the *brasiliiana* form merely was based on large specimens of *T. galea*, in which the spire decreases in height as the shell grows.

Petuch (1989: 94) referred to the “fragmentary nature of the type material” of *Malea petiti*, which made it impossible to describe the outer lip, aperture, parietal shield, and columella. The spiral sculpture of the holotype, with very low, closely spaced, alternating wide and narrow cords, and the very low spire give this specimen very much the appearance of *Tonna galea*. Two specimens from the type locality of *M. petiti*, Griffin Brothers pit, Palm Beach/Broward Co line, Florida (Bermont

Fm, Early Pleistocene; collection of Bernard Landau), agree exactly with the holotype of *M. petiti* in sculpture, and have well-preserved apertures, demonstrating that they are *T. galea*. In my opinion, *M. petiti* simply was based on incomplete material of *T. galea*. Petuch (2004: pl. 87, fig. A) illustrated a true *Malea* species identified as *M. petiti*, from the Bermont Fm *Archohelia limonensis* community, but in my opinion this is a specimen of *M. springi*.

Dimensions.—Lectotype of *Buccinum galea*: H 155, D 132 mm; neotype of *Dolium antillarum brasilianum*: H 116, D 103 mm (Turner, 1948: 176); juvenile specimen illustrated by SEM, NMB H 18037, from NMB 16928, Dominican Republic: H 14.2, D 10.3 mm; trawled off Guiana, GNS WM17122: H 148.8, D 121.1 mm. Vos (2007: 63) stated that specimens reach 300 mm H.

Types.—*Buccinum galea*, “type figure” selected by Turner (1948: 174) as Gualtieri (1742: pl. 42, fig. A); I designated (Beu, 2005: 120) this specimen as the lectotype of *B. galea*. The lectotype is in the Museo di Storia Naturale e del Territorio, Università di Pisa, in the Certosa di Calci, outside of Pisa, Gualtieri collection no. 6. Turner (1948: 174) designated the type locality as Naples, Italy. The existence of the lectotype is fortunate, because the paralectotype in Linnaeus’ collection in London is a small specimen of *Tonna canaliculata* (Linnaeus, 1758). I also designated (Beu, 2005: 120) the smaller of the two syntypes of *B. olearium* present in Linnaeus’ collection in London, marked “438” inside the outer lip, as the lectotype of *B. olearium*; this is a specimen of *T. galea*, whereas the paralectotype of *B. olearium* is a specimen of *T. canaliculata*. Acting as first reviser, I selected (Beu, 2005: 120) the name *T. galea* to be used for this species. The lectotype of *Pyrula fasciata* (in Museo di Geologia e Paleontologia dell’Università di Torino) was illustrated by Pavia (1976: text-fig. 1, pl. 1, figs 9a-b; specimen not seen) and, as pointed out by Landau *et al.* (2004: 38), is clearly a small specimen of *T. galea*, despite the fact that it has been referred to *Eudolium* by most later authors. This is the type species of *Simplicodolium*, so this “subgenus” was based on the type species of *Tonna*. Because no type material is known today of *Dolium tenue* (no possible type material is present in Menke’s collection, in SMF) or of species named by Mörch (1877), the lectotype of *B. galea* (Gualtieri collection no. 6) also is here designated the neotype of both *Dolium tenue* and *D. antillarum*. Turner (1948) did not know the location of Mörch’s type material of *D. antillarum* var. *brasilianum*, referring vaguely to his type material being in many European museums, and did not resolve a type for this name. The specimen illustrated as *T. galea brasiliiana* by Turner (1948: pl. 79, fig. 1), from off of Rio Grande do Sul, southern Brazil, USNM 125482 (Pl. 77, Fig. 1) is here designated as the neotype of *D. antillarum* var. *brasilianum*. According to the label accompanying the specimen,

it was sent to the USNM by H. von Ihering. The location of Gregorio's types is not known to me, but the infrasubspecific varieties named by Gregorio (1884) are of no consequence in taxonomy. *Malea petiti*, holotype UF 21456, from Bermont Fm (Pleistocene), Griffin Brothers pit, 11 km W of U.S. Rte. 27, Palm Beach/Broward Co line, Florida; paratype from same locality, Paleontology collection, Florida Atlantic University, FAU 414; paratype from Bermont Fm, Capeletti Brothers pit no. 11, 7 km W of Florida Turnpike, Dade Co, Florida, UF 23800 (Petuch, 1989: 94) (none seen). *Tonna galea abbotti*, holotype at Museo de Biología del Instituto Tropical, Universidad Central de Caracas, Venezuela, catalog no. MBUCV-XIV-4068 (not seen), from quadrant E-21, Margarita platform, E Venezuela, with 9 other specimens (presumably paratypes); based on a form with 22-24 closely spaced, narrow spiral cords, which the authors conceded "coincides partially in geographical distribution with *T. galea galea*." Philippi's collection is at the Department of Zoology, National Museum of Natural History, Santiago, Chile, but is not yet available for consultation.

Other material examined.—**Fossils: Florida: Pleistocene:** Bermont Fm, Griffin Brothers pit, Holey Land area, Palm Beach/Broward Co line, collection of Bernard Landau (2, topotypes of *Malea petiti*). **Dominican Republic: Late Miocene:** Cercado Fm: NMB 15909 (2, small); 16983 (1); USGS 8521 (USNM 483454, 1 incomplete); Gurabo Fm: NMB 16928 (1 small, illustrated, NMB H 18037; Pl. 76, Figs 3-5, 7); unnamed formation of E. Vokes (1989: 21); NMB 17273 (1). **Late Miocene/Early Pliocene:** Gurabo Fm: TU 1297, Río Gurabo (1). **Venezuela: Late Pliocene:** NMB 17512, Mare Fm (16).

Distribution.—*Tonna galea* lives now in the western Atlantic from North Carolina (Turner, 1948: 175), USA, south to Río Grande do Sul, Brazil (Matthews *et al.*, 1983: 33), and to Uruguay and northern Argentina (Rios, 1994: 83), throughout the Mediterranean Sea, and in the eastern Atlantic from southern Spain south to Angola (Gofas *et al.*, 1984: 132) and to Namibia (Vos, 2007). *Tonna galea* was reported by Turner (1948: 175) to occur widely throughout the Indo-West Pacific, apparently implying that she considered that the Indo-West Pacific species *T. zonata* (more usually known as *T. olearium*) is a synonym of *T. galea*, but this is not the current interpretation. Vos (2007) recognized *T. galea* (Atlantic and Mediterranean) and *T. zonata* (Indo-West Pacific) as distinct species. I have examined fossil specimens of *T. galea* from the Late Miocene-Early Pliocene rocks of the Dominican Republic, and from the Late Pliocene-Pleistocene of Florida and northern Venezuela. Böse (1906: 87) recorded a specimen from the Pliocene of the Isthmus of Tehuantepec, Mexico, Hoerle (1970: 63) recorded specimens from the Bermont Fm in Florida, Petuch's (1989) type material of *Malea petiti*

from the Bermont Fm also belongs in *T. galea*, and Robinson (1991) recorded eight small specimens from the Late Pliocene-Early Pleistocene Moín Fm at Limón, Costa Rica, in Tulane University collections that I have not examined. Rutten (1931: 664) also recorded fossils as "*Dolium antillarum*" from Pleistocene localities in Suriname, citing earlier publications that I have not seen. Also, specimens identified previously as *Eudolium fasciatum* from Pliocene rocks of the Mediterranean region include some specimens of *T. galea* (references included in the above synonymy) but other specimens identified by this name are *E. stephaniophorum* (Fontannes, 1879). *Tonna galea* is uncommon in these Mediterranean localities, and the more offshore species of *Eudolium* occur more commonly there. Pleistocene fossils of *T. galea* also have been recorded from the Cape Verde Islands (García-Talavera, 1999: 13).

***Tonna pennata* (Mörch, 1853)**

Pl. 75, Fig. 6; Pl. 76, Figs 1-2

?*Buccinum maculosum* Lightfoot, 1786: 137 (*nomen nudum*).

?*Dolium pennatum* Schröter, 1788: 30 (*nomen nudum*).

Buccinum maculosum Dillwyn, 1817: 583 (junior primary homonym of *B. maculosum* Martyn, 1784 (available, ICZN Opin. 479, 1957), and of *B. maculosum* Gmelin, 1791: 3476).

Dolium perdx. d'Orbigny, 1841a: 182; Hanley, 1860: 492; Tryon, 1885: 264; Dall, 1889: 134; 1903b: 134; Gregory, 1895: 289; Dall & Simpson, 1901: 119; Trechman, 1933: 39; Coomans, 1963: 66 (in part not *Tonna perdx* Linnaeus, 1758).

Helix sulphurea C. B. Adams, 1849: 33; 1850b: 98 (larval shell); Winckworth & Tomlin, 1933: 212; Jacobson & Boss, 1973: 428 (junior primary homonym of *H. sulfurea* Hombron & Jacquinot, 1841; ICZN Art. 58.9).

Dolium pennatum Mörch, 1853: 110; 1877: 12; Hanley, 1860: 493; Krebs, 1864: 35.

Dolium album Conrad, 1854: 31.

Dolium perdx *B. brasiliensis* Mörch, 1877: 43 (*nomen nudum*) (homonym of *D. antillarum* var. *brasiliensis* Mörch, 1877: 42).

Dolium perdx occidentalis Mörch, 1877: 43; von Martens, 1879: Moll. 35; Coomans, 1963: 81 (*nomen nudum*).

Helix sulfurea (sic). Dall, 1889: 232.

Tonna perdx. Maury, 1922: 119; Piele, 1926: 80; Winckworth & Tomlin, 1933: 212; Lebour, 1945: 474, fig. 22 (larva); Morretes, 1949: 93 (in part not *T. perdx* Linnaeus, 1758).

Tonna pennata. Winckworth & Tomlin, 1933: 211; van Regteren Altena, 1975: 40; Turgeon *et al.*, 1998: 84; Macsotay & Campos Villaroel, 2001: 71, fig. on cover; Redfern, 2001: 63, pl. 32, figs 266A-C; Lee, 2003: 44; Vos, 2007: 72, pl. 31, figs 1-5.

Tonna maculosa. Turner, 1948: 169, pl. 75, fig. 2, pl. 76, figs 1, 2; Morretes, 1949: 93; Abbott, 1954: 199, pl. 9, fig. d; 1958: 52; 1974: 167, fig. 1784; Olsson & McGinty, 1958: 15; Nowell-Usticke, 1959: 62; Warmke & Abbott, 1961: 104, pl. 2, fig. f; Kilias, 1962: 45, figs 4.2, 37b, 38; Work, 1969: 663; Kaufmann & Götting, 1970: 372, fig. 89; Matthews & Kempf, 1970: 28; Scheltema, 1971: 291, figs 2g-h, j-k (larva); Rios, 1975: 74, pl. 20, fig. 302; 1985: 71, pl. 25, fig. 313; 1994: 84, pl. 28, fig. 327;

Princz & Pacheco, 1981: table; Abbott & Dance, 1982: 118; H. & E. Vokes, 1983: 23, pl. 12, fig. 2; Jensen & Harasewych, 1986: 427, illus.; Matthews *et al.*, 1987: 37, figs 6-7; Calvo, 1987: fig. 72 (radula); Diaz & Götting, 1988: 156; Diaz, 1990: 19; Leal, 1991: 108; Lipe & Abbott, 1991: 8, 9, illus.; Wirtz, 1998: 198; Tolman, 2001: 14-15; Ardovini & Cossignani, 2004: 122, 2 upper right figs.

Tonna (Cadus) maculosa. Weisbord, 1962: 276, pl. 24, figs 5-6.

Tonna (Cadus) maculosa mareana Weisbord, 1962: 277, pl. 24, figs 7-8.

Remarks.—Since the excellent monograph by Turner (1948), this species has been known almost uniformly by the name *Tonna maculosa*. However, van Regteren Altena (1975: 40) pointed out in his synonymy that the name *Buccinum maculosum* Dillwyn is a junior primary homonym of *B. maculosum* Gmelin (1791: 3476). The name *B. maculosum* has been applied several times: Martyn (1784: vol. 1, fig. 8), the valid name for the New Zealand type species of *Cominella* Gray, 1850, made available by ICZN Opinion 479 (1957); Lightfoot (1786: 10, 50, 137), *nomen nudum*, probably referring to the present species; Gmelin (1791: 3476), a synonym of *Cassis tessellata* (Gmelin, 1791); Lamarck (1822: 269). Van Regteren Altena (1975: 40) adopted what he construed as the next available name, *T. pennata*. The “official” American Fisheries Society list of molluscan names by Turgeon *et al.* (1998) also adopted *T. pennata* as the valid name for this species. However, there are two earlier available names that might be applied to this species, despite their lack of usage for this species during the 20th century, because no one name has won general acceptance other than the preoccupied name *T. maculosa*.

The earlier name is *Dolium plumatum* Green, 1830. Green (1830: 132) identified this species by reference to a figure by Seba (1758: vol. 3, pl. 63, fig. 18). This is not a simple reference to interpret. Seba’s plate 63 has only ten figures, and shows species of *Strombus* and *Cymatium*, so there is evidently an error in Green’s citation. It seems likely that Green was referring to pl. 68, fig. 16 [the figure cited also for *Buccinum maculosum* by Dillwyn (1817: 583); see below], because the Roman numeral LXVIII on the plate easily could have been misread as LXIII. This interpretation is strengthened by Green’s (1830: 132) comment that “I have but little doubt that this shell is the *Buccinum maculosum* of Solander; figured by Seba, vol. 3, tab. 63, fig. 18. I have compared our shell with that figure, and have been surprised that Dillwyn should consider it only a variety of *Perdix*.” However, Green (1830) gave the locality of his species as “South sea islands.” Turner (1948) therefore interpreted *D. plumatum* as a synonym of *Tonna perdix*, and the lack of usage of this name for the Atlantic species by most authors implies that this has been the usual interpretation. The only exception of which I

am aware is Kobelt (1875: 265), although Tryon (1885: 264) noted that this name has been applied to the Atlantic form by some authors. It should be noted, though, that Turner (1948: 169) interpreted the engraving by Seba (1758: pl. 68, fig. 16) as clearly an illustration of the Atlantic rather than the Indo-Pacific species resembling *T. perdix*, and a further complication is that Green (1830: 132) published a description of *D. perdix*, “not uncommon on the Florida Keys,” so clearly distinguished between *T. perdix* and *T. plumatum*. Green (1830) described *D. plumatum* as having “about seventeen broad flat ribs; those near the spire are almost obliterated; spire deeply grooved at the sutures,” suggesting that he was actually describing *T. canaliculata* (Linnaeus, 1758). Green (1830) stated that “the specimen from which my description was made, was obligingly lent to me for that purpose, by P. H. Nicklin, Esq.,” who was also cited as the owner of several of the other shells described by Green, including the figured syntype of *D. zonatum*. However, nothing has been published in recent years about the location of Green’s types, and Kohn (1988: 58) was unable to determine the location of any of Green’s specimens. A neotype therefore is needed for *D. plumatum* to tie this name unambiguously to one species, and I follow Turner’s (1948) interpretation of *D. plumatum* as a synonym of *T. perdix*. A Recent specimen of *T. perdix*, 99.9 mm H, from Bobi Island, Tobelo District, Halmahera Island, Indonesia (USNM 837122) (Pl. 77, Figs 5-6) is here designated the neotype of *Dolium plumatum*. *Dolium plumatum* therefore is a synonym of *Tonna perdix*.

The second available name is *Helix sulphurea* C. B. Adams, 1849, which is based on a larval shell of the *Tonna* species that usually has been known as *T. maculosa* (C. B. Adams, 1850b: 98). Jacobson & Boss (1973: 429) quoted C. B. Adams’s (1850b: 98) comments on this species: “On p. 33 we described *Helix sulphurea* as ‘perhaps a young shell’. This opinion was founded on its papyraceous appearance. Mr. Chitty, from whom the original specimens were received, has recently furnished a series, which shows that this shell, with all the generic characters of *Helix*, is the last embryonic stage of the West Indian variety of *Dolium perdix*! ... In a young shell, near the apex, may be very easily seen a clearly defined margin of the nucleus, at which margin the smooth and polished nuclear surface is abruptly succeeded by the close spiral striae which characterise the West Indian *D. perdix*. In the change from a continuous to a notched aperture, the anterior extremity becomes first angular, and before the next whorl is completed, the notch is perfect.” This description leaves no doubt that *H. sulphurea* is indeed based on a larval shell of the *Tonna* species that usually has been known as *T. maculosa*. Mörch (1877: 43) and von Martens (1879: Moll. 35) also noted of *Dolium perdix occidentale*: “... *Helix sulfurea* being the larval shell of it.” This is therefore the first available name

for the present *Tonna* species. However, Rosenberg (1997) pointed out that this name is a junior primary homonym of *H. sulfurea* Hombron & Jaquinot, 1841; the names *sulphureus* and *sulfureus* are specifically listed in ICZN Article 58.9 as an example of homonymous alternative spellings. The valid name for the present species is therefore *T. pennata* (Mörch, 1853). The same conclusion was reached by Lee (2003) and Vos (2007), who both also used *T. pennata* as the valid name. Juvenile and larval shells were illustrated excellently by Redfern (2001).

A minor complication with the name *Dolium pennatum* is the existence of an earlier *D. pennatum* Schröter (1788: 30). Schröter (1788) referred for the name *D. pennatum* to "III, 390", i.e., Martini (1777: 390). Here the name *D. pennatum* appears in a list of *Dolium* names, without any indication of the intended species or any referred figures, other than "Perdix" listed alongside it. This name is therefore clearly a *nomen nudum*, leaving *Tonna pennata* (Mörch, 1853) available for the Atlantic species. It seems likely that Mörch (1853) intended to use the name proposed by Martini (1777; non-binominal) and Schröter (1788) rather than to propose a new name.

Tonna pennata is identified easily among Atlantic tonnoideans by its oval, high-spined, weakly inflated shape (for a species of *Tonna*), and by its sculpture of smooth, low, closely spaced, weakly convex spiral cords, separated only by narrow grooves. It is slightly the more common of the two *Tonna* species in the Dominican Republic faunas, and is represented much more widely in Plio-Pleistocene faunas than is *T. galea*. This probably reflects the slightly more near-shore environment inhabited by *T. pennata* in contrast to the slightly more offshore one of *T. galea*. *Tonna pennata* is closely similar to the common Indo-West Pacific species *T. perdix*, differing in its slightly shorter spire, its more deeply excavated columella, its narrower anterior siphonal canal, its more inflated whorls, particularly over the subsutural area where *T. perdix* is unusually little-inflated for a *Tonna* species, its deeper and more obvious grooves between the spiral cords, and in its much more subdued color pattern, lacking the bright semicircular to meniscus-like bars on the cords that make *T. perdix* such an easily identified species.

The form named *Tonna maculosa mareana* by Weisbord (1962: 277), from the Pliocene Playa Grande Fm of northern Venezuela, is well within the range of variation of Recent specimens. It is based on a specimen (PRI 26187) with the outer lip broken back for a quarter-whorl, revealing more of the inner lip callus and columella than in complete shells.

Dimensions.—Figured specimen, NMB H 18038, from NMB 19009 (TU 1246), Dominican Republic: H 43.4, D 29.4 mm; holotype of *T. maculosa mareana*: H 73.5, D 50 mm (Weisbord, 1962: 278). Vos (2007: 73) stated that the

tallest specimen of which he was aware was 178 mm H.

Types.—The first complication with types for this species is among Linnaeus' syntypes of *Buccinum perdix*, housed at the Linnean Society of London in Burlington House. Two specimens are present, in separate boxes. The first is a moderately large specimen with a tall spire and a very low, wide anterior siphonal notch (H 112.4, D 71.6 mm), typical of the Pacific species that has usually borne the name *Tonna perdix*. This specimen is labelled both "378" (the number for *B. perdix* in the 10th edition of *Systema Naturae*) and "*perdix*" inside the outer lip. The second specimen is labeled "440" (the number for *B. perdix* in the 12th edition) in the aperture; it has a markedly lower spire and a narrower anterior siphonal notch than the other specimen (H 100.1, D 68.0 mm). The second specimen therefore could possibly be a specimen of *T. pennata*. To avoid confusion over the application of the name *T. perdix*, the larger specimen in Linnaeus' collection in London, labelled "378" and "*perdix*," was designated as the lectotype of *B. perdix* by me (Beu, 2005: 124). I also designated (Beu, 2005: 124) the lectotype of *B. perdix* Linnaeus as the neotype of *Cadus meleagris* Röding, 1798, *Cadus coturnix* Röding, 1798, and *Perdix reticulatus* Montfort, 1810.

Turner (1948: 169-170) noted that Dillwyn's usage of *Buccinum maculosum* was identifiable by his reference to Seba (1758: pl. 68, fig. 16) but, because the location of Seba's material is not known, she selected as the neotype of *B. maculosum* the specimen that she illustrated (Turner, 1948: pl. 76, figs 1-2), MCZ 113091, from Simms, Long Island, Bahama Islands. Deans's (1936) list of only four lectotypes in Dillwyn's collection (see above, under *Marsupina bufo*) does not include *Buccinum maculosum*, so Turner's neotype selection is valid. *Helix sulphurea*, from Jamaica, a larval shell of the species previously known as *Tonna maculosa* (C. B. Adams, 1850b: 98; republished by Jacobson & Boss, 1973: 429); type lost (Jacobson & Boss, 1973: 310, 428). *Dolium pennatum*, location of any original material not known; as with most of Mörch's mollusks, other than Vermetidae, no type material is present at ZMC. *Dolium album*, no type material remaining at ANSP (G. Rosenberg, ANSP, pers. comm., 1999). The neotype of *Buccinum maculosum* selected by Turner (1948: pl. 76, figs 1-2), MCZ 113091, was designated the neotype of *Dolium pennatum* Mörch, 1853, by Vos (2007: 68, 73), and is here designated also as the neotype of both *H. sulphurea* C. B. Adams, 1849, and *D. album* Conrad, 1854. *Tonna maculosa mareana*, holotype PRI 26187, from Weisbord's loc. K257a, bluff 125 m W of intersection of coast road and Playa Grande Yacht Club road, Catia Member of Playa Grande Fm (Pleistocene), N Venezuela; a normal specimen of *T. pennata*.

Other material examined.—**Fossils: Bermuda: Pleistocene:** Bermuda (BMNH Palaeontology Department GG5286, 1). **Barbados: Pleistocene:** Bishopscourt (BMNH Palaeontology

Department G10863, 2); Coral Rock, Bishop's Hill, coll. C. T. Trechman (BMNH Palaeontology Department GG4078, 1); Coral Rock, Sandy Lane, coll. C. T. Trechman (BMNH Palaeontology Department G69304-5, 2); Coral Rock, Bridgetown (BMNH Palaeontology Department G3679, 3). **Atlantic Panama: Pliocene:** NMB 18373, Cayo Agua (2); 18733, Cayo Agua (1). **Dominican Republic: Late Miocene:** Cercado Fm: NMB 16852 (1); USGS 8521 (USNM 483454, 1 incomplete); unnamed formation of E. Vokes (1989: 21): TU 1444 = NMB 19021 (1). **Late Miocene/Early Pliocene:** Gurabo Fm: TU 1246 = NMB 19009, Río Gurabo (1, illustrated, NMB H 18038; Pl. 76, Figs 1-2). **Early Pliocene:** Gurabo Fm: NMB 15858, Río Gurabo (1). **Pleistocene:** La Isabella Fm, El Castillo, La Isabella, collection of Bernard Landau (1). **Venezuela: Late Pliocene:** NMB 17512, Mare Fm, Cabo Blanco (14). **Pleistocene:** NMB 17541, Araya Peninsula (1); NMB 17568, Catia Member, Playa Grande Fm (2).

Distribution.—In the western Atlantic, *Tonna pennata* lives now from Bermuda (Leal, 1991), the Bahamas (Redfern, 2001) and southern Florida, USA, to Bahia, Brazil (Turner, 1948), and at the Fernando de Noronha Islands and Atol das Rocas (Matthews *et al.*, 1987: 38; Rios, 1994: 84). Matthews (1968) recorded juvenile specimens found rarely in the gut of the toadfish or “pacomon,” *Amphychthys cryptocentrus*, caught off of Fortaleza, Ceará, Brazil. In the eastern Atlantic, it is reported only from the Canary and Cape Verde Islands (Cosel, 1982b; Garcia-Talavera, 1983; Leal, 1991; Ardivini & Cossignani, 2004: 122, Cape Verde Islands specimen illustrated in color), and Wirtz (1998: 198) recorded the first specimen from Madeira. Vos (2007: 73) reported specimens in private collections from the Cape Verde Islands, and from Tenerife and Lanzarote in the Canary Islands. A specimen from Tenerife, Canary Islands, has been examined (TFMC 2913). Scheltema (1971: 294, 300, fig. 7) recorded larvae in the plankton only in the mid-western Atlantic. Fossils are recorded from Late Miocene-Early Pliocene rocks of the Dominican Republic, and from Plio-Pleistocene rocks of Atlantic Panama, the Dominican Republic, and northern Venezuela. Gregory (1895) recorded Pleistocene fossils from Barbados. Garcia-Talavera (1999: 16) also reported Pleistocene fossils from Ilha de Sal, Cape Verde Islands. Not one *Tonna* specimen is reported from the fossil or living faunas of the tropical eastern Pacific.

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APPENDIX 1: FICIDAE OF THE DOMINICAN REPUBLIC

Superfamily **FICOIDEA** Meek, 1864 (1840)

Family **FICIDAE** Meek, 1864 (1840)

Remarks.—Riedel (1994) gave good reasons for placing the family Ficidae in a superfamily of its own, separate from its

former position in Tonnoidea. He also proposed the new family Thalassocyonidae for the ficioidean genus *Thalassocyon* Barnard, 1960, although this family was regarded as synonymous with Ficiidae by Bouchet *et al.* (2005: 250). Most Ficiidae of the tropical American region are not considered here, but the Ficiidae of the Dominican Republic are included as a further contribution to the Dominican Republic Project.

Genus *FICUS* Röding, 1798

Ficus Röding, 1798: 148. Type species (by subsequent designation, Dall, 1906: 296): *Ficus variegata* Röding, 1798, Recent, Indo-West Pacific. Verhaeghe & Poppe (2000) treated *F. variegata* and *F. ficus* (Linnaeus, 1758) as distinct species, *F. ficus* being the one more usually known as *F. subintermedia* (d'Orbigny, 1852) (as distinct from the Italian Pliocene fossil species that correctly bears this name; Landau *et al.*, 2004: 75, pl. 7, figs 2-3, pl. 8, fig. 1), and *F. variegata* being the species more usually known as *F. ficus*.

Pyrula Lamarck, 1799: 73. Type species (by monotypy): "*Bulla ficus*. Lin.", *i.e.*, *Murex ficus* Linnaeus, 1758, Recent, Indo-West Pacific.

Pirula Montfort, 1810: 486. Type species (by monotypy): *Murex ficus* Linnaeus, 1758.

Ficula Swainson, 1835: 21. No included species. Two species subsequently included by Swainson (1840: 307). Type species (by subsequent designation, Gray, 1847: 135): *Murex ficus* Linnaeus, 1758.

Sycotypus Gray, 1847: 135. Type species (by original designation): *Murex ficus* Linnaeus, 1758.

Diconoficus Covacevich & Frassinetti, 1983: 106. Type species (by original designation): *Ficus gayana* Covacevich & Frassinetti, 1980, Oligocene/Miocene, Chile.

Remarks.—Protoconch whorls are counted here in the manner defined by me (Beu, 1998b: fig. 7), *i.e.*, each protoconch is considered to commence with a hemispherical "cap" that is not included in the count. *Ficus* protoconchs commence with a smooth area, considered by B. Smith (1907) to comprise the whole protoconch, but this area passes very gradually into a cancellate-sculptured portion of *ca.* 0.1-1.5 whorls, which is clearly part of the larval shell. Most specimens show a clear sculptural break after a short cancellate-sculptured section, when the spiral cords and/or axial ridges take on a different angle with varying degrees of abruptness. This is considered to be the true protoconch-teleoconch junction; see also the very clear line of junction in the unusually small juvenile specimen of *F. gibsonsmithi* n. sp. (Pl. 78, Figs 7-9). Warén & Bouchet (1990: 83) and Landau *et al.* (2004: 77) also considered the cancellate-sculptured portion to be part of the protoconch. In many fossil specimens, the sculptured portion of the protoconch defined in this way has a different appearance from that of the teleoconch – paler, in many specimens, even under

SEM examination, and in many specimens slightly translucent grey-white, readily distinguished from the opaque cream teleoconch – suggesting that they differ slightly in mineralogy. It appears as if the protoconch might have a calcitic outer layer, whereas the teleoconch is aragonitic, although I have not tested the mineralogy. No differences have been observed between the microsculpture of the teleoconch and of the cancellate-sculptured part of the protoconch.

Verhaeghe & Poppe (2000) listed *Otus* Risso, 1826, as a further synonym of *Ficus*. However, this name appeared in a list of Pliocene fossils from La Trinité, near Nice (Risso, 1826a: 122), and, although listed after a *Pyrula* (*i.e.*, *Ficus*) species, the name *O. reticulatus* is a *nomen nudum*.

Ficus bernardi n. sp.

Pl. 79, Figs 1, 4-5, 7

?*Ficus pilsbryi*. Maury, 1917a: 277 (identity uncertain; not *F. pilsbryi* B. Smith, 1907).

Description.—Shell small for genus (available specimens to 45 mm H, but presumably immature), tall and narrowly fig-shaped, with very low, weakly conical spire, evenly inflated whorls, suture very shallow but well-defined, long, narrow, widely open aperture, and long, very gradually tapering, straight, relatively wide anterior siphonal canal (anterior end incomplete on all available specimens). Protoconch dome-shaped, of 2.5 whorls, with very narrow initiation, last 0.7-0.8 whorls gradually developing cancellate sculpture, earlier 1.7-1.8 whorls completely smooth; weakly but obviously inclined at a low angle to teleoconch coiling; separated from teleoconch by slight change in angle of growth lines and spiral cords, and by slight color difference in holotype; protoconch slightly translucent grey-white, teleoconch opaque cream. Teleoconch of 2.5 whorls in holotype, presumably increasing in number in larger specimens; last whorl enveloping all earlier ones except for narrow, gently inclined, weakly convex sutural ramp of spire whorls. Sculpture of narrow, raised, narrow-crested, moderately widely spaced spiral cords with low, vertical sides and moderately wide, almost flat spiral interspaces (very gently concave in some specimens, such as on central area of whorl sides of holotype); 17-18 primary cords on holotype, of which two on sutural ramp are lower and more closely spaced than others, and are visible on spire whorls; alternating with one only slightly weaker secondary cord in center of each spiral interspace, with secondary cords increasing in prominence slightly down last whorl to rival primary cords near base, all weakening down shell until cords merge into closely spaced, strongly oblique cords of anterior end; one very narrow, low tertiary cord in center of each secondary interspace on holotype, but arrangement of spiral cords less regular on paratypes; entire surface crossed by

very numerous, fine, raised, sharply defined, flat-crested axial ridges, about equal to secondary spiral cords in prominence but with spacing intermediate between that of secondary and tertiary spiral cords. Interior of outer lip not thickened at posterior end, presumably implying that all specimens are immature; aperture simple, unthickened, with thin outer lip and no callus on inner lip; interior of outer lip smooth, outer edge weakly sinuate in conformity with exterior spiral cords.

Dimensions.—Holotype: H 44.7, D 25.6 mm (anterior end incomplete); paratype, collection of Bernard Landau: H 25.3, D 15.0 mm; largest other paratype, NMB H 18336: H (incomplete) 24.4, D 13.4 mm.

Types.—Holotype BMNH Palaeontology Department GG22903 (Pl. 79, Figs 1, 4), Baitoa Fm (late Early Miocene), Arroyo Hondo, tributary of Río Yaque del Norte, Dominican Republic, collected by Bernard Landau; 1 small paratype from same locality, collection of Bernard Landau; NMB 15833, Mao Fm (Early Pliocene), near downstream end of exposure, E bank Río Gurabo (NMB H 18341, juvenile paratype, D 5.0 mm, protoconch D 2.7 mm; protoconch studied by SEM, Pl. 79, Figs 5, 7); NMB 17275, unnamed formation of E. Vokes (1989: 21) (Late Miocene), N bank of Río Yaque del Norte (NMB H 18336, 1 small almost complete paratype, anterior slightly incomplete).

Distribution.—*Ficus bernardi* n. sp. is known only by the type material, from the Baitoa to Mao formations in the northern Dominican Republic.

Remarks.—Although only *Ficus gibsonsmithi* n. sp. (described below) is moderately common in the Late Miocene Cercado Fm of the northern Dominican Republic, two other species from late Early Miocene to Early Pliocene rocks are each represented by a small amount of material at NMB and in Bernard Landau's collection. The spiral sculpture of both species resembling *F. pilsbryi* B. Smith, 1907, in this fauna differs from that of *F. gibsonsmithi* n. sp. in being much lower, weaker, and more closely spaced, with more numerous primary cords and flat spiral interspaces. Most specimens of both species differ from *F. gibsonsmithi* n. sp. in their lower, narrower, more steeply sloping sutural ramp, giving the shells a more oval-fusiform shape, without the more marked, gently sloping sutural ramp and more nearly parallel margins below the ramp seen in *F. gibsonsmithi* n. sp. The "drooping" shoulder is particularly marked in paratype NMB H 18336 of *F. bernardi* n. sp.; the holotype and the paratype in Bernard Landau's collection have higher shoulders and do not "droop" so obviously. The paratype NMB H 18336 also has a slightly taller protoconch than the other material and, as it is not very well preserved, it is possible that this specimen represents a fourth Dominican Republic *Ficus* species. Both species similar to *F. pilsbryi* also differ significantly from *F. pilsbryi*, in the Bowden shellbed, Jamaica, in protoconch characters. *Ficus bernardi* n.

sp. has the same number of whorls in the initial, smooth portion of the protoconch as in *F. pilsbryi*, but the protoconch is larger, with wider whorls than in *F. pilsbryi*, and also differs from that of *F. pilsbryi* in having a longer cancellate-sculptured portion. The sculptured portion occupies at least 0.7 whorls in the specimen of *F. bernardi* examined by SEM (the position of the teleoconch junction is difficult to determine in this specimen) and clearly occupies just over one whorl in the holotype, in which the protoconch is a pale, slightly translucent gray-white, whereas the teleoconch is opaque cream, and the junction between them is obvious. As noted below, the sculptured portion occupies only ca. 0.3 whorls in *F. pilsbryi*.

The sole record of *Ficus* in Maury's (1917a) Dominican Republic monograph is of a specimen identified as *F. pilsbryi*, from "Zone 1, Río Cana at Caimito." I did not see this specimen in the PRI collection. However, her description leaves no doubt that Maury was dealing with one of the species resembling *F. pilsbryi* rather than the much more common *F. gibsonsmithi* n. sp., because she noted that "the surface between the primary spirals is flat, not concave as in *P[yrula]. carbasea* Guppy" (Maury, 1917a: 277). It therefore seems likely that she had the more common of the two, *F. bernardi* n. sp. This species seems likely to be more widespread in the northern Dominican Republic than present records suggest.

Etymology.—The specific epithet is a tribute to the brilliant collecting of Bernard M. Landau, Albufeira, Portugal, who collected the holotype and a paratype, and generously allowed these and all his other excellent fossils to be included in this monograph.

Ficus gibsonsmithi n. sp.

Pl. 78, Figs 4-5, 7-9

Ficus papyratia. Gabb, 1873: 223 (not *Pyrula papyratia* Say, 1822).
Ficus carbasea. B. Smith, 1907: 215; Pilsbry, 1922: 364 (not *Pyrula carbasea* Guppy, 1866).

Description.—Shell rather small to moderate-sized for genus (apparently adult specimens 40 to ca. 75 mm H), tall and narrowly fig-shaped, with very low, almost flat spire, evenly but rather weakly inflated whorls, suture obscurely defined, and long, narrow, widely open aperture and long, very gradually tapering, straight, relatively wide anterior siphonal canal. Protoconch dome-shaped, paucispiral, of ca. 1.3 whorls, last one-eighth whorl gradually developing cancellate sculpture, earlier whorls completely smooth; protoconch separated from teleoconch by slight but abrupt change in angle of growth lines and spiral cords, at well-marked line (particularly on anterior canal) in some juvenile specimens (Pl. 78, Figs 7, 9). Teleoconch of two whorls (in holotype), up to 2.5-3 whorls in largest specimens; last whorl enveloping all earlier ones except for narrow, horizontal sutural ramp. Sculpture of narrow,

well-raised, very widely spaced spiral cords with concave sides and wide, gently concave spiral interspaces; 19-20 cords on holotype, of which two on sutural ramp are much lower and more closely spaced than others, and are the only ones visible on spire whorls; spacing increasing gradually down last whorl to a maximum at most inflated area of whorl, then decreasing again gradually down anterior canal until cords merge into fine, closely spaced, strongly oblique background sculpture of anterior end; one obvious but very narrow secondary cord in center of each interspace; two or three very narrow, raised, tertiary spiral threads in each secondary interspace, decreasing in number anteriorly and posteriorly from a maximum in widest interspaces; entire surface crossed by very numerous, fine, raised, flat-topped axial ridges, about equal to secondary spiral threads in prominence but equal to tertiary spiral threads in spacing. Interior of outer lip lightly thickened at posterior (adapical) end in large specimens, producing a low, narrow, irregular, smooth area margining suture of up to last half whorl of some large specimens, including last quarter whorl of holotype; aperture otherwise simple, unthickened, with thin outer lip and no callus on inner lip; interior of outer lip bearing weak spiral grooves (interior expression of primary spiral cords), weakly sinuating lip edge in apertural view where they reach outer margin.

Dimensions.—Holotype: H 41.9, D 21.4 mm; largest paratype, NMB 15906: H 52.0, D 25.3 mm; specimens in other locality lots reaching larger sizes: NMB 16913: H 55.6 (estimated originally *ca.* 75 mm), D 35.8 mm; TU 1378, Río Gurabo, collection of Bernard Landau: H 64.6 (estimated originally *ca.* 77 mm), D 42.4 mm; H 49.5, D 24.3 mm.

Types.—Holotype NMB H 18340 (Pl. 78, Figs 4-5), from NMB 15906, Cercado Fm (Late Miocene), upper part of small sidestream entering W bank of Río Gurabo at upper end of gorge; 23 paratypes at NMB from same locality (2 juvenile paratypes illustrated by SEM, NMB H 18338; Pl. 78, Figs 7-9).

Other material examined.—**Fossils: Dominican Republic: Late Miocene:** Cercado Fm: NMB 15898 (2 frags); 15901 (1 frag); 15903 (13 specimens, + several frags); 15904 (2 frags); 15905 (1 frag); 15907 (3 frags); 15909 (4 specimens + several frags); 15910 (9 specimens + several frags); 15911 (1); 15912 (7); 15913 (3); 15914 (1 frag); 15915 (6 frags); 16913, Bluff 1 of Maury (1 large incomplete specimen, largest seen); USGS 8521 (USNM 483458, 5 frags); USGS 8522 (2 frags); 26279 (1 incomplete); TU 1378, Cercado Fm, Río Gurabo, collection of Bernard Landau (3); NMB 17320, Cercado Fm, Río Gurabo, collection of Bernard Landau (9).

Distribution.—*Ficus gibsonsmithi* n. sp. is known only by the material listed above, all from the Cercado Fm (Late Miocene) in the Cibao Valley, northern Dominican Republic.

Remarks.—The smaller of the two small paratypes studied

by SEM (Pl. 78, Figs 7, 9) has grown only half a teleoconch whorl after the end of the protoconch, and displays the protoconch termination well in apertural view. The clear line of junction with the teleoconch and the different appearance of the sculptured portion of the protoconch from that of the teleoconch show well, and make it very clear that (a) the sculptured portion is indeed part of the protoconch, and (b) the sculptured portion of the protoconch occupies only about one-eighth of a whorl in *Ficus gibsonsmithi* n. sp., and the entire protoconch occupies *ca.* 1.3 whorls.

Three species of *Ficus* are present in the Dominican Republic collections available to me. *Ficus gibsonsmithi* n. sp. is very much the most common of them, and is the species recorded previously by B. Smith (1907) and Pilsbry (1922: 364) as *F. carbacea* (Guppy, 1866). *Ficus carbacea* was named from the Miocene of "Savanetta," Trinidad (Savaneta, Springvale Fm; Early Pliocene; Woodring, 1959: 211), but was recognized in the Middle to Late Miocene Gatun Fm of Panama by Woodring (1959: 211, pl. 36, figs 10, 13) and in the late Early Miocene Cantaure shellbeds of Paraguaná Peninsula, Venezuela, by Jung (1965: 515). It is a species with a much wider teleoconch than *F. gibsonsmithi* n. sp., more numerous and less prominent spiral cords of more uniform spacing than in *F. gibsonsmithi* n. sp., and a multispiral protoconch, with 2.0-2.5 whorls, although most specimens have 2.25 whorls, according to the counts by Jung (1965: 517) [but note that Jung's (1965: 517, text-fig. 3) diagram indicates that according to my counting method, specimens have *ca.* 0.25 whorls fewer than in Jung's counts]. There is relatively little *Ficus* material from the Dominican Republic in most collections that I have examined, and only the systematically gathered NMB collections and Bernard Landau's collection contain more than a few specimens. Pilsbry (1922: 364) seems to have had only one specimen available, from Gabb's collection.

Ficus gibsonsmithi n. sp. resembles *F. carbacea* in most characters, belonging to the extensive tropical American species group related to the Recent eastern Pacific species *F. ventricosa* (G. B. Sowerby I, 1825) (Keen, 1971: 503, fig. 952, color pl. 15), with sculpture dominated by relatively few, widely spaced, very prominent, narrow-crested spiral cords of obviously triangular section, separated by wide, deeply concave interspaces. *Ficus gibsonsmithi* n. sp. differs from all other species in this group by its much narrower, more elongate shape. The protoconch also differs from that of *F. carbacea* in having far fewer whorls, having a paucispiral, lecithotrophic form similar to that of *F. communis* (Röding, 1798), which was described by B. Smith (1907: 214) [as *F. papyratia* (Say, 1822)] as having "a very large swollen apex with not more than one smooth whorl." Of American *Ficus* species, *F. gibsonsmithi* n. sp. is the only one that combines widely spaced, prominent spiral cords and wide, concave interspaces with a tall, narrow

shape and a paucispiral protoconch. All material seen is Late Miocene, either from the Cercado Fm, or from the equivalent early strata in the Río Mao, which have been assigned rather equivocally to either the Cercado or Gurabo formations.

Etymology.—The new species is named in honor of Jack Gibson-Smith, whose publications (with Win Gibson-Smith) have enriched our knowledge of Caribbean paleontology so much, and whose magnificent collections (now at NMB) have been so important for the present work. The epithet particularly recognizes Jack's interest in the complexities of tropical American *Ficus* taxonomy.

Ficus lisselongata n. sp.

Pl. 79, Figs 2-3, 6, 8.

Description.—Shell moderate-sized for genus (60 mm H), tall and narrowly fig-shaped, with very low spire almost entirely enveloped by last whorl, with evenly and weakly inflated whorls, and long, narrow, widely open aperture, and long, very gradually tapering, straight, relatively wide anterior siphonal canal. Protoconch dome-shaped, weakly but obviously inclined at angle to coiling axis of teleoconch, of 1.5 whorls, with wide initiation, last 0.3 whorls gradually developing cancellate sculpture, earlier whorls completely smooth; protoconch separated from teleoconch by slight but abrupt change in angle of axial ridges, and (in holotype) by distinctive, gray-white coloration of protoconch and more cream coloration of teleoconch. Teleoconch of three whorls (in holotype), with last whorl enveloping all earlier ones except for narrow, gently inclined, weakly convex sutural ramp. Sculpture of narrow, well-raised, flat-crested, quite closely spaced spiral cords with low, vertical sides and narrow, flat, smooth, polished spiral interspaces; 58 cords on holotype, of which only one or two are visible on sutural ramp on spire whorls, merging into closely spaced, strongly oblique background sculpture of anterior end; one narrow, well-raised, flat-crested secondary cord in center of some spiral interspaces near most inflated area of last whorl on holotype (in 15th-18th, 20th, 32nd, and 33rd interspaces below suture), more regularly present in most interspaces on paratypes; entire surface crossed by numerous, sharply defined, raised, narrow, flat-crested axial ridges and occasional weak axial grooves of varying spacing and prominence, most axial ridges spaced at two-thirds the spacing of primary spiral cords. Interior of outer lip lightly thickened at posterior end, producing low, narrow, irregular, smooth area margining suture of last tenth of a whorl of holotype; aperture otherwise simple, unthickened, with thin outer lip and no callus on inner lip; interior of outer lip smooth except for very weakly grooved outer edge.

Dimensions.—Holotype: H 59.9, D 30.1 mm; largest moderately complete paratype, in NMB 16857: H 33.7, D 11.0

mm (incomplete, estimated originally *ca.* 14 mm).

Types.—Holotype, NMB H 18335 (Pl. 79, Figs 2, 3), from NMB 16866, Gurabo Fm (Early Pliocene), Río Cana, Dominican Republic; from W bank, next bluff downstream from NMB 16865, at the upper quarter of Saunders *et al.*'s (1986: text-fig. 15) map of localities in the Río Cana. The holotype consisted of 2 large fragments, which have been fitted together and evidently represent one specimen.

Other material examined.—**Fossils:** **Late Miocene:** NMB 16857, Cercado Fm, Río Cana, E bank, 100-250 m upstream from ford (6 small to moderate-sized paratypes; largest partial paratype NMB H 18337; 1 paratype with protoconch, studied by SEM, NMB H 18342; Pl. 79, Figs 6, 8).

Distribution.—Known only by the type material, from the Cercado and Gurabo formations in the Río Cana, Cibao Valley, northern Dominican Republic.

Remarks.—Much the more distinctive (and larger) of the two uncommon *Ficus* species in the Dominican Republic fauna is the tall and narrow, exceedingly finely sculptured species in NMB 16866 named here as *F. lisselongata* n. sp., represented also by six small specimens in NMB 16857. The protoconch is not unlike that of *F. gibsonsmithi* n. sp. in gross appearance, being relatively strongly oblique to the teleoconch coiling axis and of relatively few whorls. However, the protoconch of *F. lisselongata* n. sp. is distinctive in having a tall shape, a large smooth area, with a wide initiation, but consisting of only 1.2 whorls, followed by a short sculptured section of only *ca.* 0.3 whorls, so that the entire protoconch occupies only 1.5 whorls. It therefore has a slightly longer smooth portion than in *F. gibsonsmithi* n. sp., a slightly greater total number of protoconch whorls than *F. gibsonsmithi* n. sp., and fewer protoconch whorls than in *F. pilsbryi* and *F. bernardi* n. sp. The graceful, tall, narrow shape, having narrow, flat crests on the spiral cords and, in particular, on the axial ridges, having spiral cords of only one order of magnitude, with few secondary cords on the holotype, and the unusually fine, close spiral sculpture and even finer, more closely spaced axial ridges of *F. lisselongata* n. sp. are highly distinctive, and unique among Dominican Republic species that I have seen. It is perhaps nearest to the Recent western Atlantic species *F. communis* in most characters, and is similar in its shape and fine sculpture to *F. communis*, but the protoconch of 1.5 whorls is distinct from the more paucispiral one (of *ca.* 1.0 whorl) with a larger, bulbous initiation in *F. communis*, and the teleoconch spiral sculpture is a little coarser and the shape is a little wider in *F. communis*.

Etymology.—The specific epithet is intended to reflect the unusually fine sculpture and lightly polished surface (*liss*, from Latin, smooth) and long, narrow shape (from Latin, *elongata*) of the new species.

***Ficus pilsbryi* B. Smith, 1907**

Pl. 78, Figs 1-3, 6

Ficus carbasea. Guppy, 1873: 80 (not *F. carbasea* Guppy, 1866).*Ficus pilsbryi* B. Smith, 1907: 213, fig. 1; Woodring, 1928: 313, pl. 20, fig. 9, pl. 21, figs 1-2; B. Smith, 1945: 262, pl. 21, fig. 3.

Remarks.—*Ficus pilsbryi* is a finely sculptured species with flat spiral interspaces. Its appearance is very different from that of the more prominently sculptured *F. gibsonsmithi* n. sp., which has strongly concave spiral interspaces. The lectotype selected here is the best preserved and largest of B. Smith's (1907) syntypes, presumably the one that his illustrations were based on, and certainly bears the protoconch described by him. *Ficus pilsbryi* differs from the two similar species in the Dominican Republic in its wider teleoconch, its narrower primary spiral cords, its narrower and more widely spaced axial ridges, and its different protoconch proportions. In *F. pilsbryi* (Pl. 78, Figs 1-4) the smooth initial protoconch section (intergrading very gradually with the sculptured section) is of ca. 1.7-1.8 whorls, with a narrow initiation, and the sculptured portion is of only ca. 0.25-0.3 whorls. Protoconchs are abraded on the Bowden material, so some are difficult to use, and what is concluded to be a severely abraded protoconch was initially thought to represent a second Bowden species, but that of the lectotype is clearly almost identical to that of the small apex illustrated by SEM. Woodring (1928: pl. 20, fig. 9, pl. 21, figs 1-2) had only small, broken specimens.

Dimensions.—*Ficus pilsbryi*, lectotype: H 42.6, D 23.5 mm.

Types.—*Ficus pilsbryi*, lectotype and two paralectotypes ANSP/IP 11144 (B. Smith's figured syntype), ANSP/IP 79602, from Bowden shellbed, St. James Parish, Surrey Co, Jamaica. The largest and most complete of these, ANSP/IP 11144, is here designated the lectotype (Pl. 78, Figs 2-4).

Other material examined.—**Fossils: Late Pliocene:** Bowden: USNM, from USGS 2580 (1 small internal mold and 5 frags, several with good protoconchs; 1 illustrated by SEM, Pl. 7, Fig. 1).

Distribution.—I am aware of material of *Ficus pilsbryi*, as defined here, only from the Bowden shellbed (late Pliocene) in Jamaica.

APPENDIX 2: TAXA REMOVED FROM TONNOIDEA

OCCURRENCE OF *IPUNINA* NIELSEN & FRASSINETTI, 2008 (LITIOPIDAE) AT CANTAURE, VENEZUELA

Superfamily **CERITHIOIDEA** Fleming, 1822
Family **LITIOPIDAE** Gray, 1847

Genus *IPUNINA* Nielsen & Frassinetti, 2008

Ipunina Nielsen & Frassinetti, 2008: 254. Type species (by original designation): *I. vladimiri* Nielsen & Frassinetti, 2008, Miocene, Chiloé and Ipún Islands, southern Chile; Cantaure, Venezuela.

***Ipunina vladimiri* Nielsen & Frassinetti, 2008**

Pl. 65, Figs 2, 4-5, 8

Oocorys n. sp. aff. *elevata*. Beu, 2001: 708, table 1.*Oocorys* sp. Nielsen, 2003: 92, pl. 16, figs 23-24; Frassinetti, 2004: 76, figs 2.7-2.8.*Ipunina vladimiri* Nielsen & Frassinetti, 2008: 254, figs 2A-G.

Description.—Shell of Cantaure specimens slightly larger than type material of *Ipunina vladimiri* (maximum H 45 mm, but all specimens slightly to severely incomplete, originally ca. 48-50 mm H), with early spire whorls weakly and evenly inflated; exposed whorl area below suture decreasing progressively in inflation over penultimate whorl to leave only a narrow, more strongly convex zone at whorl base to contract to lower suture; last whorl with narrow, slightly convex subsutural area, almost flat, gently sloping whorl side for more than half whorl height, narrow, strongly convex zone forming rounded basal angulation, and very slightly convex to almost flat, steeply contracting base merging gradually into basal lip without a defined siphonal canal (base slightly incomplete on all material). Sculpture predominantly of spiral cords, 12-14 on spire whorls and ca. 25 on last whorl, three below suture more closely spaced than others on spire, but otherwise spaced evenly on last whorl; cords low, narrow, but clearly raised, flat-topped, with interspaces each approximately equal in width to one cord on spire whorls, becoming more widely spaced on last whorl, with some interspaces near aperture on last whorl each twice the width of one cord; weak traces of fine axial threads in spiral interspaces visible on some well-preserved specimens. Shell material poorly preserved or missing from Venezuelan material. Chiloé and Ipún material demonstrates that spiral cords are much more prominent, slightly narrower, and more sharply raised on more complete specimens; shell surface between spiral cords bearing many low, thin, widely spaced axial ridgelets. Base of columella strongly convex, forming narrow rim turning in toward aperture sharply, then turning out slightly to form a thin, sharp lip margin resembling that of the columellar base of *Tonna*. Protoconch, outer lip, and much of inner lip not seen in Cantaure material.

Dimensions.—Holotype: H 32 mm; SMF 330178, Chiloé: H ca. 41 mm (Nielsen & Frassinetti, 2008: 254); largest Cantaure specimen, NMB H 17991: H (incomplete) 45.3, D (incomplete) 28.6 mm; figured specimen, NMB H 17993, from NMB 17519: H 28.2, D 19.4 mm; NMB H 17992, from same locality as largest specimen: H 34.1, D (dorsoventrally

compressed) 23.2 mm.

Types.—Holotype SGO.PI.4259, with 1 paratype SGO.PI.6443, from Lacui Fm (Early Miocene?), halfway between Punta Chabranal and Puerto Scotchwell, E coast of Isla Ipún, southern Chile (Nielsen & Frassinetti, 2008: 254, fig. 1C); 3 other specimens (SGO.PI.6444, SMF 330177-330178) reported by Nielsen & Frassinetti (2008: 254) from Lacui Fm (Late Oligocene/Early Miocene? – reworked into late Miocene-Pliocene rocks; Finger *et al.*, 2007) in cliffs on coast at Cucao, W coast of Chiloé Island, southern Chile.

Other material examined.—**Fossils: Venezuela: Late Early Miocene:** NMB 17241, Cantaure Fm (late Early Miocene), near Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela, from early Cantaure collection by O. Renz (2 specimens, NMB H 17991-2; 1 illustrated, Pl. 65, Figs 4-5); Cantaure Fm, all collected by J. & W. Gibson-Smith: NMB 17516 (2, NMB H 17997-17998); 17517 (1, NMB H 17999); 17518 (3, NMB H 18000-18002); 17519 (4, one illustrated, NMB H 17993, Pl. 65, Figs 2, 8; 3, NMB H 17994-17996); 17520 (2, NMB H 18003-18004).

Remarks.—*Ipunina vladimiri* is included here because I initially thought it was a species of *Oocorys* (Cassidae Oocorythidae) related to *O. elevata* Dall, 1908 (Pl. 65, Figs 6-7, 9; Beu, 2008: figs 21I, 22D, G), from bathyal depths (over 4000 m) in the eastern Pacific. However, Nielsen & Frassinetti (2008) illustrated slightly more complete specimens from southern Chile of what seems to be the same species, described as the new genus and species *I. vladimiri*, and pointed out that its protoconch is taller and narrower than that of any planktotrophic Tonnoidea. Its protoconch has a narrow apex, concave outlines, and sculpture of curved (anteriorly concave) axial riblets over the upper half of each whorl and reticulate, thin, raised spiral cords and curved (posteriorly concave) axial riblets over the lower half, with the two segments separated by a low, narrow spiral ridge. This protoconch much more nearly resembles those of planktotrophic cerithioideans than of tonnoideans, and in particular resembles that of members of *Litiopa* Rang, 1829. The anterior area of the aperture, with a convex lower columella and a slight anterior sulcus but no true siphonal canal, also resembles that of *Litiopa*. The teleoconch is so exceedingly thin that all of the Cantaure specimens are partly moldic and partly shelly, with very little shell material present on any specimens, supporting the possibility that *Ipunina* was epiplanktonic on floating objects, in the same manner as *Litiopa*. *Litiopa melanostoma* has been reported floating attached to *Sargassum* leaves (Houbrick, 1987: 9, fig. 6) and to algae, logs, and pumice (Okutani *et al.*, 1983); adult shells reach up to 35 mm H (Okutani *et al.*, 1983).

Oocorys elevata is one of the most unusually shaped species in the Cassidae, because of its thin shell and very tall spire.

The holotype (Pl. 65, Figs 6-7, 9; apparently still the only known specimen) is quite a large specimen (60 mm H, height of aperture 35 mm, diameter 31 mm) but with a very thin shell, with a very slightly enclosed, weakly dorsally inclined, open siphonal canal, with quite evenly convex whorls, and with sculpture of low, narrow, flat-topped spiral cords, 10 on spire whorls and “about 22” on the last whorl and base (Dall, 1908: 322). The operculum (Pl. 65, Fig. 7) is standard for *Oocorys*, relatively short and wide, with spiral growth lines on the initial, juvenile area near the anterior nucleus, but with more obviously commarginal growth lines later. *Ipunina vladimiri* is similar to *O. elevata* in many characters, particularly in the flat-topped, well-raised, widely spaced spiral cords, but is easily distinguished by its shorter shape, the flattened sides of the lower few whorls, the rounded but well marked basal angulation, and the flattened base. It also seems not to have had a siphonal canal, but merely a weakly angled base of the outer lip where it joins the columella. The protoconch of *O. elevata* is not preserved, but to judge from *O. clericus* (see above) (Warén & Bouchet, 1990: fig. 119, as *O. bartschi* Rehder, 1943; reidentified by Beu, 2008) and *O. sulcata* Fischer, 1884 (Bouchet & Warén, 1993: 800, fig. 1920), *Oocorys* species all have the classic tonnoidean planktotrophic protoconch, as in *Sassia apenninica*: turbiniform with widely spaced, reticulate, axial and spiral ridges, the axial ridges simple and straight and the spiral ridges present over the entire surface. The protoconch therefore demonstrates conclusively that *Ipunina* is not a tonnoidean. A position in Litiopidae was suggested by Nielsen & Frassinetti (2008) and is accepted here. Good illustrations of *Litiopa melanostoma* (probably the one Recent species of the genus, virtually cosmopolitan in warm seas) were provided by Robertson (1971: 5, pls 2-4), Okutani *et al.* (1983), Houbrick (1987: 10-12, figs 1-9), and Healy & Wells (1998: 715, figs 15.87A, C). The protoconch of *Litiopa* differs from that of *Ipunina* in its narrower shape, its more robust axial sculpture, and in having a “*Sinusigera*” claw at the end, but the similarities are important: subdivision of the sculpture by a median spiral ridge, above and below which the axial ridges are directed slightly differently, and the “spiral” sculpture formed as groups of short ridges between the axial elements, rather than long, continuous cords as on tonnoidean protoconchs. Also, the termination is not well enough preserved in the illustrated specimen of *I. vladimiri* to tell whether it had a “*Sinusigera*” claw or not. The similarities seem likely to reflect a close phylogenetic relationship, and I regard *Ipunina* as an inflated, thin-shelled, prominently spirally sculptured litiopid.

Distribution.—*Ipunina vladimiri* is recorded only from the late Early Miocene Cantaure Fm on Paraguaná Peninsula, Estado Falcón, Venezuela, and from two Oligocene/Early

Miocene localities in southern Chile, on the eastern coast of Ipún Island and at Cucao on Chiloé Island. This very wide distribution helps to confirm the inference from protoconch characters that *Ipunina* was planktotrophic, and probably epiplanktonic on floating objects. This species can be expected at further American localities.

TRANSFERRAL OF *NEOSCONSIDA* OLSSON, 1964, FROM THE CASSIDAE TO THE BUCCINIDAE

Family **BUCCINIDAE** Rafinesque, 1815
Genus ***NEOSCONSIDA*** Olsson, 1964

Neosconsis Olsson, 1964: 167. Type species (by original designation): *N. ecuadoriana* Olsson, 1964, Pliocene, Ecuador.

Neosconsis ecuadoriana Olsson, 1964
Pl. 67, Figs 4, 6

Neosconsis ecuadoriana Olsson, 1964: 168, pl. 30, figs 5, 5a.

Remarks.—The opportunity is taken here to remove this genus and species from the Cassidae. The type species is reillustrated here for comparison with species of *Sconsis*. *Neosconsis ecuadoriana* has none of the essential characters of a tonnoidean. Instead it shares its moderately elongate shape, its sculpture of very weak spiral cords, its relatively long (at least, compared with that of *Sconsis*) but gradually contracted siphonal canal, and its narrowly callused aperture with a narrow posterior excurrent notch, with such genera of Buccinidae as *Celatoconus* Conrad, 1862 (Petuch, 1988b: 48, pl. 7, figs 1-2, pl. 13, fig. 11; 1994: 174, pl. 66, fig. L). In my opinion, *N. ecuadoriana* is a member of the family Buccinidae, and certainly it does not belong in the Cassidae.

Neosconsis ecuadoriana is common in collections from the Onzole Fm (Pliocene) in Ecuador, particularly from Quebrada Camarones. Many specimens still bear faint remnants of the color pattern, which consists of many long, narrow, slightly irregular axial stripes (Olsson, 1964: pl. 30, fig. 5a), now faded to pale orange, alternating with the background rather deep cream stain of all aragonitic fossils from this formation. The axial stripes are similar in width and spacing to the spiral cords.

Dimensions.—Figured specimen, NMB H 18017, from NMB 19018 (TU 1397), Onzole Fm (Early Pliocene), Quebrada Camarones: H 44.5, D 24.4 mm; holotype: H 52.0, D 26.1 mm; paratypes: H 37.4, D 19.5 mm; H 39.3, D 20.0 mm (Olsson, 1964: 163).

Types.—*Neosconsis ecuadoriana*, holotype USNM 644216, from Onzole Fm (Early Pliocene) at Punta Gorda, Ecuador; paratype(s?) USNM 644217, from Onzole Fm in Quebrada Camarones, 20 km by road E of bridge over Río Esmeraldas

and 11 km straight-line E of Esmeraldas town, Ecuador. Olsson (1964: 168) provided dimensions of 3 specimens but the type status and USNM numbers of only two of them; the largest, cited first, is the holotype to judge from the figure captions (Olsson, 1964: 237) so the second and third specimens with cited dimensions are apparently both paratypes, despite the citation of only one registration number.

Other material examined.—**Fossils: Ecuador: Early Pliocene:** All material from Onzole Fm in and near Quebrada Camarones: TU 1397 = NMB 19018, Quebrada Camarones, type locality of *N. ecuadoriana*, 20 km E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town (4; 1 illustrated, NMB H 18017; Pl. 67, Figs 4, 6); NMB 12821 (2); 12822 (14); 12824 (2); 12825 (4); 19137 (3); 19138 (1 small); 19141 (6).

Distribution.—*Neosconsis ecuadoriana* is limited to the Onzole Fm (Early Pliocene) at Punta Gorda, Esmeraldas Province, and in Quebrada Camarones, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town, Ecuador. Olsson (1964: 14) stated that most of the mollusks at Punta Gorda were collected from a large “rubble lens” 30 m long and 3 m thick, with admixed exotic pebbles, wood, abraded shallow-water mollusks, and well-preserved deep-water mollusks, whereas the mollusks at Quebrada Camarones are *in situ*.

TRANSFERRAL OF SOUTH AMERICAN FOSSIL TAXA FROM RANELLIDAE TO MURICIDAE

Several species that were thought to belong in the Ranellidae by Cossmann (1899) and Ihering (1897, 1907) are here transferred to the Muricidae. They were placed in the Ranellidae because they apparently have varices, but of course varices merely indicate that a species has episodic growth, and occur in many gastropod families. The species listed here only have “varices” in the sense of an irregularly expanded outer lip, in any case, indicating shell damage during life, rather than a true varix.

Family **MURICIDAE** Rafinesque, 1815
Genus ***OCENEBRA*** Gray, 1847

Ocenebra Gray ex Leach MS, 1847: 133. Type species (by monotypy): *Murex erinaceus* Linnaeus, 1758, Recent, Europe.

Ocenebra(?) rada (Ihering, 1907)

Lotorium (Lampusia) rada Ihering, 1907: 175, pl. 5, fig. 29 (not fig. 25, as stated in text).

Remarks.—The type material of “*Lotorium*” *rada*, supposedly from Rada Tilly, a beach and coastal town 10 km south of

Comodoro Rivadavia, eastern coast of Argentina, and several other lots at MLP from nearby localities, show that this species has a calcitic outer shell layer, and some specimens have low, obscurely defined varices at irregular intervals down the entire teleoconch. It is clear that *L. rada* is an ocenebrine muricid. The weak inflation and the style of low, wide, very prominent spiral cords separated by deep, wide, flat-bottomed grooves are not typical of *Ocenebra* itself, and the generic position is not certain, but what is certain is that *L. rada* does not belong in the Ranellidae.

As pointed out by the authors, the recently described ocenebrine genus and species *Argenthina emilyae* Herbert & Del Rio (2005) is very similar to *Ocenebra(?) rada*, and could well be closely related phylogenetically, although Herbert & Del Rio (2005: 940) pointed out a number of minor characters distinguishing *Lotorium rada* from *Argenthina*, including its taller spire, dentate outer lip, and lack of carinate spire whorls and posterior sulcus. However, this relationship is useful for confirming a position in the Muricidae for *L. rada*. Other South American Neogene Muricidae described by DeVries (2004a, b) from Peru and Chile show some similarities to *Ocenebra(?) rada*, and there is no doubt that *O. rada* belongs among the distinctive South American genera of Ocenebrinae, probably requiring a new genus. Another similar species, "*Fusus*" *noachinus* G. B. Sowerby I, 1846, from Miocene rocks at Port San Julian, Patagonia, was illustrated by Griffin & Nielsen (2008: 300, pl. 22, figs 1-4), who commented that "it may belong in a new, as yet undescribed, genus of muricids common in Oligocene and Miocene rocks from southern South America." A further similar species, possibly belonging in *Argenthina*, is "*Siphonalia*" *iheringi* Steinmann & Wilckens (1908: 67, pl. 7, fig. 3) from Miocene rocks at Carmen Silva, central Tierra del Fuego. These South American muricids are in need of generic revision.

Attempts by Miguel Griffin (University of La Pampa, Santa Rosa, Argentina) to recollect fossils from the supposed type locality at Rada Tilly on several occasions, including a visit with me during January 1998, were unsuccessful. The enormous, clean, beautifully exposed cliff outcrops both north and south of the beach at Rada Tilly seem entirely to lack fossils, and there is therefore considerable doubt about the provenance of the type material. However, it is conceivable that the collector of the type material, Carlos Ameghino, found a small lens of calcitic gastropods at Rada Tilly and collected all of the material.

Type material.—*Lotorium (Lampusia) rada*, holotype MACN Ihering type collection no. 793, from Rada Tilly, Patagonia (Miocene?).

Genus *XYMENE* Iredale, 1915

Kalydon Hutton 1883: 576; 1884: 222 (Marshall 1995: 495). Type species (by monotypy): *Fusus plebeius* Hutton, 1873, Pleistocene and Recent, New Zealand (suppressed, ICZN Opinion 911, 1970). Iredale (1915: 471) pointed out that *Kalydon* is a junior homonym of *Kalydon* Thomson, 1864, and this is still correct under the current ICZN Article 58.5.

Xymene Iredale 1915: 471. Type species (by original designation): *Fusus plebeius* Hutton, 1873.

Xymene obliterated (Cossmann, 1899)

Lotorium oblitteratum Cossmann, 1899: 238, pl. 11, figs 9-10.

Xymene dautzenbergi. Beu *et al.*, 1997: 93 (in part not *Triton dautzenbergi* Ihering, 1897).

Remarks.—The holotype of *Lotorium oblitteratum* looks particularly nondescript in Cossmann's (1899: pl. 11, figs 9-10) illustrations because it is heavily encrusted with a bryozoan, which hides most of the outer surface and obscures the suture. Such encrusting bryozoans are common on *Xymene* and *Urosalpinx* material from the Monte Leon Fm in southern Argentina, as well as on other, similarly shaped small gastropods such as Columbellidae, and I have observed specimens with less encrustation that are easily identified. This small shell (*ca.* 18 mm H) has evenly convex whorls, "varices" only in the sense of low ridges formed by former weakly flared, weakly thickened outer lips, situated irregularly all down the teleoconch, and sculpture of numerous narrow, cancellate spiral cords and axial costae. It is a typical species of the muricid ("trochophore") genus *Xymene* previously thought to be limited to New Zealand, but recorded from Argentina by Beu *et al.* (1997) on the basis of this species (and confused at that time with the following species).

Types.—*Lotorium oblitteratum* Cossmann, MACN Ihering type collection no. 792, from bluff on S side of the Santa Cruz River a short distance upstream from the mouth, Patagonia; from Mount Entrance Member, Monte Leon Fm, Late Oligocene/Early Miocene.

Genus *UROSALPINX* Stimpson, 1865, *sensu lato*

Urosalpinx Stimpson, 1865: 58. Type species (by original designation): *Fusus cinereus* Say, 1822, Recent, western Atlantic from Nova Scotia to northeastern Florida (Abbott, 1974: 179).

Urosalpinx (sensu lato) dautzenbergi (Ihering, 1897)

Triton (Argobuccinum) dautzenbergi (sic) Ihering, 1897: 293, fig. 16.

Lotorium (Lampusia) usurpator Ihering, 1907: 175, pl. 5, figs 28a-b.

Lotorium dautzenbergi. Ihering, 1907: 176.

?*Urosalpinx archipatagonica* Ihering, 1907: 189, pl. 6, fig. 35.

Xymene dautzenbergi. Beu *et al.*, 1997: 93 (in part not *Triton dautzenbergi* Ihering, 1897).

Remarks.—This small muricid is again based on poorly preserved specimens with “varices” only in the sense of weakly flared outer lips remaining at irregular intervals down the whole teleoconch, and definitely does not belong to the Ranellidae. Some specimens, particularly the holotype of *Lotorium dautzenbergi*, closely resemble other, better preserved specimens described by Ihering under the name *Urosalpinx archipatagonica* Ihering (1907: 189, pl. 6, fig. 35) and seem to be conspecific. Ihering’s holotype of *L. usurpator* also seems to be conspecific, although it again supposedly came from Rada Tilly (and appears to be calcitic), whereas all the other material seen of this species is aragonitic and comes from the mouth of the Santa Cruz River (and so might well be significantly older, Late Oligocene/Early Miocene rather than Middle-Late Miocene). The holotype of *L. usurpator* has several high but extremely irregular varices, the last just a quarter-whorl behind the aperture, indicating considerable shell damage during life. It is also poorly preserved in other ways, abraded and with the aperture only partly visible, and seems to be a calcite neomorph, but axial costae and spiral cords on parts of the shell are very similar to those of the type material of *Triton dautzenbergi* and to Ihering’s figure of *U. archipatagonica*. The “false varices” seem to indicate that this is a muricid, and a position in *Urosalpinx sensu lato* is suggested, but needs confirmation. *Urosalpinx dautzenbergi* resembles some of the North American *Urosalpinx* species illustrated by Abbott (1974: 179) quite closely (*U. perrugata* Conrad, 1846; *U. macra* Verrill, 1887). The shells of *U. dautzenbergi* are a little larger than those of *Xymene obliteratus*, and have a taller spire and considerably more prominent axial ridges. The very simple aperture and short siphonal canal resemble those of small buccinids such as the Australian-New Zealand genus *Buccinulum*. These Patagonian Muricidae urgently need revision based on much more material, but at present it seems appropriate to transfer them to *Urosalpinx sensu lato*, to demonstrate their position in Muricidae.

Although Ihering (1897, 1907) consistently spelled the species name “dautzenbergi,” there is no doubt that he proposed it to honor the well-known malacologist Philippe Dautzenberg, and the spelling is corrected here.

Types.—*Triton (Argobuccinum) dautzenbergi*, holotype MACN Ihering type collection no. 791, from bluff on the S side of the Santa Cruz River a short distance upstream from the mouth, Patagonia; Mount Entrance Member, Monte Leon Fm, Late Oligocene/Early Miocene; *Lotorium (Lampusia)*

usurpator, holotype MACN Ihering type collection no. 794, from Rada Tilly, Patagonia (Miocene?); *Urosalpinx archipatagonica*, type material not seen.

APPENDIX 3: FOSSIL LOCALITIES

Lists are provided here of all the Naturhistorisches Museum Basel (NMB), Tulane University (TU), and United States Geological Survey (USGS) fossil localities cited in the text (the many fewer localities for collections stored in other institutions are cited more fully in the text). Localities are listed in numerical order under countries, in the same order as in the text, with the equivalent Panama Paleontology Project (PPP) numbers (when they exist), formation, age, and a brief locality description for each locality. Latitude and longitude are provided for all PPP localities in the PPP database (<http://www.fiu.edu/~collins/pppdatabase.html>), and are not repeated here. Full details of field number, grid reference, etc., of NMB localities are listed in the NMB computer-based catalog; this list is based on that catalog, augmented by information from the PPP database for localities in Pacific Costa Rica and Pacific Panama (because these areas were not covered by Saunders *et al.*, 1986, or Collins & Coates, 1999). NMB, TU, and USGS localities were also mapped on many figures by Saunders *et al.* (1986), and (as PPP numbers) in Appendix A of Collins & Coates (1999). For localities listed here, only the locality number is cited in lists in the text, except for new taxa, or in other cases where very few localities are listed.

Specific references to Dominican Republic localities mapped on the text-figures of Saunders *et al.* (1986) are included for some individual “indicator” localities. All Dominican Republic localities are mapped on these figures, but only a few localities are highlighted here; others can easily be found on the maps, interspersed between the identified ones. For PPP localities, references have been added to maps of Coates (Appendix A in Collins & Coates, 1999) where the detailed location of almost all localities is shown by their PPP numbers. Note, though, that the latest collections (PPP > 3000) are not shown on these maps.

Locality name duplication.—Note that there is a Punta Gavilán on both the northeastern coast of Venezuela (referred to frequently) and the Atlantic coast of Panama, west of Río Indio (referred to only a few times here). In the Bocas del Toro Basin, northeastern Panama, there is a Punta di Nispero on the northern coast of both Cayo Agua (referred to only a few times here) and Valiente Peninsula (referred to frequently; also known as Chong Point). The name Colon is also in use for both the well-known city on the Atlantic coast of Panama, and the island in the Bocas del Toro Group in northeastern Panama on which the town of Bocas del Toro is situated.

NATURHISTORISCHES MUSEUM BASEL (NMB) LOCALITIES

Florida, USA

NMB 19030 = TU59, Chipola Fm (late Early Miocene), E bank of Chipola River, Calhoun County, Florida.

Mexico

NMB 19016 = TU 1318, Lower Concepción Fm (Pliocene), cutting on pipeline just to NE of Campo el Chapo, 4 km S of Mexico Highway 180 at Nueva Teapa, Isthmus of Tehuantepec, Veracruz.

NMB 19020 = TU 1046, Agueguexquite Fm (Pliocene), Perrilliat's (1963) locality, cutting on Mexico Highway 180, Isthmus of Tehuantepec.

NMB 19031 = TU 638, Agueguexquite Fm (Pliocene), cutting on Mexico Highway 180 near Perrilliat's (1963) locality, Isthmus of Tehuantepec, Veracruz.

Atlantic coast of Costa Rica

NMB 17445 = PPP 1726, Banáno Fm (Pliocene) type locality, Río Banáno, S of Limón, Bomba, left bank, 700 m S of railway bridge, soft muddy sandstone with hard, nodular sandstone, Coates (1999: 298, map 11, inset C).

NMB 17446 = PPP 1727, locality same as above, blue sandy mudstone with sandier layers, Coates (1999: 298, map 11, inset C).

NMB 17448 = PPP 1729, locality same as above, 500 m SW of railway bridge, Coates (1999: 298, map 11, inset C).

NMB 17450 = PPP 1731, locality same as above, immediately underlying NMB 17448, Coates (1999: 298, map 11, inset C).

NMB 17453 = PPP 1764, locality same as above, slipped quarry at road, overlying the above localities, Coates (1999: 298, map 11, inset C).

NMB 17477, Banáno Fm (Pliocene), La Bomba, Río Banáno, ca. 500 m SW of railway bridge, near Limón (= NMB 17448, 17450, 17779, 18095), Coates (1999: 298, map 11, inset C).

NMB 17774 = PPP 451, Banáno Fm (Pliocene), La Bomba, 600 m SW of bridge, Río Banáno, new landslide outcrop above road, Coates (1999: 298, map 11, inset C).

NMB 17779 = PPP 456, Banáno Fm (Pliocene), La Bomba, Río Banáno, ca. 500 m SW of railway bridge, near Limón (= NMB 17447-17448, 17450, 18095), Coates (1999: 298, map 11, inset C).

NMB 17784 = PPP 461, locality same as above, 700 m SW of bridge, type locality of Banáno Fm, middle of exposed section (= NMB 17445), Coates (1999: 298, map 11, inset C).

NMB 17789 = PPP 466, Moín Clay (late Pliocene-early Pleistocene), float from artificial trench, Route 32, between Cemeterio General and Progressive Baptist Church, 500 m WSW of WSW corner of city of Limón, Coates (1999: 297, map 11, inset B).

NMB 17792 = PPP 469, Moín Fm (late Pliocene-early Pleistocene), bulldozed area 150 m NNE of Standard Fruit Company box factory, 1300 m WSW of WSW corner of Limón city, Coates (1999: 297, map 11, center of inset B).

NMB 18078 = PPP 627, Moín Fm (late Pliocene-early Pleistocene), junction of roads halfway between Limón and Pueblo Nuevo, 100 m by 150 m bulldozed surface, 100-200 m E of Colegio

Tecnico Industrial, Coates (1999: 297, map 11, inset B).

NMB 18079 = PPP 757, Moín Fm (late Pliocene-early Pleistocene), clay with delicate branching corals, slope terraced by bulldozers, Lomas del Mar, W of Bella Vista, Limón, Coates (1999: 297, map 11, inset B).

NMB 18084 = PPP 1982, Moín Clay with layer of corals (late Pliocene-early Pleistocene), Lomas del Mar, W of Bella Vista, Limón, W margin of newly bulldozed area, Coates (1999: 297, map 11, inset B).

NMB 18095 = PPP 1984, Banáno Fm (Pliocene), Río Banáno, near Limón, ca. 500 m SW of railway bridge (= NMB 17448, 17450, 17477, 17779), Coates (1999: 298, map 11, inset C).

NMB 18096 = PPP 679, Banáno Fm (Pliocene), locality same as above, outcrop below road, Coates (1999: 298, map 11, inset C).

NMB 18100 = PPP 1986, Banáno Fm (Pliocene) type locality, Río Banáno, near Limón, 700 m SW of railway bridge (= NMB 17445, 17784), Coates (1999: 298, map 11, inset C).

NMB 18105 = PPP 709, Moín Fm (late Pliocene-early Pleistocene), Colonia Santa Rita, 2 km S of Liverpool, 10 km W of Limón, road outcrop, Coates (1999: 295, map 11).

NMB 18112 = PPP 723, Moín Fm (late Pliocene-early Pleistocene), locality same as above, outcrop in small creek 80 m WSW of NMB 18105, Coates (1999: 295, map 11).

NMB 18113 = PPP 1988, Moín Fm (latest Pliocene-Early Pleistocene), terraced slope, Lomas del Mar, W of Bella Vista, Limón, Coates (1999: 297, map 11, inset B).

NMB 18263 = PPP 925, top of Banáno Fm (Pliocene), Río Viscaya, ca. 3.5 km SSE of Quitaria, Limón, Coates (1999: 298, map 11, bottom of inset C).

NMB 18264 = PPP 931, Banáno Fm (Pliocene), locality same as above, 500 m further downstream, Coates (1999: 298 map 11, bottom of inset C).

NMB 18272 = PPP 943, Moín Fm (late Pliocene-early Pleistocene) with corals, bulldozed area S and SE of Lomas del Mar, SW of Bella Vista, Limón, Coates (1999: 297, map 11, inset in inset B).

NMB 18273 = PPP 944, Moín Fm (late Pliocene-early Pleistocene), locality same as above, Coates (1999: 297, map 11, inset in inset B).

NMB 18274 = PPP 948, Moín Fm (late Pliocene-early Pleistocene), locality same as above, Coates (1999: 297, map 11, inset in inset B).

NMB 18275 = PPP 951, Moín Fm (late Pliocene-early Pleistocene), locality same as above, reef with corals, Coates (1999: 297, map 11, inset in inset B).

NMB 18276 = PPP 962, Moín Fm (late Pliocene-early Pleistocene), locality same as above, float from reef, Coates (1999: 297, map 11, inset in inset B).

NMB 18277 = PPP 950, Moín Fm (late Pliocene-early Pleistocene), locality same as above, clay with mollusks, Coates (1999: 297, map 11, inset in inset B).

NMB 18278 = PPP 963, Moín Fm (late Pliocene-early Pleistocene), locality same as above, float, Coates (1999: 297, map 11, inset in inset B).

NMB 18752 = PPP 969, Moín Fm (late Pliocene-early Pleistocene), trench at construction site, Lomas del Mar, Limón.

NMB 19007 = TU 1239, Moín Fm (latest Pliocene-Early Pleistocene), hill cut above Standard Fruit Company box factory at Pueblo Nuevo, just W of cemetery at Pueblo Nuevo, 2 km W of Puerto Limón, *ca.* 13 m higher in section than TU 954, and 1.4 km S of TU 1240.

NMB 19008 = TU 1240, Moín Fm (late Pliocene-early Pleistocene), Puerto Limón.

NMB 19015 = TU 1307, Moín Fm (late Pliocene-early Pleistocene), hilltop between Puerto Limón and Barrios los Corales.

NMB 19024 = TU 589, Banáno Fm (Pliocene), La Bomba, Río Banáno, near Limón.

NMB 19026 = TU 954, Moín Fm (latest Pliocene-Early Pleistocene), 2 km W of Puerto Limón.

Pacific coast of Costa Rica

NMB 17471 = PPP 1738 (= PPP 287, 761, 825), Montezuma Fm (Pleistocene), 100 m-long outcrop at tide level, SE coast of Playa Cocalito, ENE of Montezuma village, Nicoya Peninsula.

NMB 17474 = PPP 1780, hard sandstone [late Oligocene-early Miocene(?)], 2 km N of village of Malpais, SW coast of Nicoya Peninsula.

NMB 17736 = PPP 237, Armuelles Fm (Pleistocene), at coastal road bridge over Quebrada El Higo, 5 km NE of Punta Blanco, S end of Golfo Dulce.

NMB 17739 = PPP 244, Armuelles? Fm (Pleistocene), Quebrada el Macho, *ca.* 4 km upstream from mouth and 100-200 m downstream from waterfall, 4 km NE of Punta Blanco, Golfo Dulce.

NMB 17745 = PPP 436, Armuelles Fm (Pleistocene), float from lower reaches of Quebrada El Higo, to basalt contact, 5 km NE of Punta Blanca, Golfo Dulce.

NMB 17746 = PPP 273, Armuelles Fm (Pleistocene, large *Gephyrocapsa* zone, 1.7 Ma), Quebrada El Higo, Burica Peninsula, float from upstream of first waterfall.

NMB 17749 = PPP 437, Armuelles Fm (Pleistocene), Quebrada El Higo, Burica Peninsula, blue silts with *Ficus* *ca.* 500 m downstream from basalt.

NMB 17752 = PPP 262, Armuelles Fm (Pleistocene), Quebrada El Higo, Burica Peninsula, *ca.* 1500 m downstream from basalt.

NMB 17753 = PPP 274, Late Miocene, Punta Judas, 40 km WSW of Quepos, 2 m-thick concretionary sandstone bed at middle of Punta Judas.

NMB 17754 = PPP 439, locality same as above, 10 m-thick concretionary sandstone bed overlying NMB 17753 by 5 m.

NMB 17755 = PPP 440, locality same as above, concretionary sandstone overlying NMB 17754, 100 m E of E-most bed of Punta Judas.

NMB 17757 = PPP 275, locality same as above, 20 m-thick sandstone with shellbed, 500 m E of NMB 17753.

NMB 17758 = PPP 277, locality same as above, 20 m-thick sandstone with shellbed, 1 km E of NMB 17753.

NMB 17760 = PPP 443, locality same as above, 2 concretionary beds of *Chione*, 4 m apart, 50 m E of NMB 17758.

NMB 17764 = PPP 282, locality same as above, slipped reddish bed with abundant *Anadara*, above high tide line, 2.87 km E of NMB 17753.

NMB 17767 = PPP 288 (= PPP 761, 825, 1738), Montezuma Fm (Pleistocene, with *Gephyrocapsa oceanica*), 1 m-thick greenish

sandstone at high tide line, SE coast of Playa Cocalito, ENE of Montezuma village, SE coast Nicoya Peninsula.

NMB 17771 = PPP 291, Montezuma Fm (Pleistocene), WSW end of Playa Cocalito, SE coast Nicoya Peninsula.

NMB 17799 = PPP 289, Montezuma Fm (Pleistocene), exposed at low tide, 250 m SW of NMB 17471 (= NMB 17767), Playa Cocalito, NE of Montezuma village, SE coast Nicoya Peninsula.

NMB 18035 = PPP 501, Charco Azul Group, lower member Penita Fm (Pliocene, 3.5 Ma), bend with 10 m-high outcrop, W tributary of Quebrada La Penita, Burica Peninsula.

NMB 18037 = PPP 502, Charco Azul Group, lower member Penita Fm (Pliocene), 50 m-high outcrop 450 m downstream from NMB 18035, W tributary of Quebrada La Penita, Burica Peninsula.

NMB 18039 = PPP 741, Penita Fm? (Pliocene), locality same as above, float.

NMB 18042 = PPP 507, Charco Azul Group, lower member Penita Fm (Pliocene), W tributary of Quebrada La Penita, Burica Peninsula, blue silts in right bank, outcrop 20 m high, downstream from above localities.

NMB 18043 = PPP 742, Charco Azul Group, lower member Penita Fm (Pliocene), locality same as above, 50 m further downstream.

NMB 18047 = PPP 743, Charco Azul Group, lower member Penita Fm (Pliocene), locality same as above, in Quebrada La Penita, 130 m downstream from confluence with W tributary.

NMB 18049 = PPP 519, Charco Azul Group, lower member Penita Fm (Pliocene), locality same as above, 550 m downstream from NMB 10847.

NMB 18052 = PPP 1979, Charco Azul Group, lower member Penita Fm (Pliocene), Boca Penita, coast 150 m N of mouth of Quebrada La Penita, Burica Peninsula.

NMB 18053 = PPP 745, Charco Azul Group, Penita Fm? (Pliocene), float from upper part of Quebrada la Penita, above confluence with W tributary, Burica Peninsula.

NMB 18054 = PPP 746, Charco Azul Group, Penita Fm? (Pliocene), Quebrada la Penita, Burica Peninsula, block of fossiliferous silt near waterfall *ca.* 200 m upstream from confluence with E tributary.

NMB 18055 = PPP 747, Charco Azul Group, Penita Fm (Pliocene), locality same as above, 100 m upstream from NMB 18054.

NMB 18056 = PPP 748, Charco Azul Group, Penita Fm (Pliocene), locality same as above, upper part Quebrada La Penita, 1 km upstream from NMB 18055.

NMB 18057 = PPP 749, Charco Azul Group, Penita Fm (Pliocene), locality same as above, upper part of Quebrada la Penita, downstream end of NMB 18056 outcrop.

NMB 18116 = PPP 761 (= PPP 287, 825, 1738), Montezuma Fm (Pleistocene), greenish silts, 100 m-long outcrop at tide level, SE coast of Playa Cocalito, ENE of Montezuma village, Nicoya Peninsula (= NMB 17471, 17476, 17767, 18161).

NMB 18153 = PPP 838, Armuelles Fm (Pleistocene), float, Río Claro, S coast Osa Peninsula.

NMB 18160, Montezuma Fm (Pleistocene), 80 m above sea level, trail between Quebrada Manchas and Río Montezuma, SE coast 1 km SSW of village of Montezuma, Nicoya Peninsula.

- NMB 18161 = PPP 825 (= PPP 287, 761, 1738), Montezuma Fm (Pleistocene), greenish silts, SE coast of Playa Cocalito ENE of village of Montezuma, Nicoya Peninsula (= NMB 17471, 17467, 17767, 18116).
- NMB 18284 = PPP 991, Armuelles Fm (Pleistocene), lower course of Río La Vaca, Golfo Dulce, 35 km SE of Golfito.
- NMB 18285 = PPP 992, Armuelles Fm (Pleistocene), locality same as above, 200 m downstream from NMB 18284.
- NMB 18287 = PPP 994, Armuelles Fm (Pleistocene), locality same as above, 480 m downstream from NMB 18284.
- NMB 18288 = PPP 995, Armuelles Fm (Pleistocene), locality same as above, continuation of outcrop 200 m downstream from NMB 18287.
- NMB 18289 = PPP 1991, Armuelles Fm (Pleistocene), locality same as above, just above confluence with Quebrada la Mona, Golfo Dulce.
- NMB 18293 = PPP 1992, Charco Azul Group, Penita Fm (Pliocene), Quebrada Piedra Azul, tributary of Río La Vaca, *ca.* 720 m downstream from waterfall, Golfo Dulce.
- NMB 18294 = PPP 1013, Charco Azul Group, Penita Fm (Pliocene), Quebrada Piedra Azul, tributary of Río La Vaca, 300 m downstream from confluence with Quebrada Ojo de Agua, Golfo Dulce.
- NMB 18295 = PPP 1014, Charco Azul Group, Penita Fm (Pliocene), locality same as above, 100 m downstream from NMB 18294.
- NMB 18303 = PPP 1026, Armuelles Fm (Pleistocene), Neilly, above bridge on right bank Río Corredores, Golfo Dulce.

Atlantic coast of Panama

- NMB 17621 = PPP 168, Escudo de Veraguas Fm (Late Pliocene), Escudo de Veraguas Island, Bocas del Toro Basin, W side of bay on SE side of island (= NMB 17843), Coates (1999: 298, map 4).
- NMB 17622 = PPP 170, Escudo de Veraguas Fm (Late Pliocene, NN15), Escudo de Veraguas Island, Bocas del Toro Basin, E side of bay on SE side of island (= NMB 17843), immediately overlies NMB 17621, Coates (1999: 298, map 4).
- NMB 17628 = PPP 180, Escudo de Veraguas Fm (Late Pliocene), locality same as above, NE coast of Escudo de Veraguas Island, Coates (1999: 298, map 4).
- NMB 17629 = PPP 191, Valiente Fm (mid to Late Miocene, Coates *et al.*, 2003), W side Valiente Peninsula, W Bahía Azul, "Finger" island, W of S tip of Cayo Toro, silts with 7 layers of concretions (= NMB 17824, 18375, 18711), Coates (1999: 291, map 5, inset A).
- NMB 17633 = PPP 217, Cayo Agua Fm (Late Pliocene), small island *ca.* 800 m SE of Punta Norte, Cayo Agua, Bocas del Toro Basin (= NMB 18398, 18719), Coates (1999: 293, map 6, inset B).
- NMB 17635 = PPP 201, Cayo Agua Fm (Late Pliocene), E coast Cayo Agua, SE of Punta Norte, Bocas del Toro Basin, *ca.* 600 m ESE of NMB 17633 (= NMB 17808, 18374, 18722, 18983, 18400), Coates (1999: 293, map 6, inset B).
- NMB 17637 = PPP 219, Lower Gatun Fm (Middle? Miocene), large surface outcrop NE of settlement, Residencial Dr. Martin Luther King, 1.2 km NW of Sabanita, Colon (= NMB 17871), Coates (1999: 287, map 1, inset).
- NMB 17638 = PPP 220, Lower Gatun Fm (Middle? Miocene), locality same as above, hill SE of houses, overlying NMB 17637, Coates (1999: 287, map 1, inset).
- NMB 17639 = PPP 221, Lower Gatun Fm (Middle? Miocene), locality same as above, indurated layers with pectens, large barnacles, first terrace N of trenches, Coates (1999: 287, map 1, inset).
- NMB 17643 = PPP 225, Middle Gatun Fm (Late Miocene), 100 m SE of refinery gates, Isla Payardi, Colon (= NMB 17868, 18261, 18307, 18342, 18360, 18391, 18662, TU 959), Coates (1999: 287, map 1, inset).
- NMB 17644 = PPP 226, Middle Gatun Fm (Late Miocene), Isla Payardi, hill slope above NMB 17643 (= NMB 17869, 18262, 18308, 18326, 18392, 18662, TU 960), Coates (1999: 287, map 1, inset).
- NMB 17645 = PPP 227, Middle Gatun Fm (Late Miocene), locality same as above, road cut S side dual carriageway, slightly W of junction of road to Isla Payardi with main road (R20), Coates (1999: 287, map 1, inset).
- NMB 17649 = PPP 231, Lower Gatun Fm (Middle? Miocene), large surface outcrop NE of settlement, Residencial Dr. Martin Luther King, 1.2 km NW of Sabanita, Colon, underlying NMB 17638, Coates (1999: 287, map 1, inset).
- NMB 17807 = PPP 373, Shark Hole Point Fm (Late Pliocene), *ca.* 1100 m SE of Punta Norte, E coast Cayo Agua, Bocas del Toro Basin (= NMB 17634, 18721), Coates (1999: 293, map 6, inset B).
- NMB 17808 = PPP 475, Cayo Agua Fm (Pliocene), Cayo Agua, point *ca.* 300 m ESE NMB 17807 (= NMB 17635, 18374, 18722, 18983, 18400), Coates (1999: 293, map 6, inset B).
- NMB 17812 = PPP 297, Cayo Agua Fm (Pliocene), E coast of Cayo Agua, W of Punta de Tiburón, Bocas del Toro Basin, directly overlying NMB 17811, Coates (1999: 293, map 6, inset F).
- NMB 17816 = PPP 310, Cayo Agua Fm (Pliocene), E coast of Cayo Agua, just S of Punta de Nispero, *ca.* 40 m S of double island, Coates (1999: 293, map 6, inset E).
- NMB 17822 = PPP 326, Cayo Agua Fm (Pliocene), E coast of Cayo Agua, small beach SW of promontory 230 m W of Punta de Nispero, 0.5-2.5 m above sea level (= NMB 18376, 18731), Coates (1999: 293, map 6, inset C).
- NMB 17823 = PPP 335, Cayo Agua Fm (Pliocene), 4 m above sea level, Punta Tiburón (= NMB 18732; "macromollusks from NMB 17907 included in identifications"), Coates (1999: 293, map 6, inset F).
- NMB 17824 = PPP 477, Valiente Fm (mid to Late Miocene), W side Valiente Peninsula, "Finger island" W of S tip of Cayo Toro, W of Bahía Azul, Bocas del Toro Basin, silts with 7 layers of concretions (= NMB 17629, 18375, 18711), Coates (1999: 291, map 5, inset A).
- NMB 17825 = PPP 340, Cayo Agua Fm (Pliocene), E coast Cayo Agua, 1.2 km S of Punta de Tiburón, Bocas del Toro Basin, below marker bed with solitary corals, Coates (1999: 293, map 6, inset F).
- NMB 17827 = PPP 339, Cayo Agua Fm (Pliocene), E coast Cayo Agua, 1.2 km S of Punta de Tiburón, Bocas del Toro Basin, highest horizon in section, Coates (1999: 293, map 6, inset F).
- NMB 17828 = PPP 341, Cayo Agua Fm (Pliocene), E coast Cayo

- Agua, 1.2 km S of Punta de Tiburón, Bocas del Toro, marker bed rich in solitary corals, Coates (1999: 293, map 6, inset F).
- NMB 17829 = PPP 348, Cayo Agua Fm (Pliocene), E coast Cayo Agua, 1.2 km S of Punta de Tiburón, Bocas del Toro Basin, below marker bed rich in solitary corals (= NMB 18733), Coates (1999: 293, map 6, inset G).
- NMB 17830 = PPP 345, Cayo Agua Fm (Pliocene), E coast Cayo Agua, 1.2 km SE of Punta de Tiburón, Bocas del Toro Basin, small island NE of NMB 17829, Coates (1999: 293, map 6, inset G).
- NMB 17831 = PPP 350, Cayo Agua Fm (Pliocene), E coast Cayo Agua, 1.3 km SE of Punta de Tiburón, Bocas del Toro Basin, opposite (E) of NMB 17830, Coates (1999: 293, map 6, inset G).
- NMB 17833 = PPP 359, Escudo de Veraguas Fm (mid-Late Pliocene), Escudo de Veraguas Island, Bocas del Toro Basin, NW coast of island, *ca.* 800 m E of Long Bay Point, Coates (1999: 289, map 4, inset B).
- NMB 17836 = PPP 363, Escudo de Veraguas Fm (Early-mid Pliocene), Escudo de Veraguas, Bocas del Toro Basin, N coast of island, *ca.* 730 m E of NMB 17833, island with concretionary sandstone overlain by sandstone with scattered mollusks, Coates (1999: 289, map 4, inset C).
- NMB 17840 = PPP 368, Escudo de Veraguas Fm (mid-Late Pliocene), Escudo de Veraguas, Bocas del Toro, N coast of island, 50 m NE of NMB 17839, Coates (1999: 289, map 4, inset C).
- NMB 17843 = PPP 478, Escudo de Veraguas Fm (Pliocene), Escudo de Veraguas, Bocas del Toro Basin, S coast of island, silts with scattered fossils (= NMB 17621-17622), Coates (1999: 289, map 4).
- NMB 17845 = PPP 480, Escudo de Veraguas Fm (Pliocene), locality same as above, *ca.* 60 m NNW of NMB 17844 (which is 200 m WSW of NMB 17621), Coates (1999: 289, map 4).
- NMB 17847 = PPP 431, Escudo de Veraguas Fm (mid-Pliocene), Escudo de Veraguas, Bocas del Toro Basin, S coast of island, just W of NMB 17846 (which is 80 m W of NMB 17845), Coates (1999: 289, map 4).
- NMB 17848 = PPP 482, Escudo de Veraguas Fm (Pliocene), locality same as above, *ca.* 80 m W of NMB 17847, Coates (1999: 289, map 4).
- NMB 17849 = PPP 483, Escudo de Veraguas Fm (Pliocene), locality same as above, *ca.* 100 m W of NMB 17848, Coates (1999: 289, map 4).
- NMB 17850 = PPP 373, Shark Hole Point Fm (Early Pliocene, NN15), SE-most part of outer coast, Valiente Peninsula, Bocas del Toro Basin, Bruno Bluff, Playa Colorado (= Playa Roja) (= NMB 18723).
- NMB 17854 = PPP 386, Shark Hole Point Fm (Early Pliocene), Shark Hole Point, outer coast Valiente Peninsula, Bocas del Toro Basin (= NMB 18701-18702), Coates (1999: 291, map 5, inset F).
- NMB 17855 = PPP 388, Shark Hole Point Fm (Early Pliocene), locality same as above, *ca.* 600 m W of NMB 17854 (= NMB 18703), Coates (1999: 291, map 5, inset F).
- NMB 17856 = PPP 390, Shark Hole Point Fm (Early Pliocene), locality same as above, *ca.* 300 m SW of NMB 17855 (= NMB 18726), Coates (1999: 291, map 5, inset F).
- NMB 17857 = PPP 392, Shark Hole Point Fm (Early Pliocene), locality same as above, *ca.* 130 m SW of NMB 17856 (= NMB 18727).
- NMB 17859 = PPP 397, Nancy Point Fm (Late Miocene), Chong (= Nispero) Point, outer coast Valiente Peninsula, Bocas del Toro Basin, conchoidal-fracturing silty clay overlain by 1.5 m of silt, Coates (1999: 291, map 5, inset F).
- NMB 17862 = PPP 422, Cayo Agua Fm? (Pliocene), NE coast Isla Popa, Bocas del Toro Basin, 1100 m NE of Cerro Popa, Coates (1999: 292, map 7).
- NMB 17868 = PPP 487, Middle Gatun Fm (Late Miocene), Isla Payardi, top of hill 100 m S of entrance to refinery (= NMB 17643, 18261, 18307, 18324, 18360, 18391), Coates (1999: 287, map 1, inset).
- NMB 17871 = PPP 490, Middle Gatun Fm (Late Miocene), Residencial Dr. Martin Luther King, 1.2 km NW of Sabanita, Colon, surface collection, behind settlement (= NMB 17637), Coates (1999: 287, map 1, inset).
- NMB 17904 = PPP 346, Cayo Agua Fm (Late Pliocene), E coast Cayo Agua, between Punta Piedra Roja and Punta de Tiburón, overlies NMB 17830, Coates (1999: 293, map 6, inset G).
- NMB 18257 = PPP 1031, Lower Gatun Fm (Late Miocene), Fabrica de Colchones, E of Cativa, Colon, bluish silts rich in fossils, Coates (1999: 287, map 1, inset).
- NMB 18258 = PPP 1034, Lower Gatun Fm (Late Miocene), locality same as above, 12 m of bluish silts, Coates (1999: 287, map 1, inset).
- NMB 18260 = PPP 1035, Lower Gatun Fm (Late Miocene), locality same as above, 30 m E of NMB 18258, 6 m of bluish silts, Coates (1999: 287, map 1, inset).
- NMB 18261 = PPP 1080, Middle Gatun Fm (Late Miocene), Isla Payardi, NE of Cativa, Colon, surface of hill 100 m S of entrance to refinery (= NMB 17643, 17868, 18307, 18324, 18360, 18391), Coates (1999: 287, map 1, inset).
- NMB 18262 = PPP 1081, locality same as above, 100 m S of refinery entrance, underlying NMB 18261, 6 m outcrop, includes fossils washed down hill (= NMB 17644, 17869, 18308, 18326, 18392, 18662), Coates (1999: 287, map 1, inset).
- NMB 18308 = PPP 1087, Gatun Fm (Late Miocene), Isla Payardi, NE of Cativa, Colon, 100 m S of entrance to refinery, 6 m outcrop, includes fossils washed down hill (= NMB 17644, 17869, 18262, 18326, 18392, 18662), Coates (1999: 287, map 1, inset).
- NMB 18322 = PPP 1075, Lower Gatun Fm (Late Miocene), 900 m NW of junction of road to Sabanita, Colon, 40 m outcrop S of road, Coates (1999: 287, map 1, inset).
- NMB 18324 = PPP 1077, Middle Gatun Fm (Late Miocene), Isla Payardi, NE of Cativa, Colon, surface of hill 100 m S of refinery entrance (= NMB 17643, 17868, 18261, 18307, 18360, 18391), Coates (1999: 287, map 1, inset).
- NMB 18325 = PPP 1078, Lower Gatun Fm (Late Miocene), bulldozed area, Fabrica de Colchones, E of Cativa, Colon (= NMB 18255-18260, 18389), Coates (1999: 287, map 1, inset).
- NMB 18326 = PPP 1079, Middle Gatun Fm (Late Miocene), Isla Payardi, NE of Cativa, Colon, 100 m S of refinery entrance, hill slope above NMB 18324 (= NMB 17644, 17869, 18262, 18308, 18392, 18662), Coates (1999: 287, map 1, inset).

- NMB 18360 = PPP 034, Middle Gatun Fm (Late Miocene), Isla Payardi, NE of Cativa, Colon, surface of hill 100 m S of refinery entrance (= NMB 17643, 17868, 18261, 18307, 18334, 18391), Coates (1999: 287, map 1, inset).
- NMB 18372 = PPP 1995, Swan Cay Fm (Pleistocene), Swan Cay, N of Isla Colon, Bocas del Toro Basin, 3 m-thick shelly sandstone, Coates (1999: 294, map 9).
- NMB 18373 = PPP 1188, Cayo Agua Fm (Pliocene), SE coast of Cayo Agua not far S of North Point, Bocas del Toro Basin, PPP 1189, etc., shown by Coates (1999: 293, map 6, inset B).
- NMB 18374 = PPP 1203, Cayo Agua Fm (Pliocene), E side Punta Norte, Cayo Agua, Bocas del Toro Basin (= NMB 17635, 17808, 18400), Coates (1999: 293, map 6, inset B).
- NMB 18375 = PPP 1996, Valiente Fm (mid to Late Miocene, Coates *et al.*, 2003), Laguna de Bluefield W, "Finger island," W side Valiente Peninsula, Bocas del Toro Basin (= NMB 17629, 17824, 18711), Coates (1999: 291, map 5, inset A).
- NMB 18377 = PPP 1276, Cayo Agua Fm (Pliocene), NE coast Isla Popa, Bocas del Toro Basin (= NMB 17864), Coates (1999: 292, map 7), Coates *et al.* (2003: fig. 2).
- NMB 18378 = PPP 1277, Cayo Agua Fm (Pliocene), as last, point 60 m N of NMB 18377 (= NMB 17863), Coates (1999: 292, map 7), Coates *et al.* (2003: fig. 2).
- NMB 18380 = PPP 1284, Cayo Agua Fm (Pliocene), small island at E end Deer island, N end Isla Popa, Bocas del Toro Basin, Coates (1999: 292, map 7), Coates *et al.* (2003: fig. 2).
- NMB 18381 = PPP 1286, Swan Cay Fm (Pleistocene), 700 m NE upstream in Ground Creek, NW coast Isla Colon, Bocas del Toro Basin (= NMB 18745), Coates (1999: 294, map 9).
- NMB 18387 = PPP 1256, Shark Hole Point Fm? (Pliocene), small bay on E coast of Fish Hole, E coast of Isla Bastimentos, Bocas del Toro Basin (= NMB 18982), Coates (1999: 294, map 8, inset).
- NMB 18388 = PPP 1304, Shark Hole Point Fm? (Pliocene), locality same as above, Coates (1999: 294, map 8, inset).
- NMB 18389 = PPP 1305, Gatun Fm (Late Miocene), bulldozed area SE of Fabrica de Colchones, E of Cativa, Colon (= NMB 18255-18260, 18325), Coates (1999: 287, map 1, inset).
- NMB 18390 = PPP 1306, Gatun Fm (Late Miocene), locality same as above, outcrop 20 m S, Coates (1999: 287, map 1, inset).
- NMB 18391 = PPP 1307, Gatun Fm (Late Miocene), Isla Payardi, NE of Cativa, Colon, hill above entrance to refinery (= NMB 17643, 17868, 18261, 18307, 18360, 18662), Coates (1999: 287, map 1, inset).
- NMB 18392 = PPP 1308, Gatun Fm (Late Miocene), locality same as above, from slope of hill (= NMB 17644, 17869, 18262, 18308, 19326, 18662), Coates (1999: 287, map 1, inset).
- NMB 18545 = PPP 1293, Nancy Point Fm (Late Miocene), N-most of 5 small islands off Nancy Point, Valiente Peninsula, Bocas del Toro Basin, Coates (1999: 291, map 5, inset E).
- NMB 18661 = PPP 1504, Nancy Point Fm (Late Miocene), point S of Toro Point, W end of Green Bay, Valiente Peninsula, Bocas del Toro Basin, Coates (1999: 291, map 5, inset C), Coates *et al.* (2003: fig. 1).
- NMB 18662 = PPP 2163, Gatun Fm (Late Miocene), surface of hill 100 m S of refinery gate, Isla Payardi, Cativa, Colon (= NMB 17643, 17868, 18261, 18307, 18324, 18391), Coates (1999: 287, map 1, inset).
- NMB 18663 = PPP 2164, Gatun Fm (Late Miocene), slope of hill, locality same as above (= NMB 17644, 17869, 18262, 18308, 18326, 18392), Coates (1999: 287, map 1, inset).
- NMB 18667 = PPP 2168, Gatun Fm (Late Miocene), Boyd-Roosevelt Highway SE, San Judas Tadeo, *ca.* 2 km SW of Cativa, Colon, huge quarry with 40 m of section just NW of village, collection from one spot at NW end, Coates (1999: 287, map 1, inset).
- NMB 18668 = PPP 2169, Escudo de Veraguas Fm (Pliocene), in entrance to small bay near N extremity of central coast, N coast Escudo de Veraguas, Bocas del Toro Basin (= NMB 18600), Coates (1999: 289, map 4, inset C).
- NMB 18669 = PPP 2170, Escudo de Veraguas Fm (Pliocene), locality same as above, N coast, Coates (1999: 289, map 4, right edge of inset B).
- NMB 18670 = PPP 2171, Escudo de Veraguas Fm (Pliocene), locality same as above, point opposite offshore islands, W of NMB 18669 (= NMB 17627, 17832), Coates (1999: 289, map 4, inset B).
- NMB 18671 = PPP 2172, Escudo de Veraguas Fm (Pliocene), locality same as above, small island ("Cerro Antoine") 12 m long, 600 m W of NMB 18670, Coates (1999: 289, map 4, inset A).
- NMB 18672 = PPP 2173, Escudo de Veraguas Fm (Pliocene), small island *ca.* 500 m off NW coast of Escudo de Veraguas Island, Coates (1999: 289, map 4, top left corner).
- NMB 18677 = PPP 2178, Escudo de Veraguas Fm (Pliocene), locality same as above, small island, NW coast, 100 m E of NMB 18676 (= PPP 2177), Coates (1999: 289, map 4, inset B).
- NMB 18679 = PPP 2181, Escudo de Veraguas Fm (Pliocene), locality same as above, 100 m E of E end of large beach, SE coast of Escudo de Veraguas, Coates (1999: 289, map 4, bottom right corner).
- NMB 18680 = PPP 2180, Escudo de Veraguas Fm (Pliocene), locality same as above, 100 m N of NMB 18679, Coates (1999: 289, map 4, bottom right corner).
- NMB 18681 = PPP 2182, Escudo de Veraguas Fm (Pliocene), E end of Escudo de Veraguas, Bocas del Toro Basin, the 4 E-most islands, Coates (1999: 289, map 4, bottom right corner).
- NMB 18682 = PPP 2183, Escudo de Veraguas Fm (Pliocene), locality same as above, combined collection from E-most coast of Escudo de Veraguas Island, opposite E islands, Coates (1999: 289, map 4, inset D).
- NMB 18683 = PPP 2184, Escudo de Veraguas Fm (Pliocene), locality same as above, SE coast of Escudo de Veraguas, Coates (1999: 289, map 4, bottom right corner).
- NMB 18684 = PPP 2185, Escudo de Veraguas Fm (Pliocene), locality same as above, S coast, *ca.* 500 m W of NMB 18683, Coates (1999: 289, map 4, bottom right corner).
- NMB 18685 = PPP 2186, Escudo de Veraguas Fm (Pliocene), locality same as above, S coast, 200 m W of NMB 18684, Coates (1999: 289, map 4, bottom right corner).
- NMB 18686 = PPP 2187, Escudo de Veraguas Fm (Pliocene), locality same as above, S coast, 100 m NW of NMB 18685, Coates (1999: 289, map 4, bottom right corner).
- NMB 18688 = PPP 2189, Nancy Point Fm (Late Miocene), N end of N-most island at N end of Nancy Point, N side Valiente

- Peninsula, Bocas del Toro Basin, Coates (1999: 291, map 5, inset E).
- NMB 18689 = PPP 2190, Nancy Point Fm (Late Miocene), 2 km S of Nancy Point, N side Valiente Peninsula, Bocas del Toro Basin, Coates (1999: 291, map 5, inset D).
- NMB 18690 = PPP 2191, Nancy Point Fm (Late Miocene), 200 m S of NMB 18689, Coates (1999: 291, map 5, inset D).
- NMB 18700 = PPP 2201, Nancy Point Fm (Late Miocene), tip of Chong (= Nispero) Point, Valiente Peninsula, Bocas del Toro Basin (= NMB 17859), Coates (1999: 291, map 5, inset F).
- NMB 18701 = PPP 2202, Shark Hole Point Fm (Early Pliocene), E end of Shark Hole Point, N side Valiente Peninsula, Bocas del Toro Basin (= NMB 17854), Coates (1999: 291, map 5, inset F).
- NMB 18702 = PPP 2203, Shark Hole Point Fm (Early Pliocene), locality same as above, 100 m NW of NMB 18701, Coates (1999: 291, map 5, inset F).
- NMB 18703 = PPP 2204, Shark Hole Point Fm (Early Pliocene), locality same as above, 500 m W of NMB 18702 (= NMB 17855), Coates (1999: 291, map 5, inset F).
- NMB 18705 = PPP 2206, Shark Hole Point Fm (Pliocene), 1.5 km SW of Punta del Toro, S side Valiente Peninsula, Bocas del Toro Basin, Coates (1999: 291, map 5, inset C).
- NMB 18706 = PPP 2207, Shark Hole Point Fm (Early Pliocene), locality same as above, just SW of and overlying NMB 18705, Coates (1999: 291, map 5, inset C).
- NMB 18707 = PPP 2208, Shark Hole Point Fm (Early Pliocene), locality same as above, just SW of and overlying NMB 18706, Coates (1999: 291, map 5, inset C).
- NMB 18710 = PPP 2211, Nancy Point Fm (Late Miocene), 1.7 km SW of Punta del Toro, S side Valiente Peninsula, Bocas del Toro Basin, Coates (1999: 291, map 5, inset C), Coates *et al.* (2003: fig. 1).
- NMB 18711 = PPP 2212, Valiente Fm (Late Miocene), "Finger island," 50 m W of S tip of Cayo Toro, S side Valiente Peninsula, Bocas del Toro Basin (= NMB 17629, 17824, 18375), Coates (1999: 291, map 5, inset A), Coates *et al.* (2003: fig. 1).
- NMB 18716 = PPP 2217, Shark Hole Point Fm (Pliocene), S end of Playa Lorenzo, 5 km SE of Cayo Patterson, S side Valiente Peninsula, Bocas del Toro Basin, Coates (1999: 290, map 5).
- NMB 18719 = PPP 2222, Cayo Agua Fm (Pliocene), 800 m SE of Punta Norte, Cayo Agua, Bocas del Toro Basin (= NMB 17633, 18398), Coates (1999: 293, map 6, inset B).
- NMB 18720 = PPP 2223, Cayo Agua Fm (Pliocene), 200 m SSE of Punta Norte, Cayo Agua, Bocas del Toro Basin (= NMB 18397, 18447), Coates (1999: 293, map 6, inset A).
- NMB 18721 = PPP 2224, Cayo Agua Fm (Pliocene), Cayo Agua, 300 m SSE of NMB 18719 (= NMB 17634, 17807), Coates (1999: 293, map 6, inset B).
- NMB 18722 = PPP 2225, Cayo Agua Fm (Pliocene), locality same as above, 250-300 m ESE of NMB 18721 (= NMB 17635, 17808, 18374, 18400, 18983), Coates (1999: 293, map 6, inset B).
- NMB 18723 = PPP 2226, Shark Hole Point Fm (Early Pliocene), Bruno Bluff, N coast Valiente Peninsula, Bocas del Toro Basin (= NMB 17850), Coates (1999: 290, map 5).
- NMB 18724 = PPP 2227, Shark Hole Point Fm (Early Pliocene), locality same as above, 6 m higher in section (= NMB 17851), Coates (1999: 290, map 5).
- NMB 18726 = PPP 2229, Shark Hole Point Fm (Pliocene), Shark Hole Point, N side Valiente Peninsula, 200 m WSW of NMB 18703 (= NMB 17856), Coates (1999: 291, map 5, inset F).
- NMB 18727 = PPP 2230, Nancy Point Fm (Late Miocene), 150 m SW of NMB 18726 (= NMB 17857), Coates (1999: 291, map 5, inset F).
- NMB 18729 = PPP 2233, Nancy Point Fm (Late Miocene), 450 m SW of NMB 18727, Coates (1999: 291, map 5, inset F).
- NMB 18730 = PPP 2232, Cayo Agua Fm (Pliocene), W side of end of Punta di Nispero, Cayo Agua, Bocas del Toro Basin, Coates (1999: 291, map 5, inset F).
- NMB 18731 = PPP 2234, Cayo Agua Fm (Pliocene), locality same as above, 400 m W of Punta di Nispero, 80 m SE of NMB 18730 (= NMB 17822, 18376).
- NMB 18733 = PPP 2236, Cayo Agua Fm (Pliocene), 1 km SE of Punta de Tiburón, Cayo Agua, Bocas del Toro Basin (= NMB 17829), Coates (1999: 293, map 6, inset G).
- NMB 18734 = PPP 2237, Cayo Agua Fm (Pliocene), 300 m WNW of Punta Piedra Roja, Cayo Agua, Bocas del Toro Basin (= NMB 17823), Coates (1999: 293, map 6, inset H).
- NMB 18735 = PPP 2238, Cayo Agua Fm (Pliocene), coast W of Punta de Nispero, Cayo Agua, Bocas del Toro Basin, Coates (1999: 293, map 6, inset C).
- NMB 18736 = PPP 2239, Cayo Agua Fm (Pliocene), locality same as above, Coates (1999: 293, map 6, inset D).
- NMB 18738 = PPP 2241, Cayo Agua Fm (Pliocene), locality same as above, small island 150 m NE of NMB 18735-18737, Coates (1999: 293, map 6, inset D).
- NMB 18743 = PPP 2246, Swan Cay Fm (Pleistocene), Swan Cay, N of Isla Colon, Bocas del Toro Basin (= NMB 18372), Coates (1999: 294, map 9).
- NMB 18764 = PPP 1642, Chagres Sandstone, Río Indio facies (Pliocene), bluff 1 km E of Gobeia, Río Indio, Colon, Coates (1999: 287, map 1).
- NMB 18768 = PPP 1714, Nancy Point Fm (Late Miocene), N-most of 5 small islands 300-400 m E of Nancy Point, Valiente Peninsula, Bocas del Toro Basin, Coates (1999: 291, map 5, inset E).
- NMB 18769 = PPP 1715, Valiente Fm (Late Miocene), W coast Valiente Peninsula, S of Toro Point, Bocas del Toro Basin, Coates (1999: 291, map 5, inset C), Coates *et al.* (2003: fig. 1).
- NMB 18771 = PPP 1883-1889, Valiente Fm (Late Miocene), base and small elevation W of finger, E and W sides "Finger island," Valiente Peninsula, Bocas del Toro Basin, Coates (1999: 291, map 5, inset A), Coates *et al.* (2003: fig. 1).
- NMB 18772 = PPP 1910-1917, Cayo Agua Fm (Pliocene), section NE of Punta di Nispero, Cayo Agua, Bocas del Toro, Coates (1999: 293, map 6, inset C).
- NMB 18976 = PPP 3196, Shark Hole Point Fm? (Late Pliocene), small bay on E coast of Fish Hole, E coast of Isla Bastimentos, Bocas del Toro Basin (= NMB 18387).
- NMB 18977, PPP not known, Fish Hole Member, Shark Hole Point Fm? (Late Pliocene), Fish Hole, E coast of Isla Bastimentos, Bocas del Toro Basin.
- NMB 18980 = PPP 3203, Shark Hole Point Fm? (Late Pliocene),

volcanic calcarenite and shelly sand, Fish Hole, E coast of Isla Bastimentos, Bocas del Toro.

NMB 18981 = PPP 3204, Shark Hole Point Fm? (Late Pliocene), Fish Hole, *ca.* 200 m W of NMB 18980, cliff with reef, sandy calcarenite with shells above reef, E coast of Isla Bastimentos, Bocas del Toro Basin.

NMB 18983 = PPP 3209, Cayo Agua Fm (Pliocene), silts with scattered mollusks, 1.3 km SE of Punta Norte, Cayo Agua, Bocas del Toro Basin (= NMB 17635, 17808, 18374, 18722).

NMB 18984 = PPP 3210, Cayo Agua Fm (Pliocene), locality same as above, 30 m W of NMB 18983.

NMB 18986 = PPP 3220, Río Indio facies, Chagres Fm (latest Miocene), 2 adjacent bulldozer pits in grey silts, immediately W of cemetery, 1.3 km W of Río Indio, N coast W of Colon.

NMB 18987 = PPP 3221, Río Indio facies, Chagres Fm (latest Miocene), grey silts with scattered mollusks, 6 m-high cliff, *ca.* 1 km NE of village of Gobeia (which is *ca.* 5 km E of Miguel de Borda), Morro Hueco, N coast W of Colon.

NMB 18988 = PPP 3222, Río Indio facies, Chagres Fm (latest Miocene), brownish silts with scattered mollusks, *ca.* 200 m SW of Boca Río Piloncito, *ca.* 1 km E of Punta Gavilán, Morro Rajada, *ca.* 4.3 km (straight line) W of Río Indio, N coast W of Colon.

NMB 18989 = PPP 3223, Río Indio facies, Chagres Fm (latest Miocene), locality same as above, *ca.* 40 m SW of NMB 18988, *ca.* 4.3 km (straight line) W of Río Indio, Morro Rajada, N coast W of Colon.

NMB 18990 = PPP 3224, Río Indio facies, Chagres Fm (latest Miocene), locality same as above, *ca.* 40 m SW of NMB 18989, *ca.* 900 m E of Punta Gavilán, *ca.* 4.4 km (straight line) W of Río Indio, Morro Rajada, N coast W of Colon.

NMB 18991 = PPP 3225, Río Indio facies, Chagres Fm (latest Miocene), locality same as above, *ca.* 50 m W of NMB 18990, *ca.* 850 m E of Punta Gavilán, *ca.* 4.5 km (straight line) W of Río Indio, Morro Rajada, N coast W of Colon.

NMB 18992 = PPP 3226, Río Indio facies, Chagres Fm (latest Miocene), Punta Gavilán, *ca.* 5.3 km (straight line) WSW of Río Indio, Colon.

NMB 19025 = TU 757, Gatun Fm (Late Miocene), road cut E of Cativa, Colon.

NMB 19027 = TU 962, Gatun Fm (Late Miocene), outcrop 500 m E of refinery gates, E of Cativa, Colon.

NMB 19028 = TU 958, Gatun Fm (Late Miocene), hill slope above TU 757, 100 m S of refinery gate, Isla Payardi, E of Cativa, Colon (= NMB 17644, 17869, 18262, 18308, 19326, 18662).

NMB 19029 = TU 960, Gatun Fm (Late Miocene), top of hill, just E of refinery gate, Isla Payardi, E of Cativa, Colon.

Pacific coast of Panama

NMB 17439 = PPP 1724, Armuelles Fm (Pleistocene), S of Quebrada Corotú, E coast Burica Peninsula, 2.5 m-thick bed of algal nodules and mollusks.

NMB 17441 = PPP 1725, Armuelles Fm (Pleistocene), Río Rabo de Puerco, W of Puerto Armuelles, Burica Peninsula, float.

NMB 17442 = PPP 1761, Armuelles Fm (Pleistocene), blue silts, Río Rabo de Puerco, W of Puerto Armuelles, Burica Peninsula.

NMB 17443 = PPP 1762, Armuelles Fm (Pleistocene), Río Rabo de

Puerco, W of Puerto Armuelles, blue silts 500 m upstream from NMB 17442.

NMB 18061 = PPP 592, Armuelles Fm (Pleistocene), Quebrada de Piedra (right tributary of Río San Bartolo), W and SW of San Bartolo village, 50 m upstream of confluence with Río San Bartolo, Burica Peninsula.

NMB 18066 = PPP 752, Charco Azul Group, Armuelles Fm (Pleistocene), float, Río Chiquito (left tributary of upper Río San Bartolo), Burica Peninsula.

NMB 18068 = PPP 606, Charco Azul Group, Penita Fm (Pliocene), upper course of Río Chiquito, Burica Peninsula.

NMB 18069 = PPP 754, Charco Azul Group, lower Burica Fm (early Pleistocene), Río San Bartolo, float between confluences of Río Chiquito and San Bartolo Arriba, Burica Peninsula.

NMB 18070 = PPP 561, Charco Azul Group, lower Burica Fm (early Pleistocene), locality same as above, *in situ*.

NMB 18071 = PPP 564, Charco Azul Group, lower Burica Fm (early Pleistocene), locality same as above.

NMB 18073 = PPP 755, Charco Azul group, Armuelles Fm? (Pleistocene), float, Río Rabo de Puerco, Burica Peninsula.

NMB 18074 = PPP 613, Charco Azul Group, Armuelles Fm (Pleistocene), fine blue fossiliferous sandstone, Río Rabo de Puerco, Burica Peninsula.

NMB 18076 = PPP 615, Charco Azul Group, Armuelles Fm (Pleistocene), 1.5 m blue silts 250 m upstream from NMB 18074, Río Rabo de Puerco, Burica Peninsula.

NMB 18305 = PPP 1085, Charco Azul Group, Armuelles Fm (Pleistocene), Río Rabo de Puerco, Burica Peninsula (= NMB 18076).

NMB 18306 = PPP 1029, Charco Azul Group, Armuelles Fm (early Pleistocene, 1.8 Ma), S of Quebrada Corotú, 3.3 km N of Puerto Limones, Burica Peninsula, bed with algal balls and mollusks (= NMB 17439).

NMB 18431 = PPP 148, Charco Azul Group, Armuelles Fm (Pleistocene), E coast Burica Peninsula near Quebrada Melliza, *ca.* 4.75 km N of Quebrada Corotú.

NMB 18435 = PPP 215, Charco Azul Group, Armuelles Fm (Pleistocene), 800 m N along stream from paved road, Río Rabo de Puerco, Burica Peninsula.

Panama, Darien

NMB 18184 = PPP 888, Chucunaque Fm (Late Miocene), greenish grey silts *ca.* 5 km upstream from El Salto, Río Chucunaque.

NMB 18493 = PPP 1145, Tuira Fm (Late Miocene), village of Punta Grande, Río Tupisa (= NMB 18531).

NMB 18495 = PPP 1159, Tuira Fm (Late Miocene), downstream from Boca de Tigre, 1 km below confluence with Río Cubilele, Río Chico (= NMB 18501).

NMB 18501 = PPP 1554, same locality as above.

NMB 18502 = PPP 1555, Tuira Fm (Late Miocene), Río Chico, 50 m downstream from and *ca.* 5 m stratigraphically above NMB 18501.

NMB 18503 = PPP 1565, Tuira Fm (Late Miocene), locality same as above, 1 km downstream from NMB 18501.

NMB 18504 = PPP 1566, Tuira Fm (Late Miocene), Río Chico, right bank, 1 km upstream from Corozal.

NMB 18508 = PPP 1575, lower Chucunaque Fm (Late Miocene),

- Río Chico, 200 m upstream from Comun village, first pueblo above Yaviza.
- NMB 18510 = PPP 1723, Tuira Fm (Late Miocene), Río Tuquesa, between village of Marraganti and Boca de Marraganti.
- NMB 18516 = PPP 1998, Tuira Fm (Late Miocene), Río Tuquesa, left bank, 3 km below Marraganti.
- NMB 18517 = PPP 1609, Tuira Fm (Late Miocene), Río Tuquesa, about 3 km below Marraganti, 50 m downstream from NMB 18516.
- NMB 18522 = PPP 1620, Tuira Fm (Late Miocene), Río Tupisa, right bank, a few bends above Boca de Chiatí, upstream from Punta Grande, directly overlying NMB 18521.
- NMB 18525 = PPP 1626, Tuira Fm (Late Miocene), Río Tupisa, left bank, a few bends above Boca de Chiatí, upstream from Punta Grande, *ca.* 700 m downstream from NMB 18522.
- NMB 18526 = PPP 1627, Tuira Fm (Late Miocene), Río Tupisa, left bank, concretionary sandstone 40 min walk upstream from Pulida.
- NMB 18527 = PPP 1629, locality same as above, sandstone without concretions immediately overlying NMB 18526.
- NMB 18528 = PPP 1632, Tuira Fm (Late Miocene), Río Tupisa, yellowish sandstone upstream from village of Pulida.
- NMB 18532 = PPP 1637, Tuira Fm (Late Miocene), Río Tupisa, upper landing place at Punta Grande.
- NMB 18533 = PPP 1166, Tuira Fm (Late Miocene), Río Chico, downstream from Boca Tigre.
- NMB 18534 = PPP 1138, Tuira Fm (Late Miocene), Río Tuquesa, between Charco Chivo and village of Marraganti.
- NMB 18535 = PPP 1141, locality same as above.
- NMB 18540 = PPP 1156, Tuira Fm (Late Miocene), Río Chico, downstream from Boca Grande.
- NMB 18543 = PPP 1171, locality same as above.
- NMB 18657 = PPP 1525, Tuira Fm (late Miocene), Río Tuira.

Jamaica

- NMB 10635, type locality Bowden Shellbed (Late Pliocene), St. Thomas Parish, SE coast of Jamaica, E side Port Morant, originally 5 localities, from an area not more than 200 m square.
- NMB 10651, locality same as above, type locality of Bowden Shellbed, coll. Vendryes, *ex* collection Mayer-Eymar.
- NMB 10831, locality same as above, type locality Bowden Shellbed (Late Pliocene), St. Thomas Parish, SE coast of Jamaica.
- NMB 11110, locality same as above, type locality Bowden Shellbed, Bowden Shop, SE coast of Jamaica.
- NMB 11146, locality same as above, Bowden Shellbed, locality opened by bulldozer, Bowden Shop, SE coast of Jamaica.

Dominican Republic

- NMB 15803, Gurabo Fm (Early Pliocene), Río Gurabo, upstream part of bluff at major S-bend downstream from road bridge, E bank (= NMB 15929) (just above center of Saunders *et al.*, 1986: text-fig. 4).
- NMB 15805, Gurabo Fm (Early Pliocene), Río Gurabo, downstream part of same bluff as above (= NMB 15935).
- NMB 15807, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, bluff opposite downstream end of NMB 15805 (= NMB 15942-15943).

- NMB 15809, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, second bluff downstream from NMB 15807, due W of NMB 15803-15805 (= NMB 15952-15954).
- NMB 15810, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, next bluff downstream from NMB 15809 (= NMB 15958).
- NMB 15811, Gurabo Fm (Early Pliocene), Río Gurabo, same bluff as above (= NMB 15960).
- NMB 15813, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, next major bluff downstream from NMB 15810-15811 (= NMB 15963).
- NMB 15814, Gurabo Fm (Early Pliocene), Río Gurabo, locality same as above, same bluff as NMB 15813, downstream end (= NMB 15964).
- NMB 15815, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, next major bluff downstream from NMB 15814, upstream end of long bluff (= NMB 15965).
- NMB 15816, Gurabo Fm (Early Pliocene), Río Gurabo, same bluff as NMB 15815, whole of long exposure (= NMB 15966).
- NMB 15817, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, upstream half of next bluff downstream from NMB 15816 (= NMB 15967).
- NMB 15821, basal Mao Fm (Early Pliocene), W bank, at upstream end of major S-bends, Río Gurabo (= NMB 16022-16023) (at upper quarter of Saunders *et al.*, 1986: text-fig. 4).
- NMB 15822, basal Mao Fm (Early Pliocene), Río Gurabo, E bank, next major bluff downstream from NMB 15821 (= NMB 16057).
- NMB 15824, basal Mao Fm (Early Pliocene), Río Gurabo, downstream end of same bluff as NMB 15822 (= NMB 16063).
- NMB 15833, basal Mao Fm (Early Pliocene), Río Gurabo, second bluff upstream from downstream end of exposure, E bank, *ca.* 1.7 km downstream from S-bends at NMB 15821-15824 (= NMB 16120) (near top of Saunders *et al.*, 1986: text-fig. 4).
- NMB 15836, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, in small side stream just upstream from road bridge *ca.* 300 m upstream from bluff with NMB 15803-15805 (= NMB 16124).
- NMB 15838, Gurabo Fm (Early Pliocene), Río Gurabo, next small bluff, E bank, *ca.* 300 m further upstream from NMB 15836.
- NMB 15839, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, *ca.* 100 m upstream from NMB 15838 (= NMB 16131).
- NMB 15841, Gurabo Fm (Early Pliocene), Río Gurabo, same locality as NMB 15839 (= NMB 16129).
- NMB 15842, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, small side stream *ca.* 400 m upstream from NMB 15838-15839, upper part of stream (= NMB 16134).
- NMB 15843, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, lower part of same side stream as NMB 15842 (= NMB 16135).
- NMB 15844, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, bluff *ca.* 150 m further upstream from small side stream with NMB 15842-15843 (= NMB 16136).
- NMB 15845, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, halfway between bluff with NMB 15844 and next major bluff at S-bend 250 m further upstream.
- NMB 15846, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, downstream from major W bank bluff with NMB 15848-15858 (= NMB 16137-16138).

- NMB 15848, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, downstream end of major bluff at S-bend (immediately above center of Saunders *et al.*, 1986: text-fig. 4).
- NMB 15850, Gurabo Fm (Early Pliocene), Río Gurabo, at center of W bend of S-bend, just upstream from NMB 15848 (= NMB 16882).
- NMB 15854, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, just upstream from NMB 15850 (= NMB 16911, 16883).
- NMB 15855, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, at upstream end of major bluff, *ca.* 200 m upstream from NMB 15854 (= NMB 16934, 17183).
- NMB 15856, Gurabo Fm (Early Pliocene), Río Gurabo, slightly further upstream from NMB 15855.
- NMB 15857, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, in center of next major bluff upstream from NMB 15848-15856, in E bend of S-bend.
- NMB 15858, Gurabo Fm (Early Pliocene), Río Gurabo, upstream half of same bluff as NMB 15857.
- NMB 15859, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, *ca.* 100 m upstream from NMB 15858.
- NMB 15860, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, *ca.* 200 m upstream from NMB 15859 (= NMB 16148).
- NMB 15861, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, at mouth of small side stream *ca.* 300 m upstream from NMB 15860.
- NMB 15862, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, at and for 50 m upstream from small side stream, *ca.* 150 m upstream from NMB 15861.
- NMB 15863, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, 50 m-long exposure upstream from major side stream entering Gurabo *ca.* 200 m upstream from NMB 15862 (= NMB 16152).
- NMB 15864, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, *ca.* 250 m upstream from NMB 15863 (= NMB 16154).
- NMB 15865, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, 100 m-long exposure *ca.* 100 m upstream from NMB 15864 (= NMB 16155, 16180).
- NMB 15866, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, small exposure *ca.* 100 m upstream from NMB 15865 (= NMB 16156).
- NMB 15867, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, downstream from and at mouth of side stream at minor bend, *ca.* 50 m upstream from NMB 15866 (= NMB 16808, 16157).
- NMB 15868, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, in center of minor bend *ca.* 100 m upstream from NMB 15867 (= NMB 16158).
- NMB 15869, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, downstream part of bluff at minor bend, *ca.* 50 m upstream from NMB 15868 (= NMB 16159).
- NMB 15870, Gurabo Fm (Late Miocene/Early Pliocene), Río Gurabo, E bank, downstream side of mouth of side stream entering *ca.* 150 m upstream from NMB 15869 (= NMB 16160).
- NMB 15871, Gurabo Fm (Late Miocene/Early Pliocene), Río Gurabo, E bank, in side stream 50 m upstream from NMB 15870 (= NMB 16809).
- NMB 15873, Gurabo Fm (Late Miocene/Early Pliocene), Río Gurabo, E bank, upstream side of small stream entering *ca.* 300 m upstream from NMB 15870-15871 (= NMB 16162).
- NMB 15876, Gurabo Fm (Late Miocene/Early Pliocene), Río Gurabo, W bank, in small side stream entering *ca.* 1 km upstream from NMB 15873 (= NMB 16165).
- NMB 15878, Gurabo Fm (Late Miocene/Early Pliocene), Río Gurabo, W bank, 50 m upstream from NMB 15876, at downstream end of long bluff (= NMB 16167).
- NMB 15880, Gurabo Fm (Late Miocene/Early Pliocene), Río Gurabo, W bank, in center of long bluff upstream from NMB 15878 (= NMB 16168).
- NMB 15882, Gurabo Fm (Late Miocene), Río Gurabo, E bank, next bluff upstream, *ca.* 150 m upstream from NMB 15880.
- NMB 15885, Gurabo Fm (Late Miocene), Río Gurabo, E bank, upper part of side stream entering *ca.* 150 m upstream from NMB 15882, at downstream end of major S-bend (at lower third of Saunders *et al.*, 1986: text-fig. 4).
- NMB 15887, Gurabo Fm (Late Miocene), Río Gurabo, E bank, downstream end of long bluff at downstream end of major S-bend.
- NMB 15888, Gurabo Fm (Late Miocene), Río Gurabo, E bank, center of long bluff, *ca.* 100 m upstream from NMB 15887 (= NMB 16175).
- NMB 15893, Cercado Fm (Late Miocene), Río Gurabo, E bank, *ca.* 200 m upstream from major S-bend (at lower third of Saunders *et al.*, 1986: text-fig. 4) (= NMB 16185).
- NMB 15896, Cercado Fm (Late Miocene), Río Gurabo, E bank, near downstream end of gorge, *ca.* 450 m upstream from NMB 15893.
- NMB 15897, Cercado Fm (Late Miocene), Río Gurabo, W bank, opposite NMB 15896.
- NMB 15898, Cercado Fm (Late Miocene), Río Gurabo, W bank, in gorge *ca.* 100 m upstream from NMB 15897.
- NMB 15899, Cercado Fm (Late Miocene), Río Gurabo, W bank, *ca.* 150 m upstream from NMB 15898.
- NMB 15900, Cercado Fm (Late Miocene), Río Gurabo, E bank, in gorge *ca.* 100 m upstream from NMB 15899.
- NMB 15903, Cercado Fm (Late Miocene), Río Gurabo, E bank, *ca.* 50 m upstream from NMB 15900.
- NMB 15904, Cercado Fm (Late Miocene), Río Gurabo, W bank, mouth of small side stream near upstream end of gorge, *ca.* 200 m upstream from NMB 15903.
- NMB 15905, Cercado Fm (Late Miocene), Río Gurabo, W bank, in side stream 100 m upstream from NMB 15904.
- NMB 15906, Cercado Fm (Late Miocene), Río Gurabo, W bank, upper part of side stream upstream from NMB 15905.
- NMB 15907, Cercado Fm (Late Miocene), Río Gurabo, W bank, on road *ca.* 100 m upstream from mouth of side stream.
- NMB 15909, Cercado Fm (Late Miocene), Río Gurabo, E bank, next bluff and bank upstream from NMB 15904-15907, in vicinity of sharp bend to E (= NMB 16920).
- NMB 15910, Cercado Fm (Late Miocene), Río Gurabo, E bank, lower part of same bluff as above, immediately downstream from NMB 15909.
- NMB 15911, Cercado Fm (Late Miocene), Río Gurabo, E bank, bluff *ca.* 150 m upstream from upstream end of NMB 15909 (= NMB 16913).
- NMB 15912, Cercado Fm (Late Miocene), Río Gurabo, W bank,

- next bluff upstream, *ca.* 100 m upstream from NMB 15911 (= NMB 16915).
- NMB 15913, Cercado Fm (Late Miocene), Río Gurabo, lower part of side stream entering from W *ca.* 300 m upstream from NMB 15912.
- NMB 15914, Cercado Fm (Late Miocene), Río Gurabo, E bank, upstream part of long, low bluff, upper part of major S-bend (at lower quarter of Saunders *et al.*, 1986: text-fig. 4).
- NMB 15915, Cercado Fm (Late Miocene), Río Gurabo, E bank, opposite and *ca.* 100 m upstream from NMB 15914.
- NMB 15917, Cercado Fm (Late Miocene), Río Gurabo, E bank, upstream part of bluff *ca.* 800 m upstream from NMB 15915 (= NMB 16917).
- NMB 16122, Mao Fm (Early Pliocene), Río Gurabo, E bank, isolated bluff on E side of sharp S-bend, N-most locality in Río Gurabo (at top of Saunders *et al.*, 1986: text-fig. 4).
- NMB 16801, Cercado Fm (Late Miocene), Río Mao, W bank, bend from N-S to E-W at center of Saunders *et al.* (1986: text-fig. 29) (= TU 1292, USGS 8528).
- NMB 16807, Gurabo Fm (Early Pliocene) (Saunders *et al.*, 1986: 33), Río Amina, E bank, just upstream from ford near Potrero (= TU 1219, USGS 8516, NMB 16956) (at center of Saunders *et al.*, 1986: text-fig. 34).
- NMB 16808, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, downstream from and at mouth of side stream at minor bend, *ca.* 50 m upstream from NMB 15866 (= NMB 15867, 16157).
- NMB 16809, Gurabo Fm (Late Miocene/Early Pliocene), Río Gurabo, E bank, in side stream *ca.* 50 m upstream from NMB 15870 (= NMB 15871).
- NMB 16810, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, 50 m-long exposure *ca.* 100 m upstream from NMB 15864 (= NMB 15865, 16155).
- NMB 16814, Gurabo Fm (Early Pliocene; Saunders *et al.*, 1986: 23), Cañada de Zamba, tributary of Río Cana, W bank, 50-100 m upstream from mouth.
- NMB 16817, Gurabo Fm (Early Pliocene), Cañada de Zamba, Río Cana, E bank, *ca.* 300 m upstream from mouth (= NMB 16967).
- NMB 16818, Gurabo Fm (Early Pliocene), Cañada de Zamba, Río Cana, E bank, *ca.* 350-450 m upstream from mouth (= NMB 16968-16970).
- NMB 16820, Gurabo Fm (Late Miocene/Early Pliocene), Río Cana, E bank, in center of long, nearly straight section *ca.* 1.6 k upstream from Cañada de Zamba (a little above center of Saunders *et al.*, 1986: text-fig. 15).
- NMB 16821, Gurabo Fm (Late Miocene/Early Pliocene), Río Cana, E bank, locality same as above, sample over 50 m in vicinity of spot sample NMB 16820.
- NMB 16824, Gurabo Fm (Early Pliocene), Río Cana, E bank, bluff at upstream end of major bends in vicinity of mouth of Cañada de Zamba (= NMB 16973).
- NMB 16825, Gurabo Fm (Early Pliocene), Río Cana, E bank, upstream end of bluff, immediately upstream from NMB 16824.
- NMB 16828, Gurabo Fm (Early Pliocene), Río Cana, W bank, bluff halfway between NMB 16821 and 16825, *ca.* 400 m downstream from NMB 16821.
- NMB 16833, Gurabo Fm (Late Miocene/Early Pliocene), Río Cana, W bank, exposure *ca.* 500 m upstream from NMB 18621.
- NMB 16835, Cercado Fm (Late Miocene), Río Cana, W bank, center of bluff at downstream end of major horseshoe bend just below center of Saunders *et al.* (1986: text-fig. 15) (= NMB 16983).
- NMB 16836, Cercado Fm (Late Miocene), Río Cana, W bank, next bluff *ca.* 300 m upstream from NMB 19835, at head of major horseshoe bend (= NMB 16984).
- NMB 16837, Cercado Fm (Late Miocene), Río Cana, locality same as above, 50 m upstream from NMB 16836.
- NMB 16838, Cercado Fm (Late Miocene), Río Cana, E bank, *ca.* 250 m upstream from NMB 16837, toward upper end of major horseshoe bend.
- NMB 16839, Cercado Fm (Late Miocene), Río Cana, W bank, *ca.* 50 m upstream from NMB 16838, immediately downstream from uppermost bluff on major horseshoe bend (= NMB 16986).
- NMB 16842, Cercado Fm (Late Miocene), Río Cana, W bank, just upstream from neck of major horseshoe bend near center of Saunders *et al.* (1986: text-fig. 15), *ca.* 600 m upstream from NMB 16839.
- NMB 16852, Cercado Fm (Late Miocene), Río Cana, E bank, bluff at sharp bend just downstream from ford, *ca.* 1.4 km (straight) N of El Caimito, *ca.* 1.2 km (straight) S of NMB 16842 (= NMB 16993).
- NMB 16853, Cercado Fm (Late Miocene), Río Cana, W bank, bluff just downstream from small side stream, *ca.* 700 m upstream from new road bridge 700 m upstream from El Caimito.
- NMB 16855, Cercado Fm (Late Miocene), Río Cana, E bank, *ca.* 700 m further upstream from NMB 16853.
- NMB 16857, Cercado Fm (Late Miocene), Río Cana, E bank, *ca.* 100-250 upstream from ford, *ca.* 600 m further upstream from NMB 16855.
- NMB 16862, Gurabo Fm (Early Pliocene), Río Cana, W bank, *ca.* 500 m downstream from mouth of Cañada de Zamba (= NMB 16964).
- NMB 16864, Gurabo Fm (Early Pliocene), Río Cana, hillside above W bank, *ca.* 400 m downstream from NMB 16862.
- NMB 16865, Gurabo Fm (Early Pliocene), Río Cana, E bank, at upstream end of large "square" bend *ca.* 400 m downstream from NMB 16864, at upper quarter of Saunders *et al.* (1986: text-fig. 15; = NMB 17008-17009).
- NMB 16866, Gurabo Fm (Early Pliocene), Río Cana, W bank, upstream-most part of next bluff downstream from NMB 16865 (= NMB 17010).
- NMB 16867, Gurabo Fm (Early Pliocene), Río Cana, W bank, central area of bluff immediately downstream from NMB 16866.
- NMB 16868, Gurabo Fm (Early Pliocene), Río Cana, W bank, downstream part of bluff, immediately downstream from NMB 16867 (= NMB 17011).
- NMB 16869, Gurabo Fm (Early Pliocene), Río Cana, W bank, upstream-most part of second bluff downstream from above, *ca.* 800 m downstream from NMB 16868 (= NMB 17016).
- NMB 16870, Gurabo Fm (Early Pliocene), Río Cana, locality same as above, central part of bluff, immediately downstream from NMB 16869.
- NMB 16879, Gurabo Fm (Early Pliocene), Cañada de Zamba, E

- bank, *ca.* 450 m upstream from Río Cana.
- NMB 16880, Gurabo Fm (Early Pliocene), Cañada de Zamba, W bank, opposite and 50 m upstream from NMB 16879, *ca.* 1.3 km upstream from Río Cana.
- NMB 16882, Gurabo Fm (Early Pliocene), Río Gurabo, at center of W end of S bend, 100 m upstream from NMB 15848 (= NMB 15850; immediately above center of Saunders *et al.*, 1986: text-fig. 4).
- NMB 16883, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, 100 m upstream from NMB 16882 (= NMB 15854, 16811).
- NMB 16885, Mao Fm (Early Pliocene), Río Cana, E bank, downstream-most locality, at top of Saunders *et al.* (1986: text-fig. 15; = NMB 17024).
- NMB 16910, Gurabo Fm (Late Miocene) (Saunders *et al.*, 1986: 32), Bluff 1 of Maury, Río Mao, W bank, *ca.* 200 m upstream from crossing of Cercado-Martínez road and *ca.* 1 km upstream from Cercado de Mao (= TU 1293, USGS 8519-8520, NMB 17175).
- NMB 16912, Gurabo Fm (Late Miocene), Bluff 3 of Maury, upstream-most locality in Río Mao, W bank, *ca.* 100-300 m upstream from crossing of Cercado-Bulla road, at bottom of Saunders *et al.* (1986: text-fig. 29; = TU 1294, USGS 8525).
- NMB 16913, Gurabo Fm (Late Miocene), Bluff 3 of Maury, Río Mao, W bank, downstream part of bluff, *ca.* 400-500 m upstream from crossing of Cercado-Bulla road (= NMB 17629, 17307).
- NMB 16914, Gurabo Fm (Late Miocene), Bluff 2 of Maury, Río Mao, W bank, downstream half of long bluff *ca.* 300 m downstream from mouth of Arroyo Bajón (= USGS 8526, NMB 16931, 17176).
- NMB 16915, Gurabo Fm (Late Miocene), upper Río Mao, E bank, spot collection just downstream from mouth of Arroyo Bajón (= NMB 16927; see Saunders *et al.*, 1986: text-fig. 30, for details of locality positions around mouth of Arroyo Bajón).
- NMB 16916, Gurabo Fm (Late Miocene), upper Río Mao, E bank, bluff 0-50 m downstream from mouth of Arroyo Bajón.
- NMB 16917, Gurabo Fm (Late Miocene), upper Río Mao, E bank, spot collection *ca.* 50 m upstream from mouth of Arroyo Bajón (= NMB 16923).
- NMB 16918, Gurabo Fm (Late Miocene), upper Río Mao, E bank, spot collection just upstream from NMB 16917, *ca.* 50 m upstream from mouth of Arroyo Bajón (= NMB 16934, 17177).
- NMB 16919, Gurabo Fm (Late Miocene), upper Río Mao, E bank, bluff 0-150 m upstream from mouth of Arroyo Bajón.
- NMB 16922, Gurabo Fm (Late Miocene), upper Río Mao, E bank, spot collection 100 m upstream from mouth of Arroyo Bajón.
- NMB 16923, Gurabo Fm (Late Miocene), upper Río Mao, E bank, spot collection *ca.* 50 m upstream from mouth of Arroyo Bajón (= NMB 16917).
- NMB 16924, Gurabo Fm (Late Miocene), upper Río Mao, E bank, spot collection just upstream from NMB 16923, *ca.* 50 m upstream from mouth of Arroyo Bajón (= NMB 16918, 17177).
- NMB 16927, Gurabo Fm (Late Miocene), upper Río Mao, E bank, spot collection just downstream from mouth of Arroyo Bajón (= NMB 16915).
- NMB 16928, Gurabo Fm (Late Miocene), upper Río Mao, E bank, spot collection *ca.* 50 m downstream from mouth of Arroyo Bajón (alongside NMB 16915-16916, 16927).
- NMB 16931, Gurabo Fm (Late Miocene), Río Mao, includes part of Bluff 2 of Maury, W bank, downstream half of long bluff *ca.* 300 m downstream from mouth of Arroyo Bajón (= USGS 8526, NMB 16914, 17176).
- NMB 16932, Gurabo Fm (Late Miocene), Río Mao, includes part of Bluff 2 of Maury, spot collection near center of NMB 16914, 16931.
- NMB 16934, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, at upstream end of major bluff, *ca.* 200 m upstream from NMB 15854 (= NMB 15855, 17183).
- NMB 16982, Cercado Fm (late Miocene), Río Cana, W bank, downstream end of downstream bluff on major horseshoe bend at center of Saunders *et al.* (1986: text-fig. 15), opposite NMB 16835, 16983.
- NMB 16983, Cercado Fm (late Miocene), Río Cana, locality same as above, 50 m upstream from NMB 16982 (= NMB 16835).
- NMB 17265, Baitoa Fm (late Early Miocene), López section, Río Yaque del Norte, E bank, bluff 0-100 m downstream from mouth of Arroyo Hondo, second major bend up from bottom of Saunders *et al.* (1986: text-fig. 21; = NMB 16936).
- NMB 17266, Gurabo Fm (Early Pliocene), NW of Angostura, E bank Río Yaque del Norte, upstream end of bluff at top of Saunders *et al.* (1986: text-fig. 21; = NMB 17298-17299).
- NMB 17267, Gurabo Fm (Early Pliocene), near Barranca, W bank Río Yaque del Norte, near center of bluff opposite NMB 17266 (= NMB 17302).
- NMB 17268, Gurabo Fm (Early Pliocene), near Barranca, W bank Río Yaque del Norte, downstream end of same bluff as NMB 17267, on road cutting down bluff to ford.
- NMB 17269, Cercado Fm (Late Miocene), Bluff 3 of Maury, Río Mao, W bank, downstream part of bluff, *ca.* 150 m upstream from crossing of Cercado-Bulla road (= NMB 16913, 17307).
- NMB 17270, Gurabo Fm (Early Pliocene) (Saunders *et al.*, 1986: 34), Arroyo Zalaya, Santiago-Janico Road, 9 km S of bridge at Santiago, collected over 1 km upstream from bridge over Arroyo Zalaya (= NMB 17308-17310; see Saunders *et al.*, 1986: text-fig. 36, for locations of localities in Arroyo Zalaya).
- NMB 17271, Gurabo Fm (Early Pliocene), Arroyo Zalaya, locality same as above, collected over 1 km downstream from bridge over Arroyo Zalaya (= NMB 17311-17314; see Saunders *et al.*, 1986: text-fig. 21).
- NMB 17273, unnamed formation (Late Miocene), E bank, *ca.* 300-500 m upstream from mouth of Arroyo López, Río Yaque del Norte.
- NMB 17274, unnamed formation (Late Miocene), island in Río Yaque del Norte NW of NMB 17273, *ca.* 100-250 m upstream from mouth of Arroyo López.
- NMB 17275, unnamed formation (Late Miocene), E bank Río Yaque del Norte, *ca.* 100-200 m upstream from mouth of Arroyo López.
- NMB 17278, unnamed formation (Late Miocene), Río Yaque del Norte, E bank, bluff on next major eastward bend downstream from López section, *ca.* 800 m (straight line) N of mouth of Arroyo López.
- NMB 17281, Baitoa Fm (late Early Miocene), Río Yaque del Norte, E bank, spot collection in bluff immediately upstream from

mouth of Arroyo Hondo.

NMB 17282, Baitoa Fm (late Early Miocene), Río Yaque del Norte, E bank, spot collection in bluff immediately upstream from mouth of Arroyo Hondo.

NMB 17283, Baitoa Fm (late Early Miocene), Río Yaque del Norte, E bank, spot collection in bluff immediately upstream from mouth of Arroyo Hondo.

NMB 17286, Baitoa Fm (late Early Miocene), Río Yaque del Norte, E bank, spot collection in bluff immediately upstream from mouth of Arroyo Hondo.

NMB 17320, Baitoa Fm (late Early Miocene), Río Yaque del Norte, E bank, spot collection in center of bluff immediately upstream from mouth of Arroyo Hondo.

NMB 19004 = TU 1212, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, third bluff downstream from bridge on Los Quemados-Sabaneta road (= USGS 8548).

NMB 19005 = TU 1214, Gurabo Fm (Early Pliocene), Río Gurabo, fifth to eighth bluffs, both sides of river, downstream from bridge on Los Quemados-Sabaneta road (= USGS 8550-8553).

NMB 19006 = TU 1231, Río Gurabo (Late Miocene/Early Pliocene), float near ford on Los Quemados-Sabaneta road.

NMB 19009 = TU 1246, Gurabo Fm (Late Miocene/Early Pliocene), Río Gurabo, both sides, 1-2 km upstream from bridge on Los Quemados-Sabaneta road (= Maury's zone E, USGS 8538).

NMB 19010 = TU 1249, unnamed formation (Middle Miocene), road cut 8.6 km W of plaza at San Cristobal, on road to Bani, southern Dominican Republic.

NMB 19011 = TU 1278, Gurabo Fm (Early Pliocene), large arroyo on E side Río Gurabo at ford on Los Quemados-Sabaneta road.

NMB 19012 = TU 1281, Mao Adentro Limestone (Early Pliocene), road metal quarry on highway, S side of Río Yaqué del Norte, 1 km E of Guayubin on road to Mao.

NMB 19013 = TU 1284, Gurabo Fm (Late Miocene), Río Yaqué del Norte, S bank, at junction of roads to San Jose de los Matos and Canela, 6 km W of Santiago de los Caballeros (= USGS 8702?).

NMB 19014 = TU 1280, Gurabo Fm (Late Miocene), Río Mao, bluff on W side 1 km N of Cercado de Mao (= USGS 8733).

NMB 19017 = TU 1357, Gurabo Fm (Late Miocene), bluff on W side Río Yaqué del Norte, above water plant at S edge of Bella Vista, 3 km S of bridge at Santiago de los Caballeros.

NMB 19021 = TU 1444, NMB 19021, unnamed formation (Late Miocene), Río Yaque del Norte, at Lopéz, *ca.* 0.5 km upstream from mouth of Arroyo Lopéz, between middle and lower hard limestone ledges.

NMB 19022 = TU 1450, Gurabo Fm (Late Miocene), Arroyo Dicayagua, tributary of Río Yaqué del Norte, SW of Santiago de los Caballeros, bluffs both sides for 2 km upstream from bridge on highway to San Jose de los Matas.

Carriacou Island, Grenadine Islands

NMB 10703, Grand Bay Fm (Middle? Miocene), just to NW of Point St. Hilaire (Limlair Pt.), Grand Bay.

NMB 10709, Grand Bay Fm (Middle? Miocene), 120 m W of Tarlton's Point.

NMB 10710, Grand Bay Fm (Middle? Miocene), Grand Bay promontory.

NMB 10716, locality same as above.

NMB 10759, Kendace Siltstone member, Belmont Fm (late Early Miocene), 200 m S of first junction S of Belvedere, near E. Kent's house.

NMB 10789, Kendace Siltstone member, Belmont Fm (late Early Miocene), Kendace Point.

NMB 10812, Grand Bay Fm (Middle? Miocene), coast 400 m S of Grand Bay promontory.

NMB 13759, Kendace Siltstone member, Belmont Fm (late Early Miocene), Kendace Point.

NMB 13770, Grand Bay Fm (Middle? Miocene), Grand Bay cliff.

Guadeloupe

NMB 10630, Miocene, Ravine Poucet, 4 km SE of Pointe-a-Pitre, Grande Terre.

Barbados

NMB 10118, Coral Rock (Pleistocene), Parish of Christchurch.

NMB 10121, Coral Rock (Pleistocene), Marine Hotel, Hastings.

Trinidad

NMB 10186, Holocene, Carenage Bay, Gulf of Paria.

NMB 10187, sub-Recent, Pointe-a-Pierre foreshore.

NMB 10220, Guaracare Limestone Member of Tamana Fm (Middle-Late Miocene), Nariva Quarry, near Tabaquite.

NMB 10633, Holocene, Simpsons Point, near Pointe-a-Pierre.

NMB 11301, Upper Brasso Fm (Early to Middle Miocene), Barclay Branch, Crony River system, Brasso.

NMB 11306, Upper Brasso Fm (Early to Middle Miocene), Barclay Branch, Crony River system, Brasso, float from upstream.

Venezuela

NMB 12040, Punta Gavilán Fm (Early Pliocene), Sabanas Altas, near Punta Gavilán, Estado Falcón (see map by Rutsch, 1934: fig. 2, for localities near Punta Gavilán).

NMB 12043, Punta Gavilán Fm (Early Pliocene), Boca Gucque, near Punta Gavilán, Estado Falcón.

NMB 12045, Punta Gavilán Fm (Early Pliocene), Punta Gavilán, Estado Falcón.

NMB 12842, Cantaure Fm (late Early Miocene), main Cantaure shellbed 500 m S of Casa Cantaure, Paraguaná Peninsula, Estado Falcón.

NMB 12865, Punta Gavilán Fm (Early Pliocene), 150 m S of Punta Gavilán, type locality of Punta Gavilán Fm.

NMB 12879, Cubagua Fm (Early Pliocene), 1 m-thick "*Serpulorbis* shellbed," SW part of Cerro Guamacho, Araya Peninsula, Estado Sucre.

NMB 12884, Pleistocene terrace deposit, E rim of Quebrada Araya, capas de Castillo de Araya, Araya Peninsula (= NMB 17541).

NMB 12887, Cubagua Fm (Early Pliocene), 4 m-thick shellbed, N slope of Cerro Barragón, at road *ca.* 2 km S of Araya village, Araya Peninsula, Estado Sucre.

NMB 12892, lower part of upper Caiguire Fm (Pliocene-Pleistocene?), from Cementerio de Caiguire & Quebrada Pan y Agua to Ceferino, Cumaná Hill, Ceferino, Estado Sucre.

NMB 12898, Mare Fm (Late Pliocene), 150 m W of Quebrada

- Mare Abajo, Cabo Blanco, near La Guaira, Distrito Federal.
- NMB 13112, Mataruca Member, Caujarao Fm (Late Miocene), 50 m W of Carrizal cemetery, Carrizal, E of La Vela, Estado Falcón (= NMB 12859, 13116).
- NMB 13116, Mataruca Member, Caujarao Fm (Late Miocene), locality same as above (= NMB 12859, 13112).
- NMB 13338, Cubagua Fm (Pliocene), Isla Cubagua.
- NMB 13339, Cubagua Fm (Pliocene), La Caldera, Isla Cubagua.
- NMB 13346, Holocene "raised beach," near Cumaná, Estado Sucre.
- NMB 13349, Mare Fm (Late Pliocene), Cabo Blanco, La Guaira area, Distrito Federal.
- NMB 13355, locality same as above.
- NMB 13357, locality same as above.
- NMB 13388, Veral Fm (Late Miocene), Cumarebo area, on trail 100 m W of Trig Point Juan Garcia, E of Veral Ridge, Estado Falcón.
- NMB 13640, Veral Fm (late Miocene), Cumarebo area, E of Veral Ridge, Estado Falcón.
- NMB 13641, as NMB 13388.
- NMB 13667, Caujarao Fm (Late Miocene), SW of Pueblo Cumarebo, W of Quilagua no. 1 well, Cumarebo area, Estado Falcón.
- NMB 13892, Punta Gavilán Fm (Early Pliocene), Punta Gavilán, Estado Falcón.
- NMB 16464, La Vela Fm (Late? Miocene), Saladillo, SW of Coro, Estado Falcón.
- NMB 16526, La Vela Fm (Late Miocene), La Vela, between Carretera Falcón and Well no. 2, Estado Falcón.
- NMB 16668, Paraguana Fm (Pliocene), La Luz, near Quebrada Cuarta Larga, 3 km W of Pueblo Nuevo, Paraguaná Peninsula, Estado Falcón.
- NMB 17240, Cantaure Fm (late Early Miocene), 500 m S of Casa Cantaure, Mesa de Cocodite, W of Pueblo Nuevo, Paraguaná Peninsula, Estado Falcón.
- NMB 17241, locality same as above.
- NMB 17242, locality same as above.
- NMB 17243, locality same as above.
- NMB 17248, locality same as above.
- NMB 17512, type locality of Mare Fm (Pliocene), Mare Abajo, La Guaira area, Cabo Blanco, from lower two-thirds of section, coll. Win & Jack Gibson-Smith.
- NMB 17513, Mare Fm (Pliocene), Punta Gorda, Cabo Blanco, coll. Win & Jack Gibson-Smith.
- NMB 17515, upper shellbed, Mare Fm (Late Pliocene), Punta Gorda, Cabo Blanco, coll. Win & Jack Gibson-Smith.
- NMB 17516, lower shellbed, Cantaure Fm (late Early Miocene), 300 m SSE of new (1952) Casa Cantaure, in unnamed quebrada, Paraguaná Peninsula, Estado Falcón, coll. Win & Jack Gibson-Smith.
- NMB 17517, upper shellbed, Cantaure Fm (late Early Miocene), 450 m S of Casa Cantaure, on S slope of Loma Barbasco, Paraguaná Peninsula, Estado Falcón, coll. Win & Jack Gibson-Smith.
- NMB 17518, locality same as above, along track to Casa Paraguay, 375 m ESE of Casa Cantaure, coll. Win & Jack Gibson-Smith.
- NMB 17519, locality same as above, 550 m SE of Casa Cantaure, coll. Win & Jack Gibson-Smith.
- NMB 17520, locality same as above, 1050 m WSW of Casa Cantaure and 250 m NW of Casa la Libertad, coll. Win & Jack Gibson-Smith.
- NMB 17521, La Candelaria beds (Early Miocene), 1,600 m W of Casa Cantaure and 50 m N of Casa La Candelaria, Paraguaná Peninsula, Estado Falcón, coll. Win & Jack Gibson-Smith.
- NMB 17526, El Porvenir beds (early Middle Miocene), Mesa de Cocodite, 100 m from foot of N scarp of mesa, 200-300 m S of Caserio El Porvenir, SSW of Buenevara, Paraguaná Peninsula, Estado Falcón, coll. Win & Jack Gibson-Smith.
- NMB 17527, Buenevara Adentro beds (early Middle Miocene), Mesa de Cocodite, 100 m from foot of scarp of mesa, 50-100 m W of reservoir to SSE of Buenevara, Paraguaná Peninsula, Estado Falcón, coll. Win & Jack Gibson-Smith.
- NMB 17530, Mataruca Member, Caujarao Fm (Late Miocene), 30 m W of Cementario de Carrizal, Estado Falcón, coll. Win & Jack Gibson-Smith.
- NMB 17531, Punta Gavilán Fm (Early Pliocene), Punta Gavilán, Estado Falcón, coll. Win & Jack Gibson-Smith.
- NMB 17532, Cubagua Fm (Early Pliocene), first major bend along track leading S from Castillo de Araya, N scarp of Cerro Barragón, Araya Peninsula, coll. Win & Jack Gibson-Smith.
- NMB 17541, Castillo de Araya Fm (Pleistocene), Araya Peninsula, coll. Win & Jack Gibson-Smith.
- NMB 17542, Boca Chica Fm (Pleistocene), Araya Peninsula, coll. Win & Jack Gibson-Smith.
- NMB 17561, Caiguire Fm (Pliocene), Quebrada Maria de la Cruz, N flank of Cerro de Caiguire, Cumaná, coll. Win & Jack Gibson-Smith.
- NMB 17563, El Manglillo Fm (Pleistocene), El Manglillo, S coast of Isla Margarita, coll. Win & Jack Gibson-Smith.
- NMB 17565, Holocene terrace, Punta Tonel, Isla Margarita, coll. Win & Jack Gibson-Smith.
- NMB 17568, Catia Member of Playa Grande Fm (Pleistocene), Cabo Blanco, coll. Win & Jack Gibson-Smith.
- NMB 17606, Caiguire Fm (Middle? Pliocene), S flank of Cerro de Caiguire, Cumaná, coll. Win & Jack Gibson-Smith.
- NMB 17607, Maiquetia Member, Playa Grande Fm (Pleistocene), Quebrada Las Pailas, Cabo Blanco, coll. Win & Jack Gibson-Smith.
- NMB 18169, Caiguire Fm (Middle? Pliocene), SE flank of Cerro de Caiguire, Cumaná, coll. Win & Jack Gibson-Smith.

Ecuador

- NMB 12816, Borbón Fm (middle-late Miocene), first cliff E of Punta Same, Esmeraldas area, Esmeraldas Province.
- NMB 12818, Onzole Fm (Pliocene), float from river bed *ca.* 1 km from coast, Quebrada Camarones, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town.
- NMB 12820, Onzole Fm (Pliocene), float downstream from NMB 12821, Quebrada Camarones, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town.
- NMB 12821, Onzole Fm (Pliocene), 40 cm bed of rich mollusks in greenish sandstone, Quebrada Camarones, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of

- Esmeraldas town.
- NMB 12822, Onzole Fm (Pliocene), artificial outcrop on top of hill, km 493.05 on Trans-Ecuadorian Pipeline, 10 km S of Esmeraldas.
- NMB 12823, Onzole Fm (Pliocene), Quebrada Camarones, 20 km by road E of bridge over Río Esmeraldas (= 11 km straight line E of Esmeraldas town), greenish sandstone rich in mollusks.
- NMB 12824, Onzole Fm (Pliocene), 30-100 cm above NMB 12823, Quebrada Camarones, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town.
- NMB 12825, Onzole Fm (Pliocene), green sandstone, Quebrada Camarones, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town; early *Hirsutella margaritae* zone, overlying NMB 12824.
- NMB 19018 = TU 1397, Onzole Fm (Pliocene), 200 m up Quebrada Camarones from coast, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town, type locality of *Neosconsia ecuadoriana* Olsson, 1964.
- NMB 19019 = TU 1398, Onzole Fm (Pliocene), mixed shallow and deep facies in cutting on Esmeraldas-Camarones-Onzole road, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town, immediately E of Quebrada Camarones, Esmeraldas Province.
- NMB 19078 = PPP 3369, Angostura Fm (Late Miocene), ca. 50 m upstream from Angostura village, Cueva de Angostura, Río Santiago, Borbón, Esmeraldas Province.
- NMB 19084 = PPP 3314, Onzole Fm? (Pliocene), downstream from Picaderos village, Río Santiago, Borbón, Esmeraldas Province.
- NMB 19122 = PPP 3391, Angostura Fm (Late Miocene), shellbed 2.5 m below oyster bed, Punta Verde, 30 km ENE of Esmeraldas, Esmeraldas Province.
- NMB 19124 = PPP 3394, Pliocene?, deeper water silts with occasional mollusks, some shallow-water taxa washed in from Onzole Fm, Punta Verde, 30 km ENE of Esmeraldas, Esmeraldas Province.
- NMB 19125 = PPP 3435, Angostura Fm (Middle Miocene), boulder horizon in middle of cave wall (1.5 m above lower horizon), Cueva de Angostura, Río Santiago, Borbón, Esmeraldas Province.
- NMB 19126 = PPP 3437, Angostura Fm (Middle Miocene), near Angostura village, Río Santiago, Borbón, Esmeraldas Province.
- NMB 19136 = PPP 3485, Onzole Fm (Early Pliocene), 50 cm sandy layer, lower course of Quebrada Camarones, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town, Esmeraldas Province.
- NMB 19137 = PPP 3487, 3.5 m above NMB 19136.
- NMB 19138 = PPP 3495, Onzole Fm (Early Pliocene), scree collection, lower course of Quebrada Camarones, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town, Esmeraldas Province.
- NMB 19141 = PPP 3500, Onzole Fm (Early Pliocene), large road cut immediately W of Camarones, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town, Esmeraldas Province.
- NMB 19142 = PPP 3514, Canoa Fm (Late Pliocene), Punta Canoa, 10 km SSE of San Lorenzo, which is 23 km SW of Manta, Manabi Province.

- NMB 19145 = PPP 3535, Canoa Fm (Late Pliocene), 2 km SSE of El Mangle and 13 km SSE of San Lorenzo, which is 23 km SW of Manta, Manabi Province.
- NMB 19146 = PPP 3536, 500 m SSE of NMB 19145.
- NMB 19149 = PPP 3551, Pleistocene shell bed, road cuts 5 km from roundabout at Manta, road from Manta to Montecristi, Manabi Province.
- NMB 19151 = PPP 3565, Jama Fm (Pliocene), section SSE of Punta Ballena, 7.5 km NW of Jama, 48 km NNE of Bahía de Caráquez, Manabi Province.
- NMB 19152 = PPP 3560, locality same as above; exposure at low tide, underlying NMB 19151.
- NMB 19153 = PPP 3566, type section of Jama Fm (Pliocene), 100 m S of Punta Cereza, SSE of Punta Ballena, 7.5 km NW of Jama, 48 km NNE of Bahía de Caráquez, Manabi Province.
- NMB 19154 = PPP 3558, Jama Fm (Pliocene), Punta Cereza, SSE of Punta Ballena, 7.5 km NW of Jama, 48 km NNE of Bahía de Caráquez, Manabi Province.
- NMB 19156 = PPP 3587, Angostura Fm? (Miocene?), pueblito Marco, 5 km N of Restaurante San Jose, 20 km ENE of Flavio Alfaro on road to Santo Domingo, 46 km WSW of El Carmen, Manabi Province.

TULANE UNIVERSITY (TU) LOCALITIES

Florida, USA

- TU 69a, Shoal River Fm (Middle Miocene), first ravine upstream from Shell Bluff, Shoal River, ca. 5.6 km NW of Mossy Head, Walton County.
- TU 70, Chipola Fm (late Early Miocene), Tenmile Creek, Chipola River, Calhoun County.
- TU 456, Chipola Fm (late Early Miocene), Tenmile Creek, Chipola River, Calhoun County.
- TU 458, Chipola Fm (late Early Miocene), E bank Chipola River, above Farley Creek, Calhoun County.
- TU 459, Chipola Fm (late Early Miocene), E bank of Chipola River, Calhoun County (= NMB 19030).
- TU 546, Chipola Fm (late Early Miocene), basal bed, Tenmile Creek, 3 km W of Chipola River, Calhoun County.
- TU 547, Chipola Fm (late Early Miocene), W bank Chipola River 600 m upstream from Fourmile Creek, Calhoun County.
- TU 655, Chipola Fm (late Early Miocene), Tenmile Creek, Chipola River, Calhoun County.
- TU 729, Pinecrest Fm (Pliocene), 0.1-0.5 mi S of Florida Rte. S-65D, Highlands County.
- TU 770, Pinecrest Fm (Pliocene), 2-5 km W of Florida State Rte. 70, W side Kissimmee River, Okeechobee County.
- TU 787, Chipola Fm (late Early Miocene), Tenmile Creek, ca. 2.2 km W of Chipola River, Calhoun County.
- TU 820, Chipola Fm (late Early Miocene), Farley Creek, at bridge on Florida Rte. 275, Calhoun County.
- TU 826, Chipola Fm (late Early Miocene), locality same as above.
- TU 830, Chipola Fm (late Early Miocene), Tenmile Creek, tributary of Chipola River, at power line crossing ca. 1.6 km W of Chipola River, Calhoun County.
- TU 951, Chipola Fm (late early Miocene), Tenmile Creek, tributary of Chipola River, ca. 2 km W of Chipola River, Calhoun

County.

- TU 998, Chipola Fm (late Early Miocene), Tenmile Creek, Chipola River, Calhoun County.
- TU 999, Chipola Fm (late Early Miocene), Farley Creek, S bank, *ca.* 300 m downstream (W) of bridge on Fla. Rte. 275, Calhoun County.
- TU 1051, Chipola Fm (late Early Miocene), Tenmile Creek, just downstream from Sexton's Gully, S bank, Calhoun County.
- TU 1098, Chipola Fm (late Early Miocene), Tenmile Creek, *ca.* 100 m downstream from TU 830.

Mexico

- TU 638 = NMB 19031, Agueguexquite Fm (Pliocene), cutting on Mexico Highway 180 near Perrilliat's (1963) locality, Isthmus of Tehuantepec, Veracruz.
- TU 1025, Lower Concepción Fm (Pliocene), road cut 0.8 km S of Mexico Highway 180 at Nueva Teapa, Isthmus of Tehuantepec, Veracruz.
- TU 1046 = NMB 19020, Perrilliat's (1963) locality, Agueguexquite Fm (Pliocene), cutting on Mexico Highway 180, Isthmus of Tehuantepec, Veracruz.
- TU 1318 = NMB 19016, Lower Concepción Fm (Pliocene), cutting on pipeline just to NE of Campo el Chapo, 4 km S of Mexico Highway 180 at Nueva Teapa, Isthmus of Tehuantepec, Veracruz.

Atlantic coast of Costa Rica

- TU 589, Banáno Fm (Pliocene), 0.6-0.8 km above railway bridge at La Bomba, Río Banáno, near Limón (= NMB 19024).
- TU 953, Moín Fm (latest Pliocene-Early Pleistocene), type locality, railroad cut and adjacent ditches at Empalme Moín, E side of road from Moín junction to Sandoval, 4.5 km W of Puerto Limón.
- TU 954, Moín Fm (latest Pliocene-Early Pleistocene), hill cut above Standard Fruit Company box factory, just W of cemetery at Pueblo Nuevo, 2 km W of Puerto Limón (= NMB 19026).
- TU 956, Moín Fm (latest Pliocene-Early Pleistocene), hill slope behind Baptist church, road between Puerto Limón and Pueblo Nuevo, *ca.* 0.75 km W of Pueblo Nuevo, Limón.
- TU 1239, Moín Fm (latest Pliocene-Early Pleistocene), hill cut above Standard Fruit Company box factory at Pueblo Nuevo, just W of cemetery at Pueblo Nuevo, 2 km W of Puerto Limón, *ca.* 13 m higher in section than TU 954, and 1.4 km S of TU 1240 (= NMB 19007).
- TU 1240, Moín Fm (latest Pliocene-Early Pleistocene), hill top on Calle King Fish in Barrio Los Corales 2, 1.4 km N of Standard Fruit Company box factory, which is 2 km W of Puerto Limón (= NMB 19008).
- TU 1307, Moín Fm (latest Pliocene-Early Pleistocene), hilltop half-way between Puerto Limón and Barrio Los Corales 1, *ca.* 0.5 km N of highway at Pueblo Nuevo (= NMB 19015).
- TU 1489, Moín Fm (latest Pliocene-Early Pleistocene), hilltop on Calle King Fish in Barrio Los Corales 3, *ca.* 1.8 km N of Standard Fruit Company box factory, which is 2 km W of Puerto Limón.

Atlantic coast of Panama

- TU 757, Gatun Fm (Late Miocene), road cut E of Cativa, Colon (= NMB 19025).
- TU 958, Gatun Fm (Late Miocene), hill slope above TU 757 (= NMB 19028).
- TU 959, Gatun Fm (Late Miocene), outcrop 100 m S of refinery gate, Isla Payardi, E of Cativa, Colon.
- TU 960, Gatun Fm (Late Miocene), top of hill, just E of refinery gate, Isla Payardi, E of Cativa, Colon (= NMB 19029).
- TU 961, Gatun Fm (Late Miocene), Woodring's loc. 138, Trans-isthmian Highway just E of Cativa, Colon.
- TU 962, Gatun Fm (Late Miocene), outcrop 500 m E of refinery gates, E of Cativa, Colon (= NMB 19027).

Dominican Republic (see Saunders *et al.*, 1986: appendix 4; localities were also mapped by Saunders *et al.*, 1986: text-figs 5, 21, 29, 34, 38).

- TU 1205, Gurabo Fm (Late Miocene/Early Pliocene), road cut at K. 15-16, on highway from Santiago to San Jose de los Matas, W of bridge over Río Yaque del Norte at Santiago de los Caballeros (= Pflug, 1961: K. 13-14).
- TU 1206, Gurabo Fm (Late Miocene/Early Pliocene), road cut at K. 17, on highway from Santiago to San Jose de los Matas, W of bridge over Río Yaque del Norte at Santiago de los Caballeros (= Pflug, 1961: K. 15).
- TU 1210, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, first bluff downstream from bridge on Los Quemados-Sabaneta road (= USGS 8544; see localities on Saunders *et al.*, 1986: text-fig. 5).
- TU 1211, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, second bluff downstream from bridge on Los Quemados-Sabaneta road (= USGS 8546).
- TU 1212, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, third bluff downstream from bridge on Los Quemados-Sabaneta road (= USGS 8548, NMB 19004).
- TU 1213, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, fourth bluff downstream from bridge on Los Quemados-Sabaneta road (= USGS 8549).
- TU 1214, Gurabo Fm (Early Pliocene), Río Gurabo, fifth to eighth bluffs, both sides of river, downstream from bridge on Los Quemados-Sabaneta road (= USGS 8550-8553, NMB 19005).
- TU 1215, Gurabo Fm (Early Pliocene), Río Gurabo, Maury's zone D, from bridge on Los Quemados-Sabaneta road to 1 km upstream (= USGS 8539-8543).
- TU 1219, Gurabo Fm (Early Pliocene), Río Amina, bluffs E side, immediately above ford that is 2 km W of Potrero and 3 km downstream from dam at "La Represa" (= USGS 8516; just below center of Saunders *et al.*, 1986: text-fig. 34).
- TU 1220, Gurabo Fm (Early Pliocene), Río Amina, bluffs on W side *ca.* 100-500 m above ford, which is 2 km W of Potrero, and *ca.* 3 km downstream from "La Represa" (= USGS 8517).
- TU 1225, Gurabo Fm (Late Miocene/Early Pliocene), Arroyo la Sabrima, W side Río Mao, upstream from Mao Adentro and first side stream downstream from Cercado de Mao, 11 road km S of Mao (at center left edge of Sanders *et al.*, 1986: text-fig. 29).
- TU 1226, Baitoa Fm (late Early Miocene), type locality, Río Yaque

- del Norte, E bank, downstream from Baitoa, and above confluence of Río Bao and Río Yagué del Norte.
- TU 1227, Gurabo Fm (Early Pliocene; Saunders *et al.*, 1986: 34), Arroyo Zalaya, which crosses road to Janico from Santiago de los Caballeros 11 km S of bridge over Río Yague del Norte at Santiago.
- TU 1227A, Gurabo Fm (Early Pliocene), turbidity flow lens in above, 25 m downstream from road bridge.
- TU 1230, Cercado Fm (Late Miocene), Río Cana, E bank, just above ford at Caimito, on Los Quemados-Sabaneta road (= Maury's zone H; USGS 6534).
- TU 1231, Río Gurabo (Late Miocene/Early Pliocene), float near ford on Los Quemados-Sabaneta road (= NMB 19006).
- TU 1245, Mao Adentro Limestone (Late Pliocene), road cut 5 km S of Guayubin Bridge, on road to Sabanetta.
- TU 1246, Gurabo Fm (Late Miocene/Early Pliocene), Río Gurabo, both sides, 1-2 km upstream from bridge on Los Quemados-Sabaneta road (= Maury's zone E, USGS 8538, NMB 19009).
- TU 1248, Gurabo Fm (Early Pliocene), Río Amina, W bank, first bluff downstream from ford at Potrero.
- TU 1249, unnamed formation (Middle Miocene), road cut 8.6 km W of plaza at San Cristobal, on road to Bani, southern Dominican Republic (= NMB 19010).
- TU 1250, Gurabo Fm (Late Miocene/Early Pliocene), Río Verde, S bank, just above ford on side road connecting Duarte Highway with La Vega-Moca Highway, 10 km N of La Vega (see Saunders *et al.*, 1986: text-fig. 38).
- TU 1277, Gurabo Fm (Late Miocene/Early Pliocene), Río Gurabo, Maury's zone F, from horse trail to 0.5 km upstream from trail, ca. 2-2.5 km upstream from bridge on Los Quemados-Sabaneta road.
- TU 1278, Gurabo Fm (Early Pliocene), large arroyo on E side Río Gurabo at ford on Los Quemados-Sabaneta road (= NMB 19011).
- TU 1279, Late Miocene/Early Pliocene, road cut, Los Quemados-Sabaneta Road, 2.5 km W of los Quemados.
- TU 1280, Gurabo Fm (Late Miocene), Río Mao, bluff on W side, 1 km N of Cercado de Mao (= USGS 8733, NMB 19013).
- TU 1281, Mao Adentro Limestone (Early Pliocene), road metal quarry on highway, S side of Río Yagué del Norte, 1 km E of Guayubin on road to Mao (= NMB 19012).
- TU 1284, Gurabo Fm (Late Miocene), Río Yagué del Norte, S bank, at junction of roads to San Jose de los Matos and Canela, 6 km W of Santiago de los Caballeros (= USGS 8702?, NMB 19013).
- TU 1292, Gurabo Fm (Late Miocene/Early Pliocene), Río Mao, W bank, bluffs on long corner where river turns to E, 1.5-2 km upstream from Mao Adentro, about 9 road km S of Mao (= USGS 8528, NMB 16801).
- TU 1293, Gurabo Fm (Late Miocene), Río Mao, W bank, Maury's bluff 1, bluff just below Paso Chorrero, ca. 12 road km S of Mao (= USGS 8519-8520).
- TU 1294, Cercado Fm (Late Miocene), Río Mao, W bank, bluff 3 of Maury, bluffs just above Paso de los Perros, ca. 5 road km N of Mancion-San Jose de los Matos road (= USGS 8525).
- TU 1295, Gurabo Fm? (Late Miocene/Early Pliocene), road cuts around junction of road to Naranjo with Moncion-San Jose de los Matas Road, ca. 3 km E of crossing of Río Mao at Bulla.
- TU 1296, Gurabo Fm (Late Miocene/Early Pliocene), Río Gurabo, Maury's zone F, 0.5-1 km above horse trail, ca. 2.5-3 km (straight line) above ford on Los Quemados-Sabaneta road, from immediately upstream to ca. 500 m upstream from TU 1277.
- TU 1297, Gurabo Fm (Late Miocene/Early Pliocene), Río Gurabo, Maury's zone G, 1-1.5 km above horse trail, ca. 3-3.3 (straight line) km above ford on Los Quemados-Sabaneta road.
- TU 1298, Gurabo Fm (Late Miocene), Río Gurabo, E bank at large E-ward bend ca. 2 km upstream from horse trail, or 3.5 km (straight line) upstream of ford on Los Quemados-Sabaneta road, downstream part of large S-bend at lower quarter of Saunders *et al.* (1986: text-fig. 5; = USGS 8737).
- TU 1301, Cercado Fm (Late Miocene), Río Cana, E bank, 2 km upstream from ford at Caimito on Los Quemados-Sabaneta road.
- TU 1354, Gurabo Fm (Early Pliocene; Saunders *et al.*, 1986: 23), Cañada de Zamba, tributary on W side of Río Cana, ca. 2 km E of village of Zamba, which is 7 km N of Cruz de Santiago, on road to Guayubin, or 4.5 m below ford at Caimito.
- TU 1357, Gurabo Fm (Late Miocene), bluff on W side Río Yagué del Norte, above water plant at S edge of Bella Vista, 3 km S of bridge at Santiago de los Caballeros (= NMB 19017).
- TU 1358, Cercado Fm (Late Miocene), Río Gurabo, W side, at and downstream from mouth of Arroyo La Cabra, ca. 6 km (straight line) upstream from ford on Los Quemados-Sabaneta road, second bend from bottom of map (Saunders *et al.*, 1986: text-fig. 5).
- TU 1359, Cercado Fm (Late Miocene), Río Gurabo, E bank, long bluff extending upstream from mouth of Arroyo Palero, ca. 5.5 (straight line) km upstream from ford on Los Quemados-Sabaneta road, next bluff ca. 300 m downstream from TU 1358.
- TU 1363, Baitoa Fm (late Early Miocene), Boca de los Rios, above the waterfall in Arroyo Hondo, which enters Río Yagué del Norte from E just below confluence with Río Bao, downstream from Baitoa (these TU localities are shown near bottom of map, Saunders *et al.*, 1986: text-fig. 21).
- TU 1364, Baitoa Fm (late Early Miocene), Boca de los Rios, below the waterfall in Arroyo Hondo, which enters Río Yagué del Norte from E just below confluence with Río Bao, downstream from Baitoa (= NMB 18560).
- TU 1365, Mao Fm (Early Pliocene), Río Gurabo, W bank, bluff ca. 4 km below ford on Los Quemados-Sabaneta road, third-from-top locality on map (Saunders *et al.*, 1986: text-fig. 5).
- TU 1378, Cercado Fm (Late Miocene), Río Gurabo, W bank, high bluff ca. 1 km upstream from mouth of Arroyo La Cabra, or ca. 6.6 km (straight line) upstream from ford on Los Quemados-Sabaneta road, bottom locality on map (Saunders *et al.*, 1986: text-fig. 5).
- TU 1379, Gurabo Fm (Late Miocene), Río Mao, E bank, for 100 m either side of mouth of Arroyo Bajón, just below Paso de los Perros, ca. 5 road km N of Moncion-San Jose de los Matas road (near bottom of Saunders *et al.*, 1986: text-fig. 29).
- TU 1406, Cercado Fm (Late Miocene), road cuts, Santiago-Janico road, 3-5 km W of junction with road to Baitoa, 16-17 km NW of bridge over Río Yagué del Norte at Santiago de los Caballeros.

- TU 1410, Gurabo Fm (Late Miocene), Río Mao, bluff on E bank 1 km upstream from Paso de Chorrero, halfway between Maury's Bluffs 1 and 3 (= USGS 8521-8523, NMB 16802-16803; not identified by Saunders *et al.*, 1986: text-fig. 29).
- TU 1411, Gurabo Fm (Late Miocene/Early Pliocene), Río Guanajuma, tributary of Río Amina from W, bluffs on N side just downstream from trail at Higuerito Penuelas, which meets river *ca.* 2.5 km upstream from confluence with Río Amina, and 1 km above ford on road to Potrero.
- TU 1412, Gurabo Fm (Late Miocene/Early Pliocene), locality same as above; bluffs on S side.
- TU 1422, Cercado Fm (Late Miocene), Arroyo Bellaco (= Beyaco), tributary of Río Cana from the E, coral reef exposed *ca.* 1 km below ford at Las Caobas Adentro, 3 km SW of Las Caobas.
- TU 1444 = NMB 19021, unnamed formation (Late Miocene), Río Yaque del Norte, at Lopéz, *ca.* 0.5 km upstream from mouth of Arroyo Lopéz, between middle and lower hard limestone ledges (= NMB 19021).
- TU 1449, Gurabo Fm (Early Pliocene), Río Yaqué del Norte, W bank, large gravity flows exposed along road to river at village of La Barranca (not identified by Saunders *et al.*, 1986: text-fig. 21).
- TU 1450, Gurabo Fm (Late Miocene), Arroyo Dicayagua, tributary of Río Yaqué del Norte, SW of Santiago de los Caballeros, bluffs both sides for 2 km upstream from bridge on highway to San Jose de los Matas (= NMB 19022).
- TU 1451, Gurabo Fm (Early Pliocene), Arroyo Babosico, bluffs both sides upstream from bridge at La Barranca to junction with Arroyo Zalaya, *ca.* 1 km above bridge.
- TU 1455, Gurabo Fm (Late Miocene/Early Pliocene), Río Guanajuma, W side at large bend *ca.* 1.5 km upstream (S) from ford at Higuerito Penuelas.
- TU 1456, Gurabo Fm (Late Miocene/Early Pliocene), as for TU 1455.

Ecuador

- TU 1397, Onzole Fm (Pliocene), mixed shallow and deep facies 200 m up Quebrada Camarones, at E edge of village of Camarones, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town, Esmeraldas Province (= NMB 19018).
- TU 1398, Onzole Fm (Pliocene), mixed shallow and deep facies in cutting on Esmeraldas-Camarones-Onzole road, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town, 400 m E of Quebrada Camarones, Esmeraldas Province.
- TU 1399, Onzole Fm (Pliocene), mixed shallow and deep facies in cutting on Esmeraldas-Camarones-Onzole road, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town, immediately E of Quebrada Camarones, Esmeraldas Province (= NMB 19019).
- TU 1400, Onzole Fm (Pliocene), deep-water facies collected along Esmeraldas-Camarones-Onzole road, parallel to coast, over 8 km to E of airport, Esmeraldas Province.

UNITED STATES GEOLOGICAL SURVEY (USGS) LOCALITIES

Louisiana, USA

- USGS 26471, Mississippi delta "mudlumps," late Pleistocene/Holocene, mouth of South Pass, Plaquemines Parish.
- USGS 26949, Mississippi delta "mudlumps," late Pleistocene/Holocene: mudlump 90, mouth of South Pass, Plaquemines Parish.

Florida, USA

- USGS 3742, Shoal River Fm (late Middle Miocene), Shell Bluff, WNW of Mossy Head, Walton County, Shoal River.
- USGS 3856, Shoal River Fm (late Middle Miocene), W of Mossy Head, Walton County, Shoal River.
- USGS 5184, Shoal River Fm (late Middle Miocene), Shoal River, head of first drain below Shell Bluff, *ca.* 200 m W of river, Walton County.
- USGS 5195, same as above.
- USGS 10603, Shoal River Fm (late Middle Miocene), *ca.* 2.5 km SW of Eucheeanna, road from Eucheeanna to Knox Hill, Walton County, below Shell Bluff, Shoal River.
- USGS 26552, spoil on levee L-49, 5 km W of Indian Prairie Canal at bridge 16A, on Florida Rte. 78, NW of Lake Okeechobee, Elderberry, Glades County, Florida, probably from Pinecrest Fm (middle Pliocene), coll. Carmen Hughes, 17 September 1961, *ex* A. A. Olsson collection.

Mexico

- USGS 10699, Pliocene, Río Jaltepec, Isthmus of Tehuantepec, Veracruz.
- USGS 12084, Plio-Pleistocene, Punta Gorda area, Puerto Mexico [Coatzacoalcas], Veracruz.
- USGS 12086, Agueguexquite Fm (Pliocene), Agueguexquite Creek, Isthmus of Tehuantepec, Veracruz.
- USGS 18688, Pliocene(?), Puerto Mexico area [Coatzacoalcas], Veracruz.
- USGS 22279, Agueguexquite Fm (Pliocene), between Coatzacoalcas and Villa Hermosa, Isthmus of Tehuantepec, Veracruz.

Atlantic coast of Costa Rica

- USGS 2693, Moín Fm (latest Pliocene-Early Pleistocene), track bal- last along railway, taken from old reef, Limón.
- USGS 4269, Moín Fm (latest Pliocene-Early Pleistocene), Port Limón.
- USGS 5882a, Banáno Fm (Pliocene), Río Banáno, near Limón, up- permost fossiliferous zone.
- USGS 5882h, Banáno Fm (Pliocene), Río Banáno, near Limón, to- ward base of fossiliferous exposure.
- USGS 5883a, Banáno Fm (Pliocene), Río Bananito, near Limón, uppermost fossiliferous zone.
- USGS 8343, Moín Fm (latest Pliocene-Early Pleistocene), Port Limón.
- USGS 18273, locality same as above.
- USGS 18693, locality same as above, hill excavation at Port Limón.
- USGS 20468, locality same as above, excavation at new Colegio de Limón building, on NW outskirts of Puerto Limón.
- USGS 21035, locality same as above, hillside cut at new site of

Colegio de Limón, on NW outskirts of Puerto Limón.
 USGS 21036, locality same as above, scraped hillside slope in Barrio Cemetario district in S outskirts of Puerto Limón.
 USGS 21051, locality same as above, Moín Hill, early collection.

Pacific coast of Costa Rica

USGS 24792, Plio-Pleistocene, stream courses including Río la Vaca, crossed by Progreso-Lagarto trail, Puntarenas Province.

Atlantic coast of Panama

USGS 5211, Pleistocene, Woodring's loc. 159, Gatun locks, Canal Zone.
 USGS 5850, Pleistocene or Holocene, Mt. Hope, Canal Zone.
 USGS 5854, Gatun Fm (Late Miocene), Mt. Hope, Canal Zone.
 USGS 5899, Gatun Fm (Late Miocene), railroad 1 km S of Gatun.
 USGS 8307, "Bocas del Toro Fm" (Pliocene), Colon Island [assumed to refer to the "unnamed" formation shown underlying Swan Cay Fm by Coates (1999: text-fig. 5), and included here in Fish Hole Reef Member, Shark Hole Point Fm, because that is shown as laterally equivalent to the unnamed formation by Coates (1999: text-fig. 5); these collections (USGS 8307-8323) are listed here within Shark Hole Point Fm].
 USGS 8323, locality same as above, coralline zone, Minnitimmi Creek, Bocas del Toro Island (= Colon Island, Minnitimmi Creek; Coates, 1999: 294, map 9).
 USGS 8326 (assigned here to Valiente Fm; Coates *et al.*, 2003: fig. 1A), 2 cays just off Bluefields Point, Valiente Peninsula (= PPP 2145, not assigned a formation in PPP database; Coates, 1999: 290, map 5, top left corner).
 USGS 8375, Gatun Fm (Late Miocene), cuts W of Gatun dam, Canal Zone.
 USGS 8383, Gatun Fm (Late Miocene), Atlantic coast near Río San Miguel, Colon.
 USGS 8408, Gatun Fm (Late Miocene), Caribbean coast E of San Miguel, Colon.
 USGS 8409, Gatun Fm (Late Miocene), Mt. Hope facies, along road bordering eastern diversion channel ("old French canal"), near Mt. Hope.
 USGS 8410, locality same as above, cuts on N side of "old French canal."
 USGS 8487, Gatun Fm (Late Miocene), Caribbean coast E of Río San Miguel, Colon.
 USGS 8488, locality same as above.
 USGS 16909, Gatun Fm (Late Miocene), cuts on both sides of Transisthmian Highway 3.3 km E of entrance to Coco Solo Naval Hospital, Canal Zone.
 USGS 16926, Gatun Fm (Late Miocene), W-most cut on railroad S of Fort Davis, 1.7 km NNE of Gatun third locks, Canal Zone.
 USGS 16949, Gatun Fm (Late Miocene), spoil dump from Gatun third locks, Panama Canal.
 USGS 21956, Gatun Fm (Late Miocene), 100 m N of Transisthmian Highway and 75 m W of road to refinery, Isla Payardi, immediately E of Cativa, Colon.
 USGS 22016, same as above.
 USGS 22018, Gatun Fm (Late Miocene), 100 m SW of refinery gate, Isla Payardi, Cativa, Colon (= NMB 17643, 17868, 18261, 18307, 18342, 18360, 18391, 18662, TU 959).

USGS 22019, Gatun Fm (Late Miocene), top of hill above USGS 22018 (= NMB 17644, 17869, 18262, 18308, 18326, 18392, 18662, TU 960).
 USGS 22391, lower part of Gatun Fm (Late Miocene), dredged below sea level at refinery site, Payardi Island, Cativa, Colon.
 USGS 23663, Gatun Fm (Late Miocene), S side Transisthmian Highway, hillside excavation at Colchoneria Yero, *ca.* 450 m SW of Cativa, Colon.
 USGS 24173, Gatun Fm (Late Miocene), Gatun locks excavation, Canal Zone.
 USGS 25278, middle part of Gatun Fm (Late Miocene), hillside excavation in housing development adjoining Canal Zone boundary (*i.e.*, Residencial Dr. Martin Luther King).
 USGS 25281, lower part of Gatun Fm (Late Miocene), cut on S side of cart track leading past house on refinery road, Cativa, Canal Zone.

Pacific coast of Panama (Darien)

USGS 8477, Late Miocene, Río Tuyra [Tuirá], between Limones and Río Cué, Darien.

Colombia

USGS 7852, Middle Miocene, on surface on top of knoll, Las Sierras, between El Carmen and Zambrano, Jesus del Monte-Zambrano area, Departamento de Bolivar.
 USGS 8734, Pleistocene, 2 km E of mouth of Río Cordoba, Departamento de Bolivar.
 USGS 10101, Middle Miocene, Villa Nueva, Arenal-Turbaco area, Departamento de Bolivar.
 USGS 10927, Miocene, Cerro de San Antonio, edge of town of Balsanco, N of Usiacuri, Departamento de Magdalena.
 USGS 11010, Pleistocene raised terrace, 2 km W of Río San Juan, Departamento de Antioquia.
 USGS 11012, Pleistocene, Zapotá, Departamento de Antioquia.
 USGS 11325, Pliocene(?), *ca.* 400 m S of coast, traverse from Juan de Acosta to Caribbean Sea, Cibarco-Tubará area.
 USGS 11335, Pliocene, *ca.* 800 m S of Saco, on trail from Saco to Juan de Acosta, Departamento de Atlantico.
 USGS 11344, Sado Fm (Pliocene?), road from Cibarco to Tubará, *ca.* 400 m S of Tubará, Departamento de Atlantico.
 USGS 11356, Usiacuri Fm (Late Miocene), on Juan de Acosta-Cibarco traverse, 3.2 km W of Cibarco, Departamento de Atlantico.
 USGS 11520, Tubará Fm (Miocene-Pliocene?), just below limestone scarp, *ca.* 2 km NW of Las Perdices, Cibarco-Tubará area, Departamento de Atlantico.
 USGS 11593, Miocene?, sta. 32, Quebrada Canouffage, Río San Juan-Río Sinu area, Antioquia, Departamento de Bolivar.
 USGS 11594, sta. 41, locality same as above.
 USGS 11595, Miocene?, Quebrada Cordova, locality same as above.
 USGS 11625, Miocene-Pliocene?, Quebrada Pajuil, W of Río Sinu, Antioquia, Departamento de Bolivar.

Jamaica

USGS 2374, Bowden Shellbed (Late Pliocene), St. Thomas Parish.
 USGS 2580, locality same as above.

USGS 18205, locality same as above; 50 m NW of road fork, granule-cobble gravel, *ca.* 3 m above road.

USGS 23476, Bowden, Jamaica, early collection.

USGS 23741, Bowden, Jamaica.

USGS 24743, locality same as above.

USGS 61537, locality same as above.

Cuba

USGS 3318, "raised beach" (Pleistocene terrace), Cabanas Bay.

USGS 7943, Pleistocene, naval station, Guantanamo Bay.

USGS 12103a, Pleistocene, 800 m S of naval station, Guantanamo Bay.

USGS 12103b, Pleistocene, naval station, Guantanamo Bay.

Haiti

USGS 9604, Late Miocene, Rivière Gosseline, *ca.* 9 km W of Jacmel.

USGS 18397, Late Miocene, Rivière Gauche, 5 km SE of Trouin.

USGS 18398, Late Miocene, Rivière Gauche, 6 km E of Trouin.

Dominican Republic (see Saunders *et al.*, 1986: appendix 5; localities were also mapped by Saunders *et al.*, 1986: text-figs 5, 21, 29, 34)

USGS 8516, Gurabo Fm (Early Pliocene), Río Amina, bluff on E bank 100-400 m upstream from ford near Potrero (= TU 1219) (near center of Saunders *et al.*, 1986: text-fig. 34).

USGS 8519, Gurabo Fm (Late Miocene), Río Mao, Bluff 1 of Maury, W bank *ca.* 250-400 m upstream from ford at Cercado de Mao, mostly from lower part of bluff (= TU 1293, USGS 8520).

USGS 8521, Cercado Fm (Late Miocene), Río Mao, fossils from basal 4.5 m of section, bluff on E bank 1.7 km upstream from Paso Bajito at Cercado de Mao (USGS 8522-8524, NMB 16802-16803 from same bluff).

USGS 8522, Cercado Fm (Late Miocene), Río Mao, fossils from 4.5-9 m above water, bluff on E bank 1.7 km upstream from ford (Paso Bajito) at Cercado de Mao (same bluff as USGS 8521, 8523-8524, NMB 16802-16803).

USGS 8525, Cercado Fm (Late Miocene), Río Mao, Bluff 3 of Maury, long bluff on W bank 200-400 m upstream from ford on Cercado-Bulla road and *ca.* 2.5 km (straight line) upstream from ford at Cercado de Mao (= TU 1294, NMB 16912-16913, 17269).

USGS 8526, Cercado Fm (Late Miocene), Río Mao, Bluff 2 of Maury, second bluff on W side *ca.* 2.1 km (straight line) above ford at Cercado de Mao (= NMB 16914, 16930-16932).

USGS 8527, Gurabo Fm (Late Miocene/Early Pliocene), Río Mao, bluff right bank, opposite Cercado de Mao, first bluff 1 km downstream from ford at Paso Bajito.

USGS 8528, Gurabo Fm (Late Miocene/Early Pliocene), Río Mao, second bluff on left bank below Paso Bajito, long bluff at head of long E-ward reach *ca.* 1.2 km downstream from road junction in Cercado de Mao (= TU 1292, NMB 16801).

USGS 8534, Cercado Fm (Late Miocene), E bank of Río Cana at Caimito, road from Las Caobas to Sabaneta (= Maury's zone H; TU 1230).

USGS 8537, basal Gurabo Fm (Late Miocene), Río Gurabo, W

bank, head of sharp W bend on major S-bend at lower quarter of Saunders *et al.* (1986: text-fig. 5), *ca.* 4 km (straight line) upstream from new road bridge on Los Quemados-Sabaneta road.

USGS 8538, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, 1.6 km S of upper ford at Gurabo Adentro, on road from Las Caobas to Los Quemados, 1.4 km (straight line) upstream from new road bridge on Los Quemados-Sabaneta road (= downstream part of area collected for TU 1246).

USGS 8539, Gurabo Fm (Early Pliocene), Río Gurabo, W bank, 1.3 km upstream from upper ford at Gurabo Adentro, downstream part of downstream bluff of large S-bend just below center of Saunders *et al.* (1986: text-fig. 5) (= upstream-most part of TU 1215).

USGS 8540, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, 400 m upstream from upper ford at Gurabo Adentro, next bend below USGS 8538, *ca.* 1 km upstream from new road bridge on Los Quemados-Sabaneta road (= part of TU 1215).

USGS 8541, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, 300 m upstream from upper ford at Gurabo Adentro, downstream part of bluff immediately N of USGS 8540, *ca.* 850 m upstream from new road bridge on Los Quemados-Sabaneta road (= part of TU 1215).

USGS 8544, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, 150 m upstream from middle ford at Gurabo Adentro, downstream part of bluff at major S-bend *ca.* 600-700 m downstream from new road bridge on Los Quemados-Sabaneta road (= TU 1210).

USGS 8545, Gurabo Fm (Early Pliocene), Río Gurabo, 60 m downstream from middle ford at Gurabo Adentro, W bank, opposite and next bluff downstream from USGS 8544, 300 m (straight line) downstream from new road bridge on Los Quemados-Sabaneta road (= upper part of TU 1211).

USGS 8546, Gurabo Fm (Early Pliocene), Río Gurabo, W bank just above lower ford at Gurabo Adentro, next bluff 350-450 m downstream from USGS 8545 (= lower part of TU 1211).

USGS 8547, Río Gurabo, mixed specimens (Early Pliocene) from fallen packages, collected above Gurabo Adentro (USGS 8538-8546).

USGS 8548, Gurabo Fm (Early Pliocene), Río Gurabo, E bank, *ca.* 150 m below lower ford at Gurabo Adentro, next bluff *ca.* 200-300 m downstream from USGS 8546 (= TU 1212).

USGS 8549, Gurabo Fm (Early Pliocene), Río Gurabo, E bank *ca.* 400 m below lower ford at Gurabo Adentro, next bluff 100-250 m downstream from USGS 8548 (= TU 1213).

USGS 8550, Gurabo Fm (Early Pliocene), Río Gurabo, second bluff on W bank below lower ford at Gurabo Adentro, next bluff 100-300 m downstream from USGS 8549 (= upstream part of TU 1214).

USGS 8551, Gurabo Fm (Early Pliocene), Río Gurabo, third bluff on E bank below lower ford at Gurabo Adentro, next bluff 100-250 m downstream from USGS 8550 (= middle part of TU 1214).

USGS 8555, Mao Fm (Early Pliocene), Río Gurabo, E bank *ca.* 400 m NW of bluff G (= USGS 8553), bluff S of traverse, *ca.* 1.4 km below lower ford at Gurabo Adentro, minor E bend in complex S-bends in center of upper fifth of Saunders *et al.*, 1986: text-fig. 5, between TU 1343 and 1344.

- USGS 8591, Cerros de Sal Fm (Miocene), Barahona, southern Dominican Republic.
- USGS 8668, Baitoa Fm (late Early Miocene), bluff of yellow sandstone on E bank Río Yaque del Norte, 400-600 m downstream from road bridge at Baitoa, just above bottom of Saunders *et al.*, 1986: text-fig. 21 (= TU 1226, USGS 8558, NMB 16909).
- USGS 8702, Gurabo Fm (Early Pliocene), bluff on S bank Río Yaque del Norte, 8.6 km W of Santiago.
- USGS 8714, Gurabo Fm (Early Pliocene), Río Yaque del Norte, *ca.* 3.2 km S25°W of wireless tower at Santiago.
- USGS 8726, ?upper Gurabo Fm (Early Pliocene), S side of Río Yaque del Norte, La Canita, 15 km W of Santiago.
- USGS 8733, Gurabo Fm (Late Miocene), Río Mao, bluff W side 1.7 km NW of Paso Bajito, near Cercado de Mao, N-ward bend 400-550 m N of road junction in Cercado de Mao, just below center of Saunders *et al.*, 1986: text-fig. 29 (= TU 1280).
- USGS 8737, basal Gurabo Fm (Late Miocene), Río Gurabo, *ca.* 4 km upstream from Gurabo Adentro, base of coralliferous limestone and above conglomerate, long bluff on E bank just downstream from prominent narrow W-ward bend at lower quarter of Saunders *et al.*, 1986: text-fig. 5 (= partly overlapping TU 1298).
- USGS 8739, Cercado Fm (late Miocene), Río Gurabo, *ca.* 5 km upstream from Gurabo Adentro, fossils from below conglomerate, bluff on E bank near center of gorge, upstream-most USGS locality of Saunders *et al.*, 1986: text-fig. 5 (= TU 1374).
- USGS 26273, Cercado Fm (Late Miocene), Río Mao, Bluff 3 of Maury, A. A. Olsson collection, bluff on W bank 100-300 m upstream from ford on Caimito-Bulla road, upstream-most locality of Saunders *et al.*, 1986: text-fig. 29 (= TU 1294, USGS 8525, NMB 16912-16913, 17269).
- USGS 26274, Baioa Fm (late Early Miocene), A. A. Olsson's loc. 179 (= 739), lower bluff on river at Baitoa.
- USGS 26275, Gurabo Fm? (Late Miocene/Early Pliocene), Río Mao, Bluff 1a of Maury, A. A. Olsson collection, W bank *ca.* 250-400 m upstream from ford at Cercado de Mao, mostly from lower part of bluff (= TU 1293, USGS 8519-8520, NMB 16910).
- USGS 26277, Gurabo Fm (Late Miocene-Early Pliocene?), Río Gurabo, A. A. Olsson collection locs 182, 731, 736, bluff at first river crossing (on old trail), Gurabo Adentro.
- USGS 26279, Cercado Fm (Late Miocene), Maury's bluff 3, Río Mao, A. A. Olsson's locs 202, 734, 738, 741.
- USGS 26280, locality same as above, A. A. Olsson's locs 203, 738.
- USGS 26281, Gurabo Fm (Late Miocene-Early Pliocene?), Gurabo Adentro, Río Gurabo, A. A. Olsson's locs 208, 735.
- USGS 26283, locality same as above, A. A. Olsson's loc. 219.
- USGS 26286, Miocene?, Arroyo Chepadera, Azua, A. A. Olsson's locs 707, 719.
- USGS 26292, Cercado Fm (Late Miocene), Río Mao, Bluff 3 of Maury, A. A. Olsson collection, bluff on W bank 100-300 m upstream from ford on Caimito-Bulla road, upstream-most locality of Saunders *et al.*, 1986: text-fig. 29 (= TU 1294, USGS 8525, NMB 16912-16913, 17269).
- USGS 26294, Cercado Fm (Late Miocene), Río Mao, Bluff 2 of Maury, A. A. Olsson's loc. 218, second bluff on W side *ca.* 2.1 km (straight line) above ford at Cercado de Mao (= USGS 8526, NMB 16914, 16930-16932).
- USGS 26298, Cercado Fm (Late Miocene), Río Mao, Bluff 3 of Maury, A. A. Olsson's loc. 278, bluff on W bank 100-300 m upstream from ford on Caimito-Bulla road, upstream-most locality of Saunders *et al.*, 1986: text-fig. 29 (= TU 1294, USGS 8525, NMB 16912-16913, 17269).
- USGS 26534, Lowermost Las Cahobas Fm (Miocene), bluff in blue-gray siltstone, 10 m downstream from crossing of small stream known as Río El Marco, on trail from Comendador to San Pedro, 10 km N32°W of Comendador, Provincia Benefactor, San Juan region, coll. B. N. Moore, 06 November 1940.
- USGS 26535, Lowermost Las Cahobas Fm (Miocene), high bluff in siltstone *ca.* 100 m downstream from trail crossing Río de El Pino *ca.* 3 km N63°E of Comendador, Provincia Benefactor, San Juan region, coll. B. N. Moore, 07 November 1940.

Barbados

- USGS 18381, Coral Rock (Pleistocene), Pine, late Quaternary terrace fauna near airport.
- USGS 18382, Coral Rock (Pleistocene), Britton's Hill, Barbados.
- USGS 18383, Coral Rock (Pleistocene), Erdiston, Barbados.

Trinidad

- USGS 18204, Pleistocene, Matura, loose blocks at inner edge of beach on E coast, *ca.* 1.6 km S of S edge of metamorphic rocks.
- USGS 18634, Melajo Clay member of Springvale Fm (Early Pliocene; Donovan, 1994), Melajo River, *ca.* 3 km upstream from Loco Main Road and 8 km from coast, St. Andrews County.
- USGS 19860, type locality Matura Fm (Pleistocene), Matura coast, St. Andrews County.
- USGS 19865, Trinity Hill Sandstone member of Moruga Fm (Middle Miocene), Cats Hill Oilfield, Guayaguayara area, SE Trinidad.
- USGS 21234, rich pteropod marl (early Middle Miocene, *Globorotalia fohsi barisanensis* zone), Mayo River, near 6.8 km on Mayo-Tortuga Road.
- USGS 21809, Savaneta glauconitic sandstone member of Springvale Fm (Early Pliocene), Springvale Quarry, *ca.* 1.6 km N of Forrest Park (= USGS 18255, etc.).

Venezuela

- USGS 6288, Pleistocene "raised beach" on shore, Puerto Caballo, Estado Carabobo.
- USGS 6825, Pleistocene/Holocene?, Margarita Island.
- USGS 18252, *Chione* bed, 4 m above *Turritella* bed, Mare Fm (Late Pliocene), N side Quebrada Las Pailas, 450 m SE of Maiquetia Airport beacon, Cabo Blanco, Distrito Federal.
- USGS 18253, Mare Fm (Late Pliocene), steep slope above sea, *ca.* 75 m W of Maiquetia Airport drain and *ca.* 1 km SW of airport beacon, Cabo Blanco, Distrito Federal.
- USGS 18410, Pleistocene, vertical bluff of sandy limestone interbedded with dark sandy siltstone, footpath near N border of hills, 6 km E of Cumaná.
- USGS 24548, Cubagua Fm (Pliocene), Isla de Cubagua.
- USGS 24564, Cerro Negro Mbr, Cubagua Fm (Pliocene), top sandy bed, Cañon de Las Calderas, central Cubagua Island.

USGS 24573, Pleistocene terrace, left side of road from wharf to town of Araya, Araya Peninsula, Estado Sucre.

USGS 24704, Cumaná Fm (Pliocene), Manicaure, S coast of Araya Peninsula, Estado Sucre.

USGS 25171, Cantaure Fm (late Early Miocene), near Casa Cantaure, Paraguaná Peninsula, Estado Falcón.

Ecuador

USGS 23478, Jama Fm (Late Pliocene?), S side of Jama Bay S to

Punta Barrocho, near Jama.

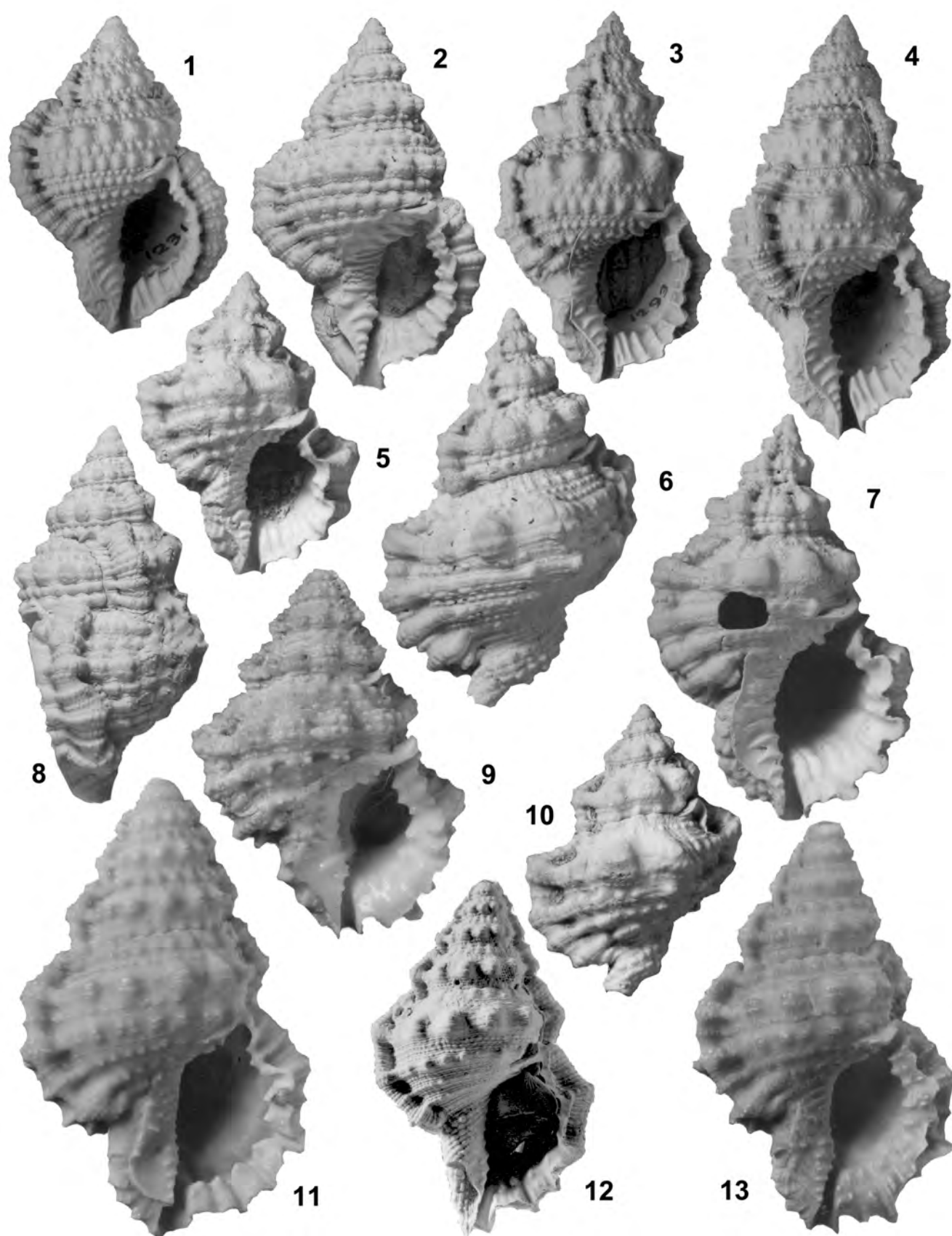
USGS 23479, Onzole Fm (Pliocene), Punta Gorda area, from 2.5 km W of mouth of Río Esmeraldas to Punta Gorda, 9 km further W, principally from beach platform at 5 km, NW Ecuador, A. A. Olsson collection.

USGS 23487, Angostura Fm (Late Miocene), Cueva de Angostura, Río Santiago, A. A. Olsson collection.

USGS 23507, "*Loripes* zone" (Pliocene?), Punta Blanca, A. A. Olsson collection.

PLATE I

Figure		Page
1-4, 8.	<i>Bursa amphitrites</i> Maury, 1917	42
	1. GNS WM16925, unusually short specimen, Gurabo Fm (Late Miocene/Early Pliocene), loc. TU 1231, float near ford on Los Quemados-Sabaneta road, Río Gurabo, Dominican Republic; H 38.1 mm.	
	2, 8. PRI 28763, holotype, Cercado Fm (Late Miocene), Maury's bluff 3, Cercado de Mao, Dominican Republic; H 46.4 mm.	
	3. GNS WM18850, most common form, Gurabo Fm (Late Miocene), loc. TU 1293, Maury's bluff 1, Río Mao, W bank, just below Paso Chorrero, Dominican Republic; H 53.8 mm.	
	4. GNS WM18849, unusually tall specimen, Gurabo Fm (Early Pliocene), loc. TU 1278, large arroyo on E side Río Gurabo at ford on Los Quemados-Sabaneta road, Dominican Republic; H 60.9 mm.	
5-7, 10.	<i>Bursa chipolana</i> Schmelz, 1997	44
	5, 10. USNM 647108, second specimen accompanying paratype (Pl. 1, Figs 6-7), coral reef facies of Chipola Fm (late Early Miocene), loc. TU 547, W bank Chipola River 400 m above Four Mile Creek, Calhoun County, Florida, USA; H 28.7 mm.	
	6-7. USNM 647108, paratype, specimen illustrated by Vokes (1973: text-figs 2a-b), all data same as for Pl. 1, Figs 5, 10; H 48.4 mm.	
9.	<i>Bursa asperima</i> Dunker, 1862. GNS WM12441, Recent, coll. scuba diver in 7-17 m, off of Nanakuli, Oahu, Hawaii, USA; H 44.6 mm.	43
11-13.	<i>Bursa corrugata</i> (Perry, 1811)	45
	11. BMNH 1967654, syntype of <i>Ranella ponderosa</i> Reeve, 1844, Recent, without locality (western Atlantic?), ex Cuming collection; H 67.3 mm.	
	12. NMB H 17980, specimen from type locality of <i>Bursa mexicana</i> Perrilliat, 1963, Agueguexquite Fm (Late Pliocene), loc. TU 1046 (= NMB 19020), cutting on Mexico highway 180, Isthmus of Tehuantepec, Veracruz, Mexico; H 32.8 mm.	
	13. BMNH 1998031, syntype of <i>Ranella ponderosa</i> Reeve, 1844, Recent, without locality (western Atlantic?), ex Cuming collection; H 59.1 mm.	



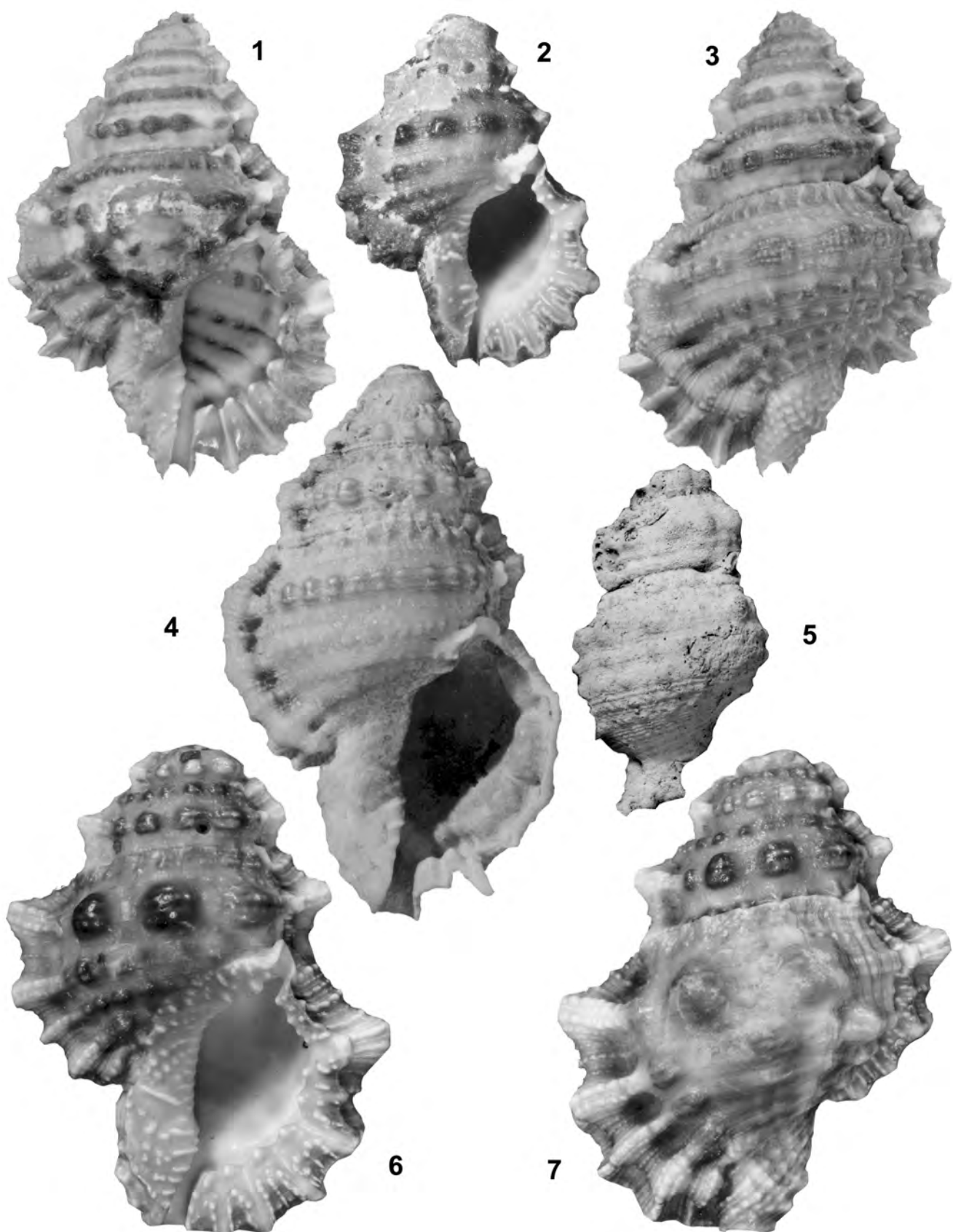
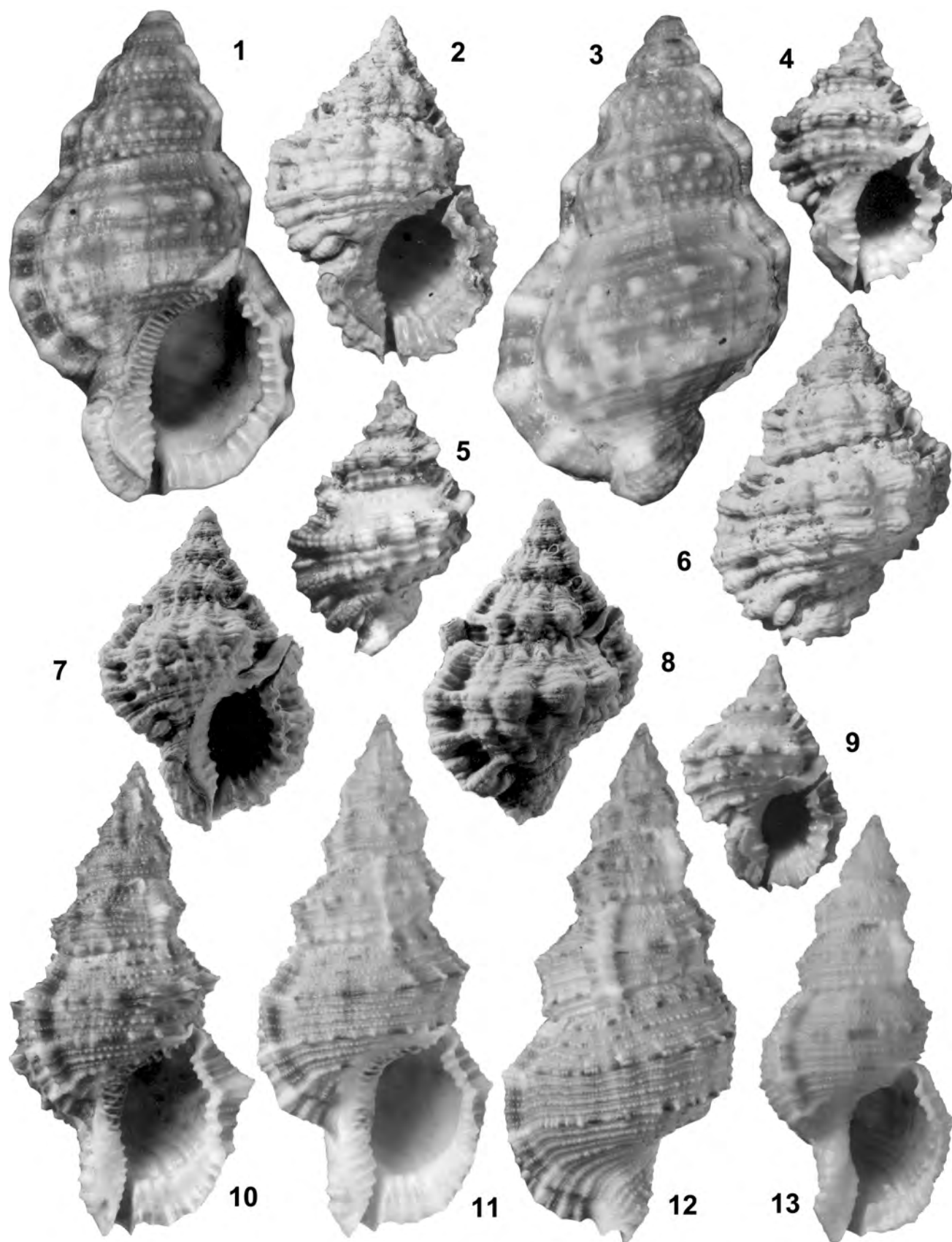


PLATE 2

Figure	Page
1-4, 6-7. <i>Bursa corrugata</i> (Perry, 1811)	45
1, 3. BMNH 1950.11.28.7, lectotype of <i>Ranella caelata</i> Broderip, 1833, Recent, "Panama," ex Cuming collection; H 50.1 mm.	
2. MCZ 232217, Recent, Ascension Island, South Atlantic; H 44.7 mm.	
4. MHNG 1098/86/2, lectotype of <i>Ranella semigranosa</i> Lamarck, 1822, probably the specimen illustrated by Kiener (1842, <i>Ranella</i> : pl. 11, fig. 2), Recent, without locality (eastern Pacific or western Atlantic?); H 40.8 mm.	
6-7. BMNH 1967653, lectotype of <i>Ranella pustulosa</i> Reeve, 1844, Recent, Ascension Island, South Atlantic, ex Cuming collection; H 54.0 mm.	
5. <i>Bursa victrix</i> Dall, 1916. USNM 166728, holotype (latex cast from natural impression in chert), "upper beds" (Flint River Fm, Late Oligocene), loc. USGS 7079, Mascot Point, Flint River, Georgia, USA; H 43 mm.	65

PLATE 3

Figure		Page
1, 3.	<i>Bursa granularis</i> (Röding, 1798). BMNH 1854.10.4.412, holotype of <i>Ranella cubaniana</i> d'Orbigny, 1841, Recent, "St Lucia," West Indies; H 51.7 mm.	48
2, 4-9.	<i>Bursa grayana</i> Dunker, 1862	50
	2, 6. NMB H 18053, Gurabo Fm (Early Pliocene), loc. NMB 15863, 50 m-long exposure upstream from major side stream, E bank, Río Gurabo, Dominican Republic; H 41.9 mm.	
	4, 5. ANSP 276358, Recent, Itapoa, Bahia, Brazil; H 33.2 mm.	
	7-8. NMB H 17891, Cayo Agua Fm (Late Pliocene), loc. NMB 18734 (= PPP 2237), 300 m WNW of Punta Piedra Roja, Cayo Agua, Bocas del Toro Basin, Atlantic Panama; H 29.5 mm.	
	9. BMNH 1988064/1, lectotype, Recent, "Red Sea" [wrong, western Atlantic; type locality designated here as off of Mucuripe, Fortaleza, Brazil], ex Cuming collection; H 29.3 mm.	
10-13.	<i>Bursa natalensis</i> Coelho & Matthews, 1970	52
	10-12. Two specimens in collection of D. Lamy, Recent, 180 m, Saba Bank, off of Guadeloupe, West Indies; H 85.3 mm (Fig. 10), 94.2 mm (Figs 11-12).	
	13. Specimen in collection of D. Lamy, Recent, 120-180 m, Racket Bank, off of St. Barthelemy, West Indies; H 78.0 mm.	



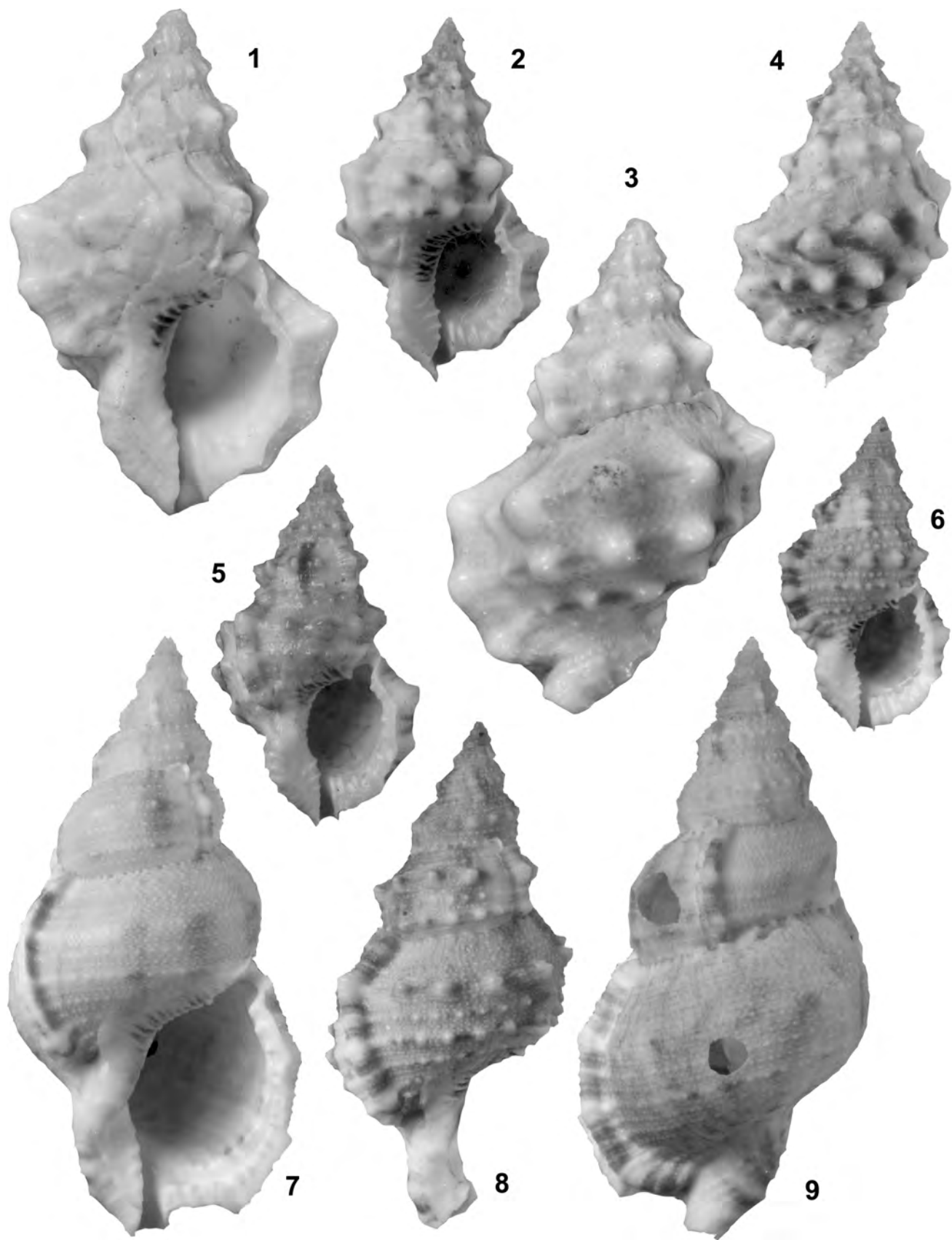
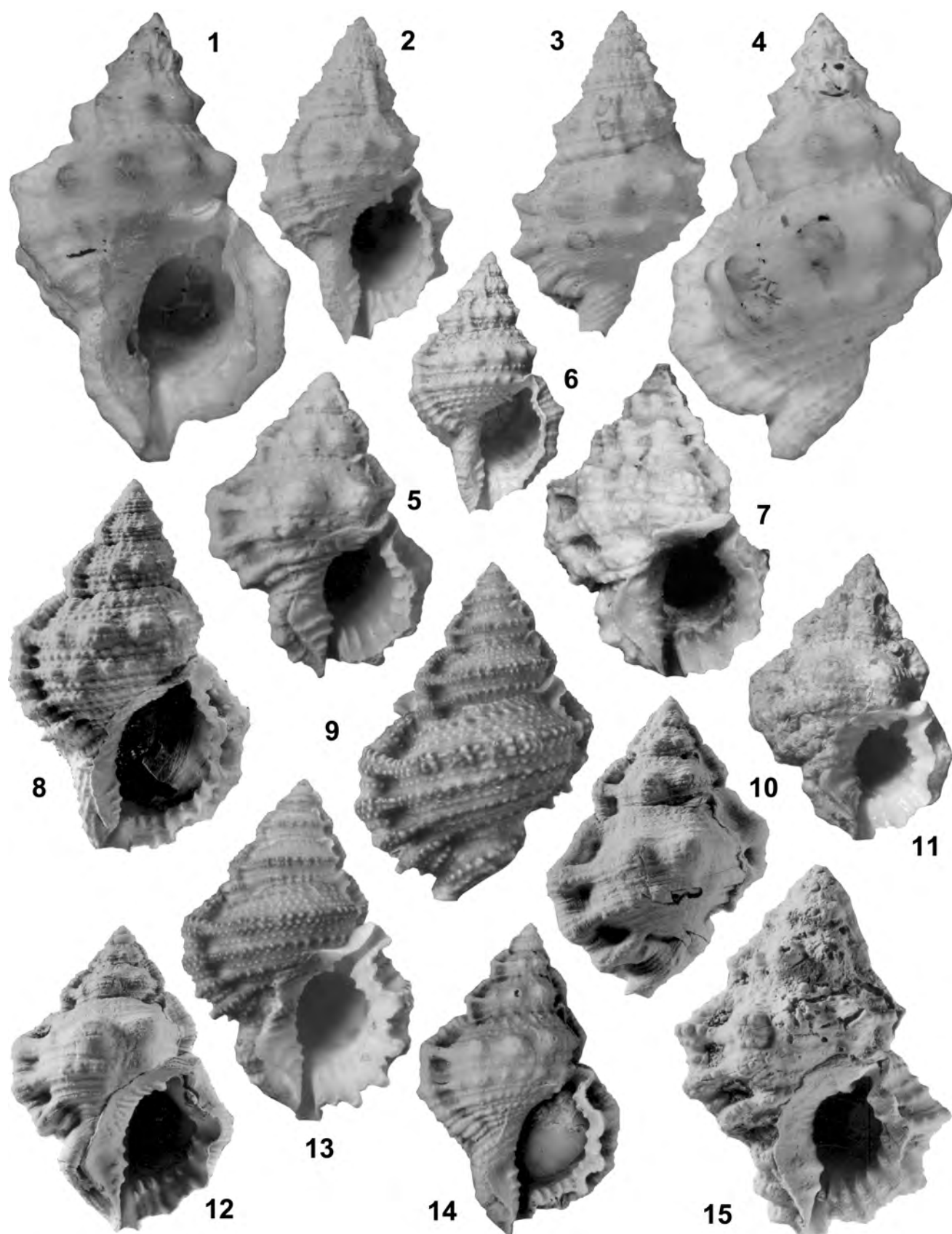


PLATE 4

Figure		Page
1-9.	<i>Bursa ranelloides</i> (Reeve, 1844)	54
	1, 3. BMNH 1967594, holotype, Recent, "Philippines" [wrong, a beach specimen from southern Japan; type locality here designated as Sagami Bay, Honshu], ex Cuming collection; H 49.6 mm.	
	2, 4, 5-9. Five specimens from one lot of 23 in collection of D. Lamy, Recent, 600 m, Racket Bank, off of St. Barthelemy, West Indies; H 66.2 mm (Figs 2, 4), 64.0 mm (Fig. 5), 57.3 mm (Fig. 6), 109.7 mm (Figs 7, 9), 93 mm (Fig. 8) (specimen in Pl. 4, Figs 2, 4 resembles Japanese specimens of <i>B. ranelloides</i> ; specimen in Fig. 6 is forma <i>benvegnuae</i> Penna-Neme & Leme, 1978; specimen in Figs 7, 9 is forma <i>tenuisculpta</i> Dautzenberg & Fischer, 1906; others are intermediate).	

PLATE 5

Figure	Page
1-4, 6, 8. <i>Bursa ranelloides</i> (Reeve, 1844)	54
1, 4. BMNH 1967680, holotype of <i>Simpulum papillosum</i> A. Adams, 1870, Recent, Japan, ex Cuming collection; H 40.3 mm.	
2-3. MNHN unreg., Cruise MD 32/Réunion 1982, sta. DC128, 280-340 m, off of Réunion Island, Indian Ocean; H 39.3 mm.	
6. MNHN unreg., same as above, Cruise MD 32/Réunion 1982, sta. CP129, 290-300 m, off of Réunion Island, Indian Ocean; H 32.3 mm.	
8. NMB H 17892, Cayo Agua Fm (Pliocene), loc. NMB 17830 (= PPP 345), small island 1.2 km SE of Punta de Tiburón, Cayo Agua, Bocas del Toro Basin, Atlantic Panama; H 33.8 mm.	
5, 7, 10-12, 15. <i>Bursa rhodostoma</i> (G. B. Sowerby I, 1835)	57
5. BMNH 1854.10.4.414, holotype of <i>Ranella thomae</i> d'Orbigny, 1841, Recent, "St. Thomas," West Indies; H 18.4 mm.	
7. BMNH 1966542/3, larger paralectotype of <i>B. rhodostoma</i> , Recent, "Isl. of Masbate, Philippines," ex Cuming collection; H 28.4 mm (photo S. D. Kaicher).	
10, 12. NMB H 17894, Cantaure Fm (late Early Miocene), loc. NMB 17516, lower shellbed, Casa Cantaure, Paraguaná Peninsula, Venezuela; H 27.7 mm.	
11. MCZ 261293, Recent, dredged in 45-60 m, off of Boynton Beach, Florida, USA; H 24.2 mm.	
15. NMB H 17893, Moín Fm (latest Pliocene-Early Pleistocene), loc. TU 1239 (= NMB 19007), hill cut above Standard Fruit Company box factory at Pueblo Nuevo, just W of cemetery at Pueblo Nuevo, 2 km W of Puerto Limón, Atlantic Costa Rica; H 22.6 mm.	
9, 13-14. <i>Bursa rugosa</i> (G. B. Sowerby II, 1835)	59
9, 13. BMNH 1989133/1, lectotype of <i>Ranella rugosa</i> , Recent, "Manila" [incorrect, Pacific Panama; type locality here designated as Perlas Islands, Panama Bay], ex Cuming Collection; H 49.1 mm.	
14. NMB H 1870, holotype of <i>B. (Marsupina) albofasciata boussingaulti</i> Rutsch, Punta Gavilán Fm (Early Pliocene), loc. NMB 1769, Punta Gavilán, northern Venezuela; H 36.7 mm.	



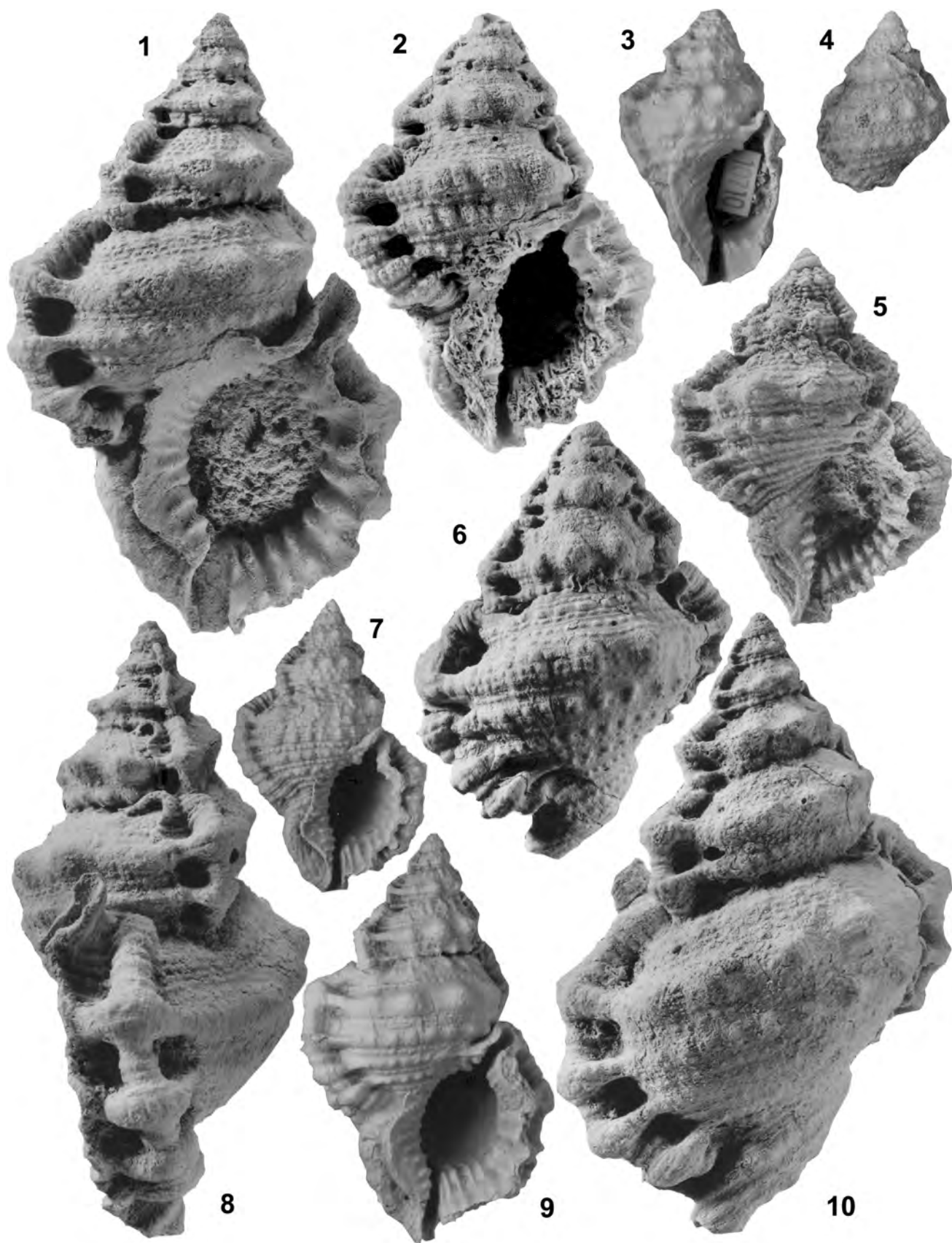
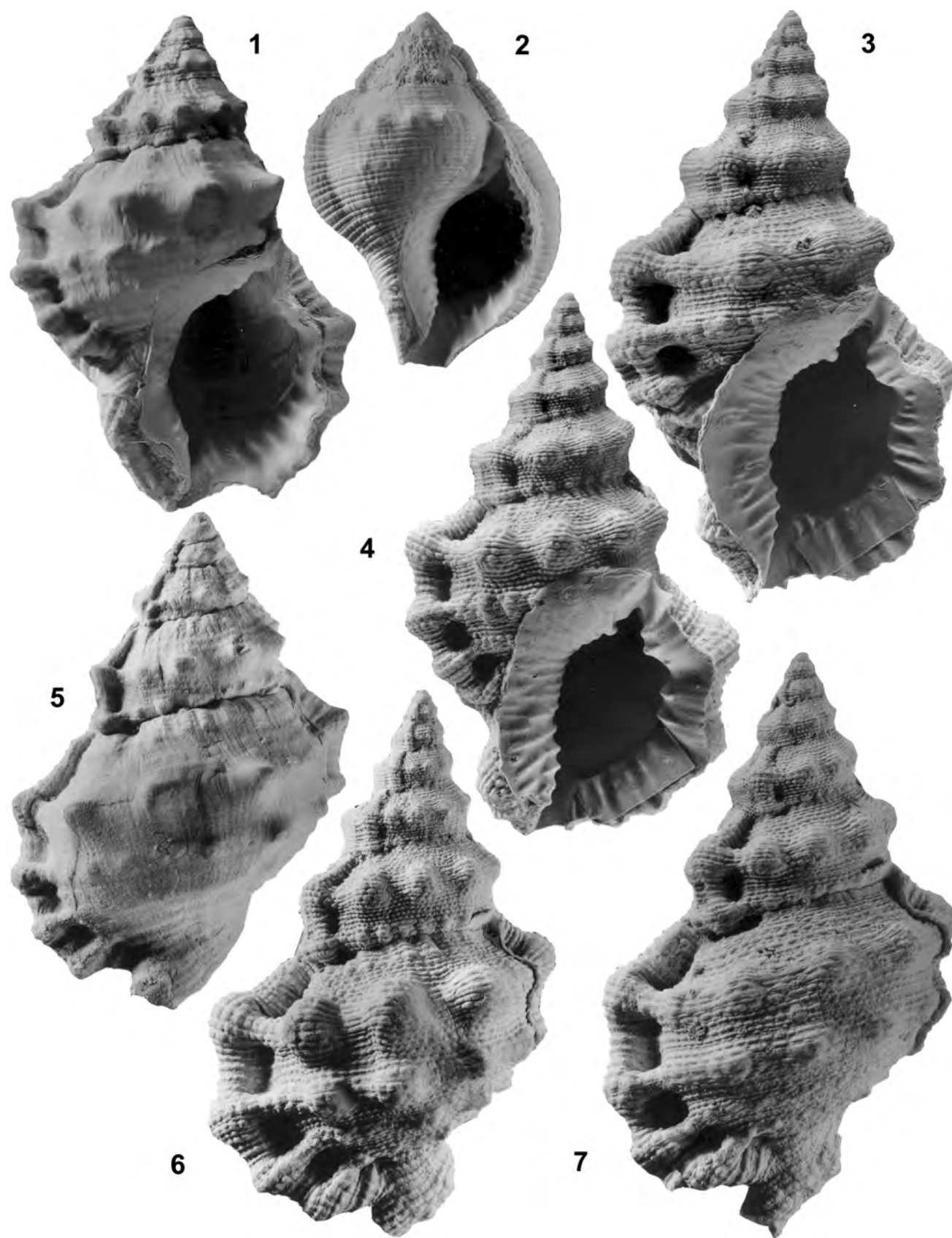


PLATE 6

Figure		Page
1-10.	<i>Bursa rugosa</i> (G. B. Sowerby I, 1835)	59
	1, 5, 8, 10. NMB H 17896-17897, large (Pl. 6, Figs 1, 8, 10) and small (Fig. 5) specimens from type locality of <i>Bursa albofasciata boussingaulti</i> Rutsch, 1934, Punta Gavilán Fm (Early Pliocene), loc. NMB 17531, Punta Gavilán, Venezuela; H 71.2 mm (Figs 1, 8, 10), 22.9 mm (Fig. 5).	
	2, 6. NMB H 17895, Armuelles Fm (Pleistocene), loc. NMB 18306, S of Quebrada Corotú, 3.3 km N of Puerto Limones, Burica Peninsula, Pacific Panama; H 41.2 mm.	
	3-4. NMB H 15448-15449, Grand Bay Fm (Middle Miocene), loc. NMB 10710, Grand Bay promontory, Carriacou Island, West Indies; H 28.2 mm (Fig. 3), 21.0 mm (Fig. 4) (specimens illustrated by Jung, 1971: pl. 11, figs 5-7).	
	7. NMB H 13699, Cantaure Fm (late Early Miocene), Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; H 32.7 mm (specimen illustrated by Jung, 1965: pl. 68, figs 12-13).	
	9. NMB H 18050, Cubagua Fm (Early Pliocene), loc. NMB 12887, 4 m-thick shellbed, 2 km S of Araya village, W slope of Cerro Barragón, Araya Peninsula, Estado Sucre, Venezuela; H 46.7 mm (largest of 18 specimens).	

PLATE 7

Figure		Page
1, 5.	<i>Crossata ventricosa</i> (Broderip, 1833). NMB H 17902, Shark Hole Point Fm (Early Pliocene), loc. NMB 17854, Shark Hole Point, outer coast of Valiente Peninsula, Bocas del Toro Basin, Atlantic Panama; H 45.0 mm.	68
2.	<i>Aspa marginata</i> (Gmelin, 1791). NMB H 17901, Moín Fm (latest Pliocene-Early Pleistocene), loc. TU 1240 (= NMB 19008), hill top on Calle King Fish in Barrio Los Corales 2, 1.4 km N of Standard Fruit Company box factory, 2 km W of Puerto Limón, Atlantic Costa Rica; H 21.4 mm (for dorsal view, see Pl. 11, Fig. 3).	66
3-4, 6-7.	<i>Bursa scrobilator</i> (Linnaeus, 1758). NMB H 17899, H 17900, 2 specimens, Moín Fm (latest Pliocene-Early Pleistocene), loc. TU 1240 (= NMB 19008), as above, Limón, Atlantic Costa Rica; H 54.7 mm (Figs 3, 7), 50.3 mm (Figs 4, 6).	62



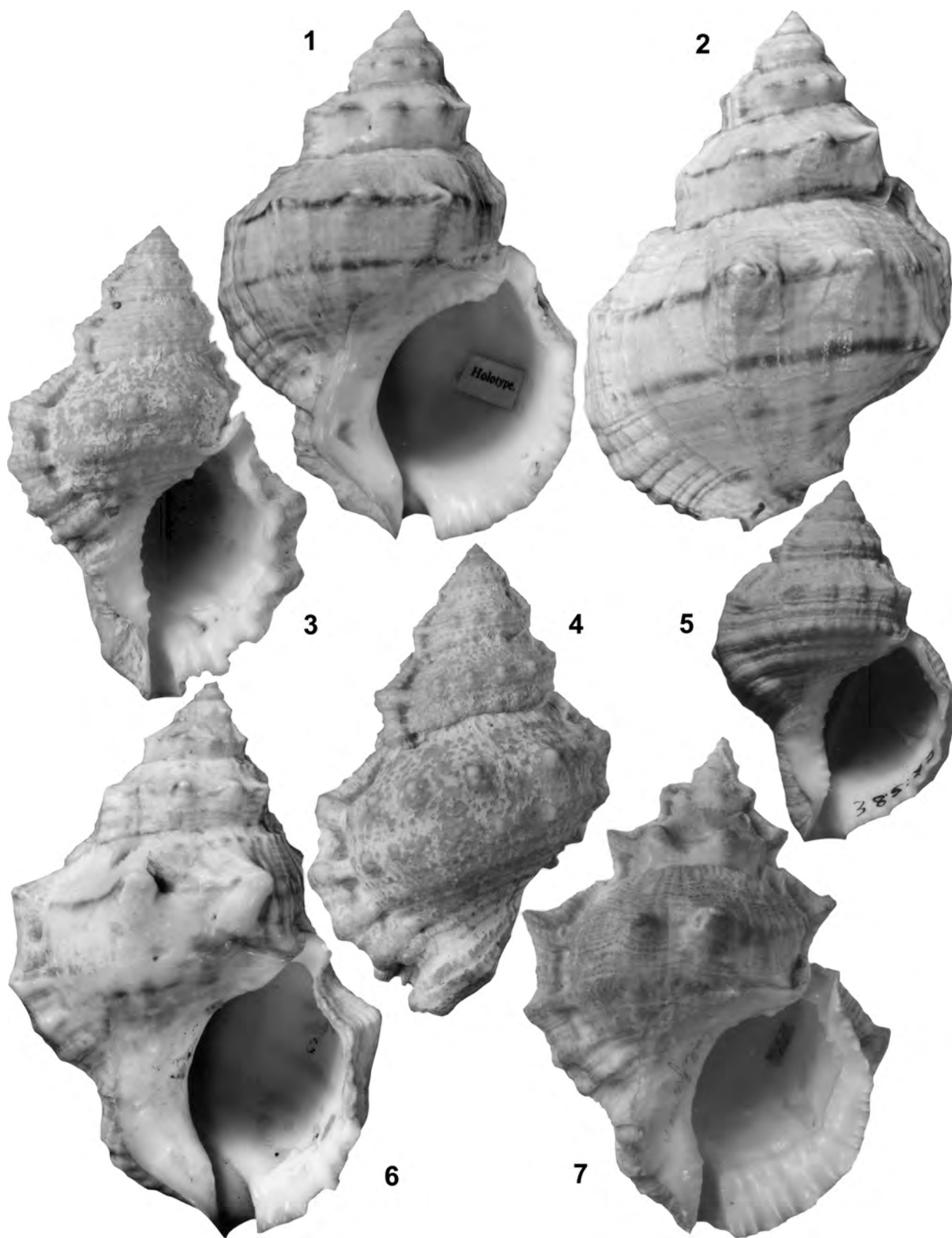
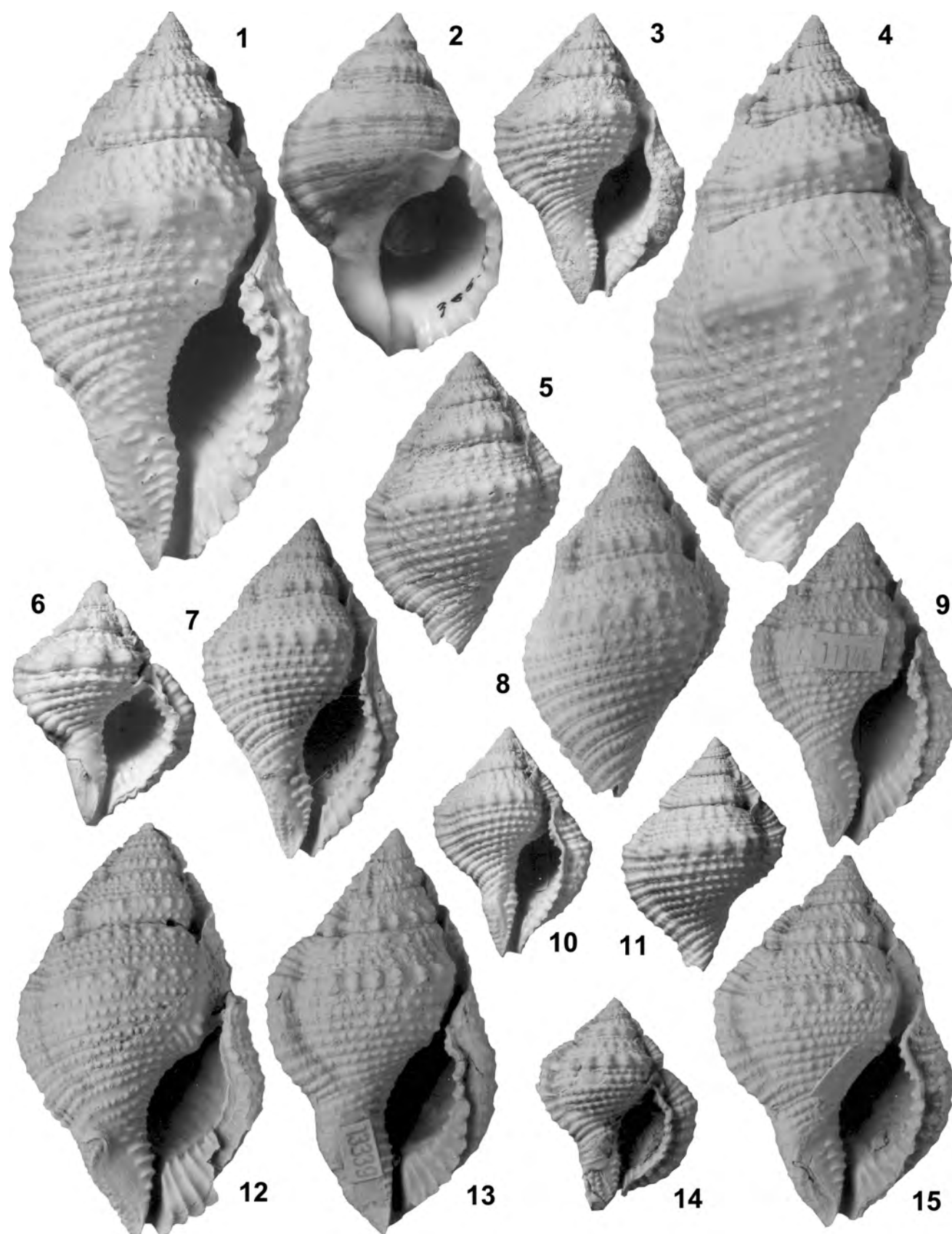


PLATE 8

Figure		Page
1-7.	<i>Crossata ventricosa</i> (Broderip, 1833)	68
	1-2, 6. BMNH 1950.11.28.1-2, lectotype (Figs 1-2) and one of two paralectotypes of <i>Ranella ventricosa</i> , Recent, "Bay of Callao, Peru," ex Cuming collection; H 81.3 mm (Figs 1-2), 67.5 mm (Fig. 6).	
	3-4. USNM 123027, holotype of <i>Bursa (Lampadopsis) calcipicta</i> Dall, 1908, Recent, U. S. Fish Commission sta. 3368, 120 m, near Cocos Island, Costa Rica; H 44 mm.	
	5. LACM 385-24, immature specimen, Recent, 16-18 m, 14°13'S, 76°09.3'W, Bahia Independencia, Peru; H 48.1 mm (second specimen shown on Pl. 9, Fig. 2).	
	7. BMNH 1842.1.2.634, neotype (designated here) of <i>Ranella californica</i> Hinds, 1843, Recent, "California, R. B. Hinds, esq.," type locality San Diego, California, USA; H 90.4 mm.	

PLATE 9

Figure	Page
1, 3-15. <i>Marsupina bufo</i> (Bruguière, 1792)	72
1, 4. USNM 369464, specimen illustrated by Woodring (1928: pl. 19, fig. 4), Bowden Shellbed (Late Pliocene), loc. USGS 23741, Bowden, Jamaica; H 67.8 mm.	
3, 5. PRI 22964, holotype of <i>Bursa crassa colombiana</i> Weisbord, 1929, Middle Miocene, near Tuhera Cedral, Morro Hermoso, Departamento de Atlantico, Colombia; H 34.8 mm.	
6. USNM 647109, specimen illustrated by Vokes (1973: text-fig. 1), Shoal River Fm (Middle Miocene), loc. TU 69A, Shell Bluff, 3.5 miles N of Mossy Head, Florida, USA; H 22.2 mm.	
7-8. ANSP/IP 3747, holotype of <i>Bursa crassa bowdenensis</i> Pilsbry, 1922, Bowden Shellbed (Late Pliocene), Bowden, Jamaica; H 49.1 mm.	
9. NMB H 18045, Bowden Shellbed (Late Pliocene), loc. NMB 11146, Bowden, Jamaica; H 39.3 mm.	
10-11. USNM unreg., juvenile specimen, Bowden Shellbed (Late Pliocene), loc. USGS 23741, Bowden, Jamaica; H 27.5 mm.	
12. NMB H 15150, large specimen illustrated by Jung (1969: pl. 49, figs 5-6), Matura Member, Talparo Fm (Pleistocene), Matura, Trinidad; H 74.7 mm.	
13, 15. NMB H 18055-18056, 2 specimens, Cubagua Fm (Pliocene), loc. NMB 13339, Cañon de las Calderas, Cubagua Island, Venezuela; H 49.2 mm (Fig. 13), 44.6 mm (Fig. 15).	
14. ANSP/IP 3227, holotype of <i>Bursa crassa proavus</i> Pilsbry, 1922, Late Miocene or Early Pliocene, "Santo Domingo," ex W. M. Gabb collection; H 25.3 mm.	
2. <i>Crossata ventricosa</i> (Broderip, 1833). LACM 385-24, second immature specimen in same lot as the specimen in Pl. 8, Fig. 5; Recent, 16-18 m, Bahia Independencia, Peru; H 63.5 mm.	68



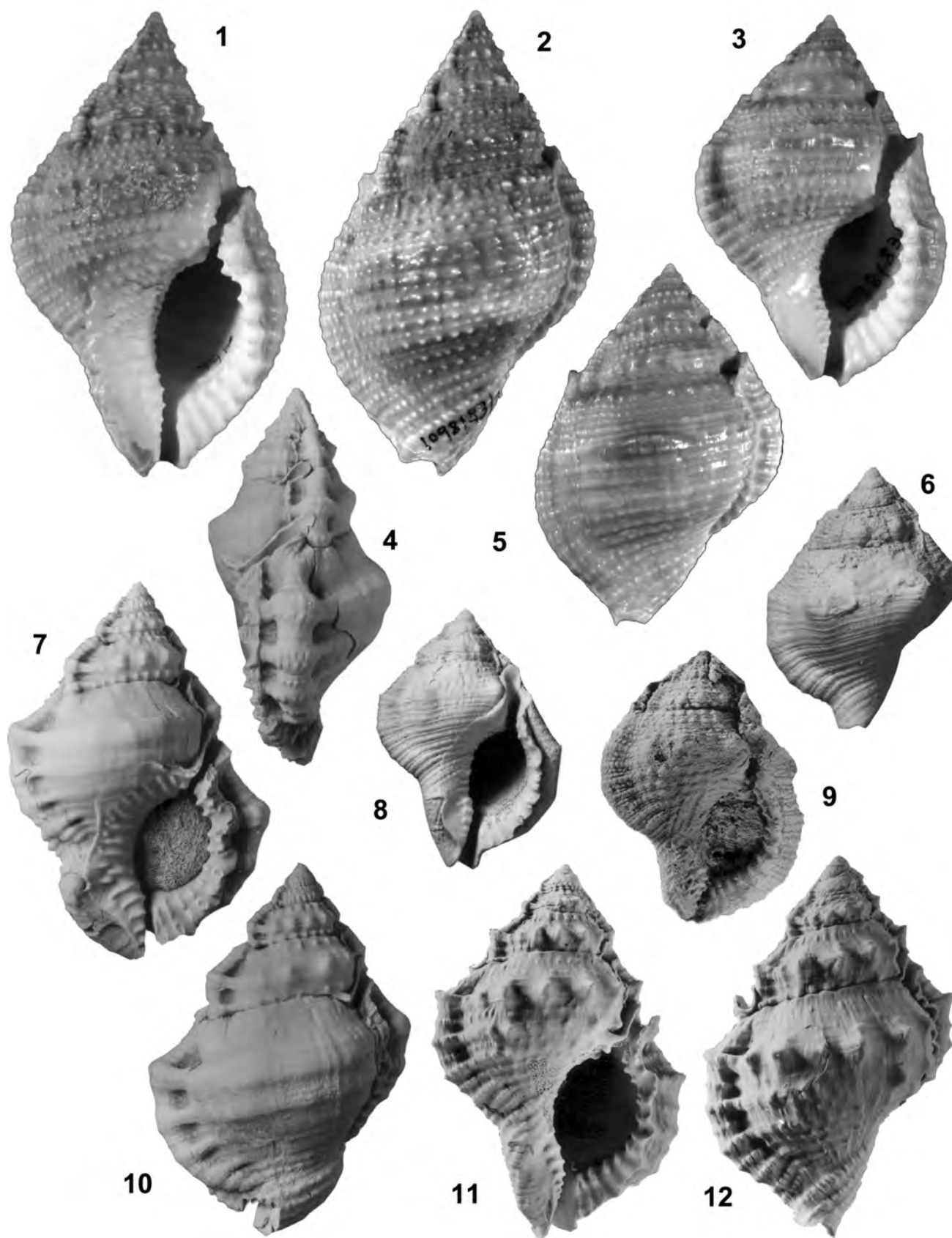
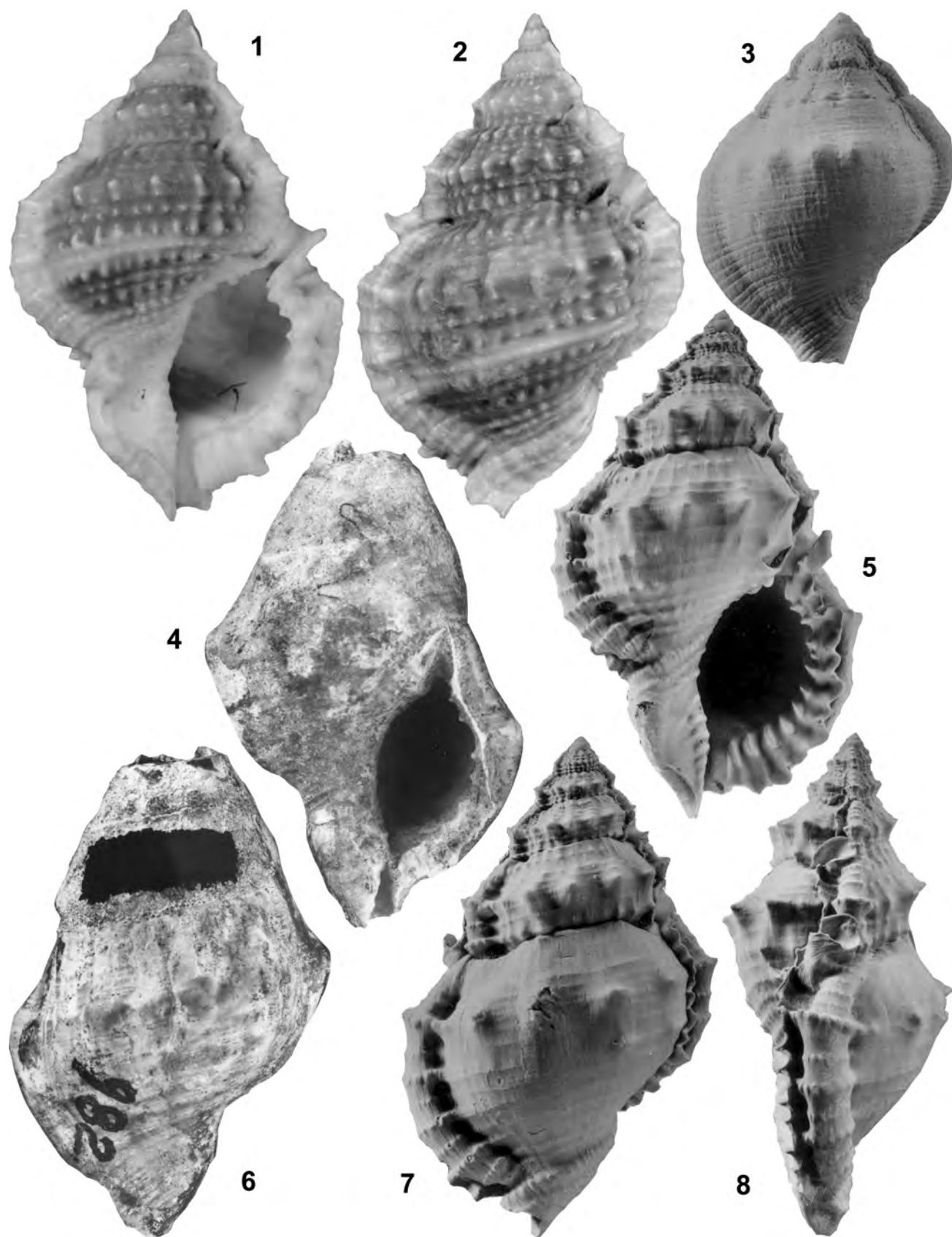


PLATE 10

Figure	Page
1-3, 5. <i>Marsupina bufo</i> (Bruguière, 1792)	72
1-2. MHNG 1098/84, lectotype (designated here) of <i>Ranella granulata</i> Lamarck, 1816, specimen illustrated by Lamarck (1816: pl. 412, fig. 4) and Kiener (1841, <i>Ranella</i> : pl. 12, fig. 1), neotype of <i>Murex bufo</i> Bruguière, 1792, of <i>Bursa gibbosa</i> Röding, 1798, of <i>Buffo spadiceus</i> Montfort, 1810, and of <i>Murex crassus</i> Dillwyn, 1817, Recent, without locality [western Atlantic; type locality here designated as off of Cayenne, Guiana]; H 58.3 mm (from a color transparency).	
3, 5. MHNG 1098/85, paralectotype of <i>Ranella granulata</i> Lamarck, 1816; H 41.5 mm (from a color transparency).	
4, 7, 10. <i>Marsupina judensis</i> n. sp. NMB H 18308, holotype, Late Miocene, Punta Judas, Pacific Costa Rica, ex Bernard Landau collection; H 54.0 mm.	75
6, 8-9. <i>Marsupina freya</i> (Olsson, 1932)	75
6, 8. PRI 2312, holotype, "Zorritos Miocene," divide between Quebrada Conchudo Bravo and Quebrada Seca, Mancora, Peru; H 23.1 mm.	
9. NMB H 17903, Late Oligocene-Early Miocene, loc. NMB 17474, 2 km N of Malpais, SW coast of Nicoya Peninsula, Pacific Costa Rica; H 24.8 mm (calcite neomorph in cemented sandstone, upper right margin partly hidden).	
11-12. <i>Marsupina nana</i> (Broderip & G. B. Sowerby I, 1829). NMB H 17904, forma <i>albofasciata</i> G. B. Sowerby II, 1841, Montezuma Fm (Pleistocene), loc. NMB 18161, SE coast of Playa Cocalito, ENE of Montezuma village, SE coast of Nicoya Peninsula, Pacific Costa Rica; H 34.4 mm.	76

PLATE I I

Figure		Page
1-2, 5, 7-8.	<i>Marsupina nana</i> (Broderip & G. B. Sowerby I, 1829)	76
	1-2. BMNH 1950.11.28.20, lectotype of <i>Ranella albofasciata</i> G. B. Sowerby II, 1841, Recent, Pacific Panama, ex Cuming collection; H 56.4 mm.	
	5, 7-8. NMB H 17905, Montezuma Fm (Pleistocene), loc. NMB 17471, SE coast of Playa Cocalito, ENE of Montezuma village, SE coast of Nicoya Peninsula, Costa Rica (<i>i.e.</i> , same locality as Pl. 10, Figs 11-12); H 49.8 mm.	
3.	<i>Aspa marginata</i> (Gmelin, 1791). NMB H 17901, Moín Fm (latest Pliocene-Early Pleistocene), loc. TU 1240 (= NMB 19008), hill top on Calle King Fish in Barrio Los Corales 2, 1.4 km N of Standard Fruit Company box factory, which is 2 km W of Puerto Limón, Atlantic Costa Rica; H 21.4 mm (dorsal view of this specimen shown in Pl. 7, Fig. 2).	66
4, 6.	<i>Marsupina strongi</i> (Jordan, 1936). CAS 5480, holotype, late Pleistocene terrace (Last Interglacial, oxygen isotope stage 5e), beach S of village, Bahia Magdalena, Baja California Sur, Mexico; H 46.8 mm (photo L. G. Hertlein).	78



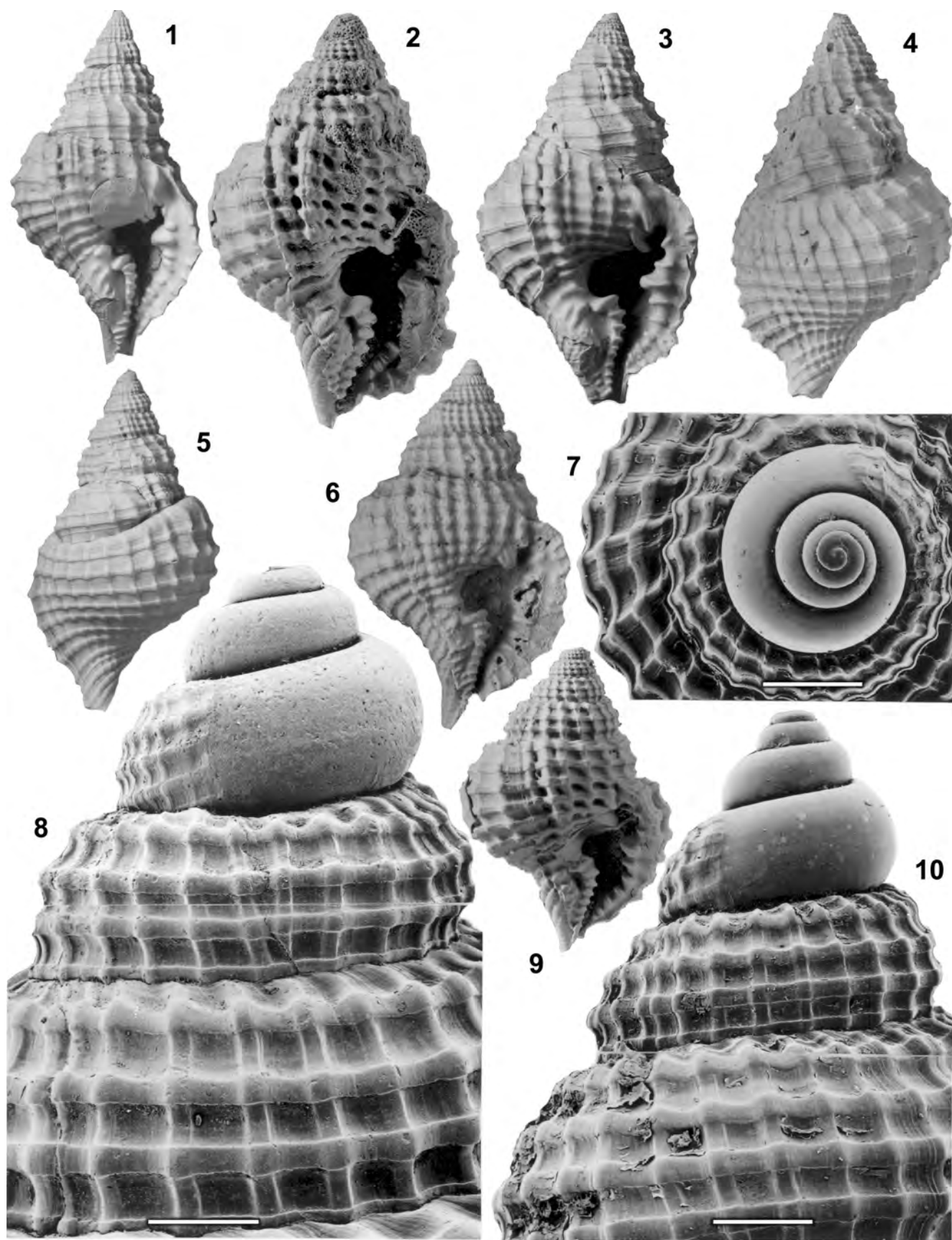
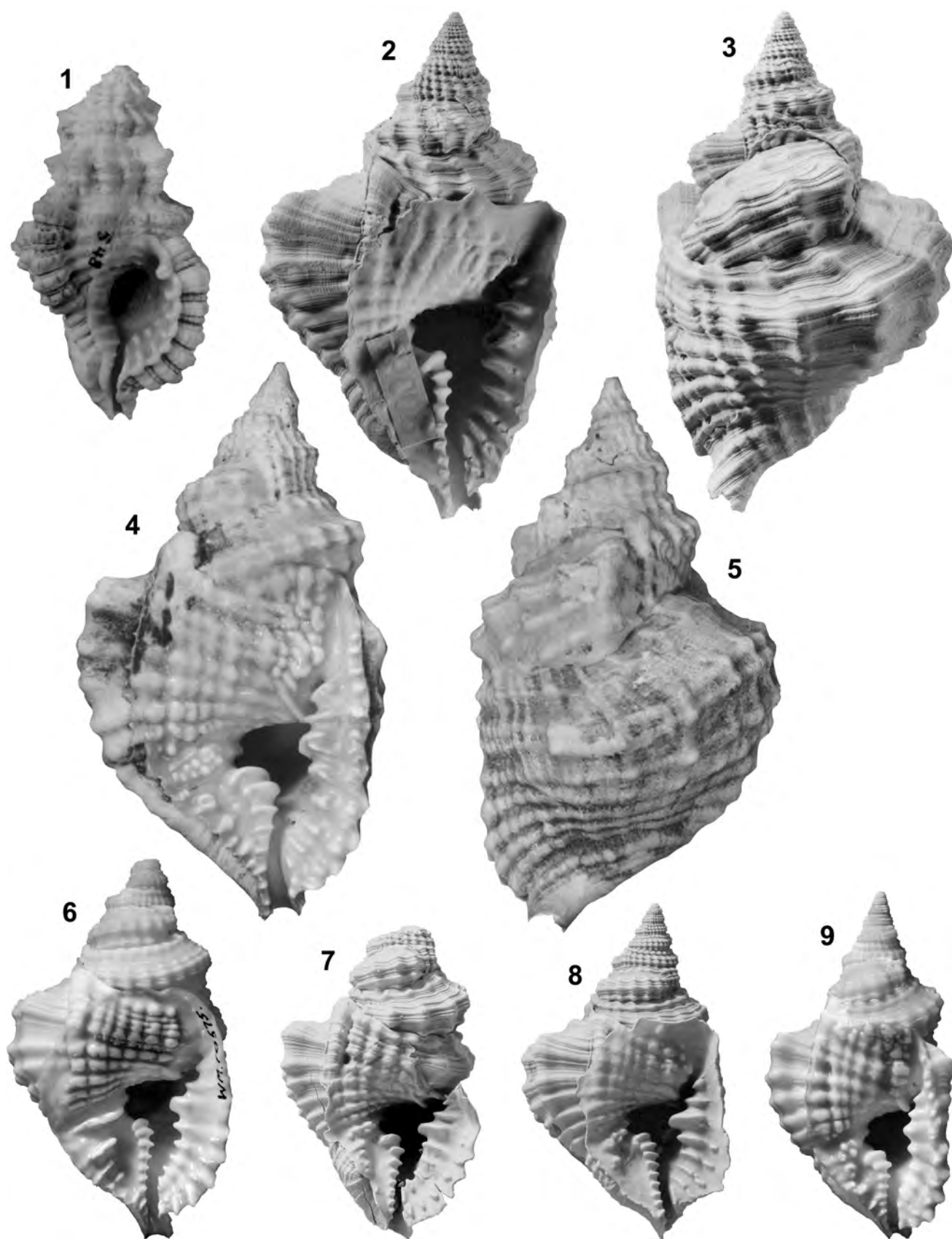


PLATE 12

Figure		Page
1-10.	<i>Distorsio clathrata</i> (Lamarck, 1816)	81
	1, 5. USNM unreg., Gurabo Fm (Early Pliocene), loc. USGS 8544, E bank Río Gurabo, 150 m upstream from middle ford at Gurabo Adentro, Dominican Republic; H 41.2 mm (slightly aberrant specimen).	
	2. NMB H 17906, Agueguexquite Fm (Pliocene), loc. TU 1046 (= NMB 19020), cutting on Mexico Highway 180, Isthmus of Tehuantepec, Veracruz, Mexico; H 37.9 mm (largest in lot of 74 “dwarf” specimens).	
	3-4. Specimen in collection of Bernard Landau, Gurabo Fm (Early Pliocene), loc. TU 1214, fifth to eighth bluffs downstream from bridge on Los Quemados-Sabaneta road, Río Gurabo, Dominican Republic; H 70.2 mm.	
	6. NMB H 1868/2, specimen illustrated by Rutsch (1930: pl. 17, figs 5-6), Punta Gavilán Fm (Early Pliocene), Punta Gavilán, N Venezuela; H 45.0 mm (calcite neomorph).	
	7, 10. GNS WM16592, Recent, 40 m, off of Suriname, Caribbean, SEM micrographs of protoconch and spire apex; scale bar = 1 mm.	
	8. NMB H 18066, Lower Concepción Fm (Pliocene), loc. TU 1318 (= NMB 19016), cutting on pipeline just NE of Campo El Chapo, 4 km S of Mexico Highway 180 at Nueva Teapa, Veracruz, Mexico; SEM micrograph of protoconch and spire apex to compare with Pl. 12, Fig. 10 (apex incomplete); scale bar = 1 mm.	
	9. NMB H 17907, typical small specimen in same lot as Pl. 12, Fig. 2; H 27.8 mm.	

PLATE 13

Figure	Page
1. <i>Monoplex nicobaricus</i> (Röding, 1798). GNS WM16367, Recent, rocks in 1-1.5 m of water, Pelican Shoals, Florida Keys, USA; H 52.1 mm.	163
2-3, 6-8. <i>Distorsio mcgintyi</i> Emerson & Puffer, 1953	92
2-3. NMB H 17920, Moín Fm (latest Pliocene-Early Pleistocene), Loc. TU 1240 (= NMB 19008), hill top on Calle King Fish in Barrio Los Corales 2, 1.4 km N of Standard Fruit Company box factory, which is 2 km W of Puerto Limón, Costa Rica; H 46.9 mm (outer lip incomplete).	
6. GNS WM10575, Recent, dredged, 55 m, W of Cedar Key, Florida, USA; H 55.2 mm.	
7-8. GNS WM16953, Moín Fm (latest Pliocene-Early Pleistocene), loc. TU 1240, all data same as for Pl. 13, Figs 2-3; two further specimens; H 37.7 mm (Fig. 7), 40.7 mm (Fig. 8).	
4-5, 9. <i>Distorsio constricta</i> (Broderip, 1833)	84
4-5. BMNH 1989161, lectotype, Recent, "Monti Christi and Xipixapi" [here corrected to Manta], Ecuador, ex Cuming collection; H 60.8 mm.	
9. GNS WM18094, Recent, intertidal, Gobernadora I, Pacific Panama; H 41.8 mm.	



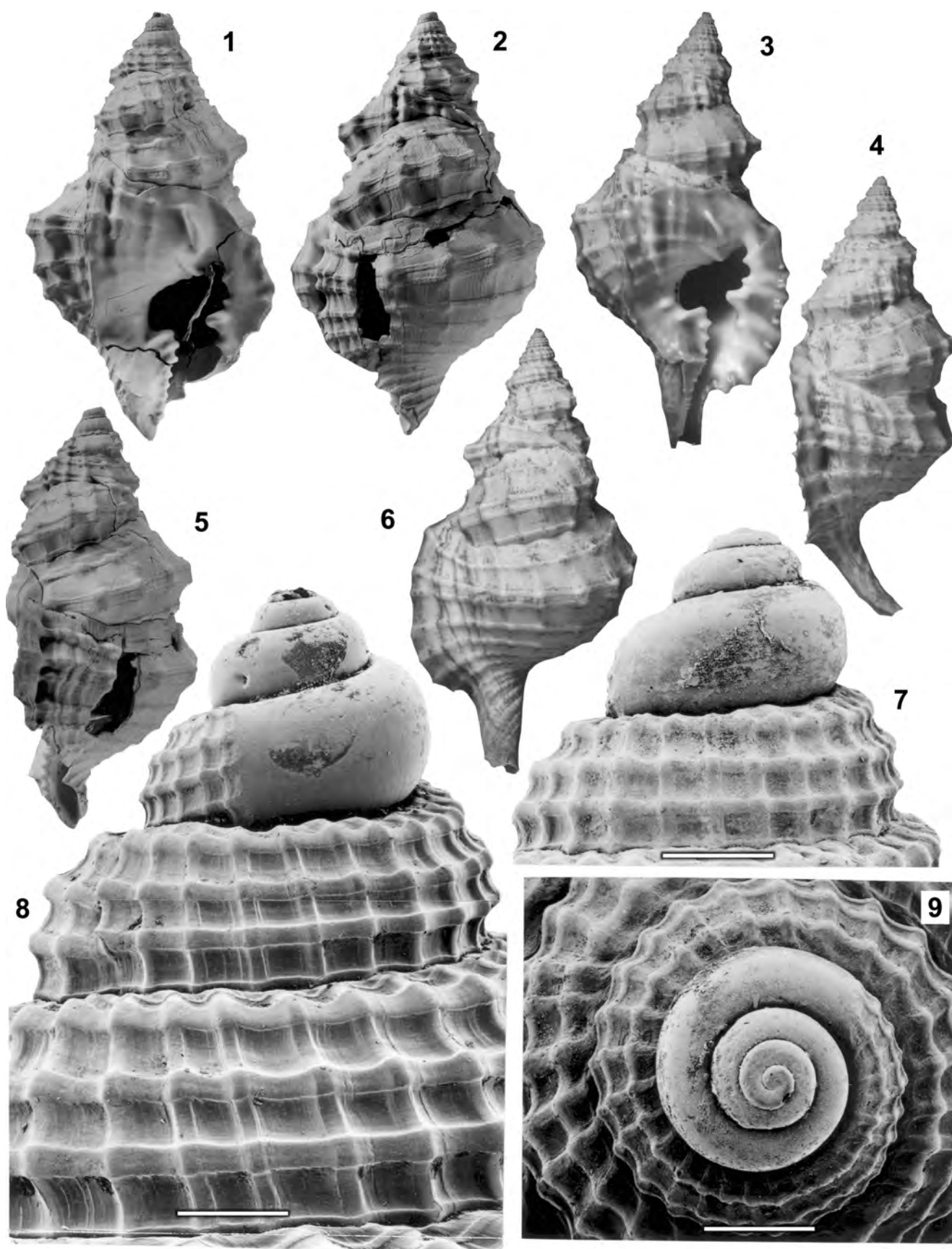
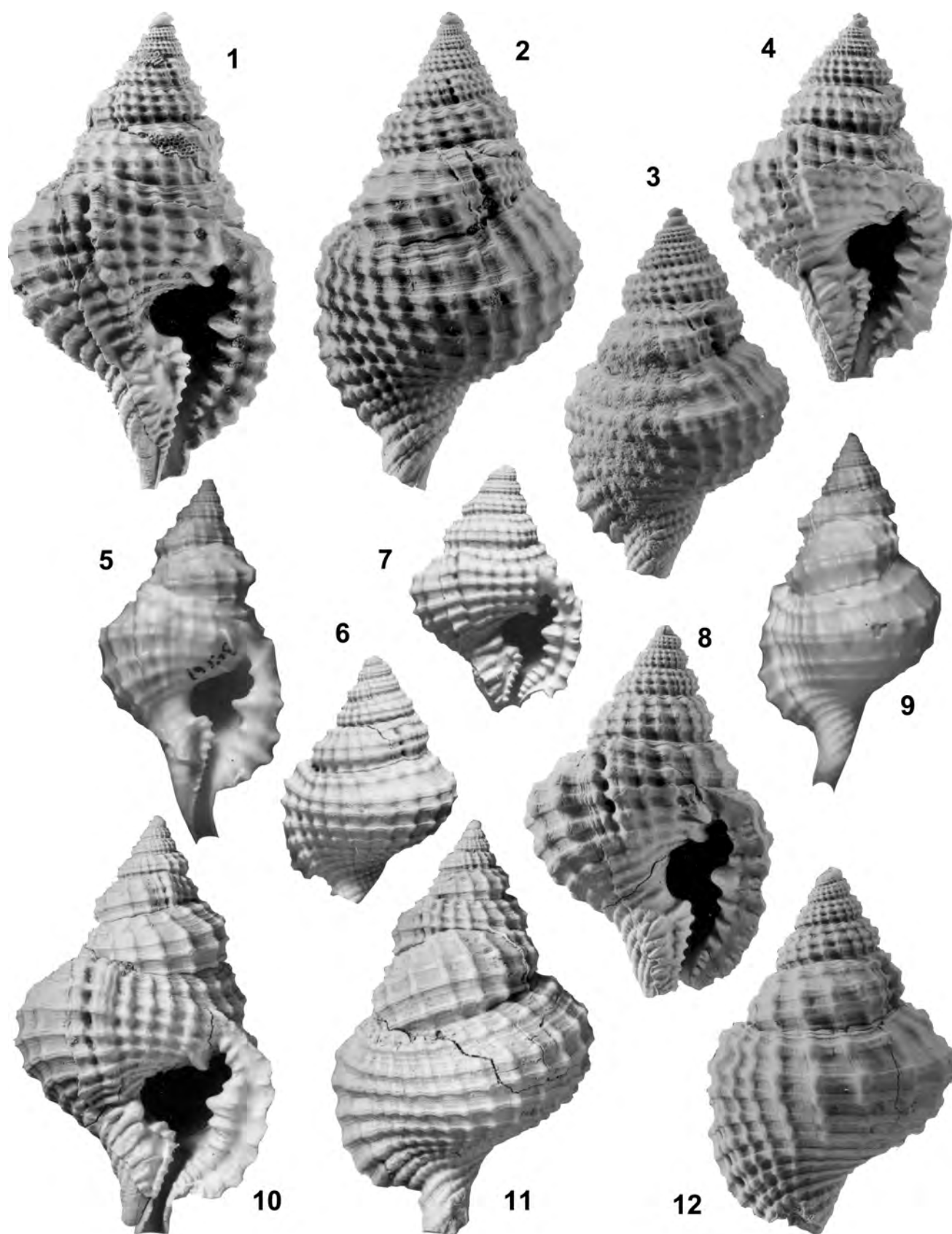


PLATE 14

Figure		Page
1-9.	<i>Distorsio decussata</i> (Valenciennes, 1832)	87
	1-2, 5. NMB H 17908, large "typical" specimen, Armuelles Fm (Pleistocene), loc. NMB 18289, just above confluence with Quebrada la Mona, lower course of Río la Vaca, Golfo Dulce, Pacific Costa Rica; H 77.6 mm.	
	3-4, 6. LACM 59-11, extreme <i>decussata</i> form, Recent, shrimp boats operating out of Mazatlan, Sinaloa, Mexico; H 78.9 mm.	
	7, 9. NMB H 18063, Escudo de Veraguas Fm (Pliocene), loc. NMB 17840, N coast of Escudo de Veraguas Island, Bocas del Toro Basin, Atlantic Panama; SEM micrographs of protoconch; scale bar = 1 mm.	
	8. NMB H 18062, Escudo de Veraguas Fm (Pliocene), loc. NMB 17628, NE coast of Escudo de Veraguas Island, Bocas del Toro Basin, Atlantic Panama; SEM micrograph of protoconch and spire apex (rotated slightly further to right than in Pl. 14, Figs 7, 9); scale bar = 1 mm.	

PLATE 15

Figure	Page
1-5, 9. <i>Distorsio decussata</i> (Valenciennes, 1832)	87
1-2. NMB H 17918, <i>gatumensis</i> form, Cayo Agua Fm (Pliocene), loc. NMB 18373, not far S of North Point, SE coast of Cayo Agua, Bocas del Toro Basin, Atlantic Panama; H 44.4 mm.	
3-4. NMB H 17917, <i>gatumensis</i> form, Tuirá Fm (Late Miocene), loc. NMB 18510, between Marraganti village and Boca Marraganti, Río Tuquesa, Darien, Pacific Panama; H 33.6 mm.	
5, 9. LACM 34661, Recent, Perlas Islands, Pacific Panama; H 63.9 mm.	
6-7, 10-11. <i>Distorsio floridana</i> (Gardner, 1947)	89
6-7. USNM 371879, holotype, Shoal River Fm (late Middle Miocene), loc. USGS 3742, Shell Bluff, WNW of Mossy Head, Florida, USA; H 23.1 mm.	
10-11. USNM unreg., adult specimen, Shoal River Fm (late Middle Miocene), loc. USGS 10603, road from Eucheeanna to Knox Hill, 2.5 km SW of Eucheeanna, Walton County, Florida, USA; H 50.5 mm.	
8, 12. <i>Distorsio</i> cf. <i>floridana</i> (Gardner, 1947). NMB H 17916, Penita Fm (Pliocene), loc. NMB 18055, Quebrada la Penita, Burica Peninsula, Pacific Costa Rica; H 33.5 mm.	89



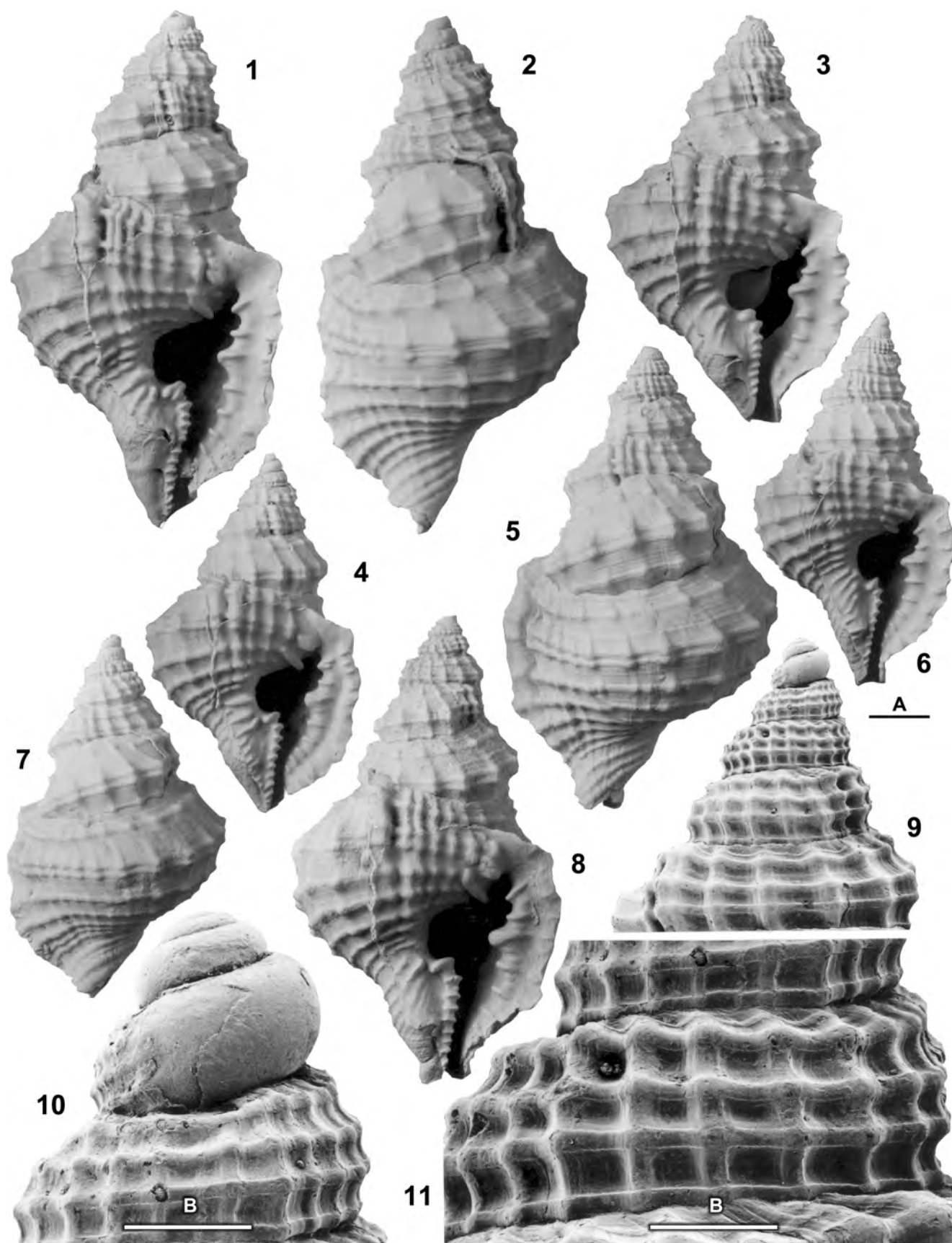
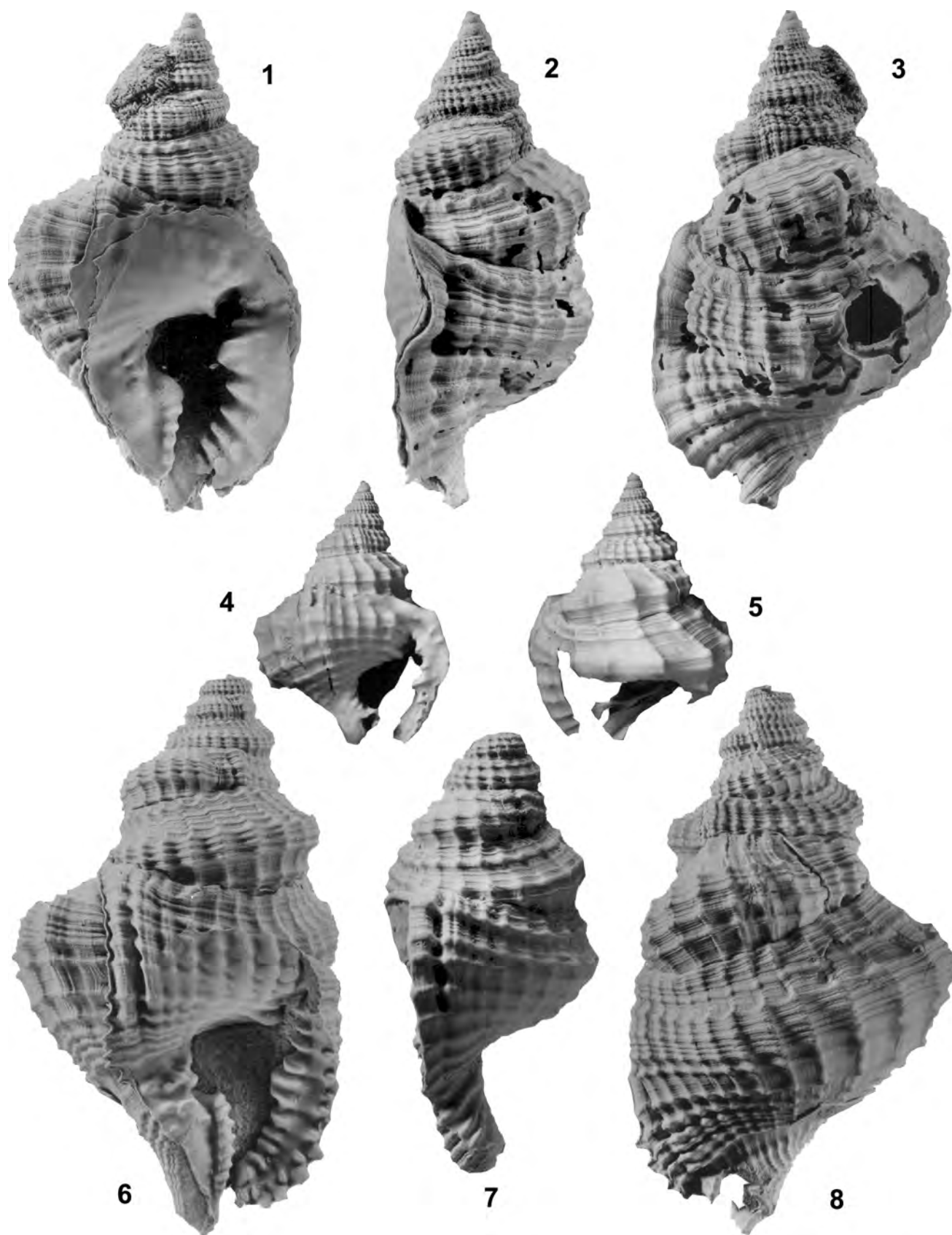


PLATE 16

Figure		Page
1-11.	<i>Distorsio jungi</i> n. sp. Cantaure Fm, lower shellbed (late Early Miocene), loc. NMB 17516, Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela.	90
	1-2. NMB H 18330, holotype; H 55.8 mm.	
	3. NMB H 18332, paratype; H 49.0 mm.	
	4, 7. NMB H 18333, paratype; H 43.3 mm.	
	5, 8. NMB H 18331, paratype; 56.6 mm.	
	6. NMB H 13697, paratype, specimen illustrated by Jung (1965: pl. 68, figs 9, 11); H 44.3 mm.	
	9-11. NMB H 18061, paratype, SEM micrographs of protoconch, spire apex, and second spire whorl; scale bar A = 2 mm, scale bar B = 1 mm.	

PLATE 17

Figure		Page
1-3.	<i>Distorsio jenniernestae</i> Emerson & Piech, 1992. NMB H 17919, Armuelles Fm (Pleistocene), loc. NMB 18288, lower course of Río la Vaca, Golfo Dulce, Pacific Costa Rica; H 45.2 mm.	90
4-5, 7.	<i>Distorsio jungi</i> n. sp.?, specimens assigned. Chipola Fm (late Early Miocene), Chipola River, Calhoun County, Florida, USA.	90
	4-5. USNM unreg., loc. TU 820, Farley Creek, at bridge on Florida Highway 275, ex S. Hoerle collection; H 32.0 mm.	
	7. NMB H 17914, loc. TU 459 (= NMB 19030), E bank Chipola River; H 37.6 mm.	
6, 8.	<i>Distorsio mcgintyi</i> Emerson & Puffer, 1953. NMB H 18921, Gurabo Fm (Early Pliocene), loc. NMB 15863, 50 m-long exposure upstream from major side stream, E bank Río Gurabo, Dominican Republic; H 51.5 mm (aberrant specimen with numerous peripheral cords).	92



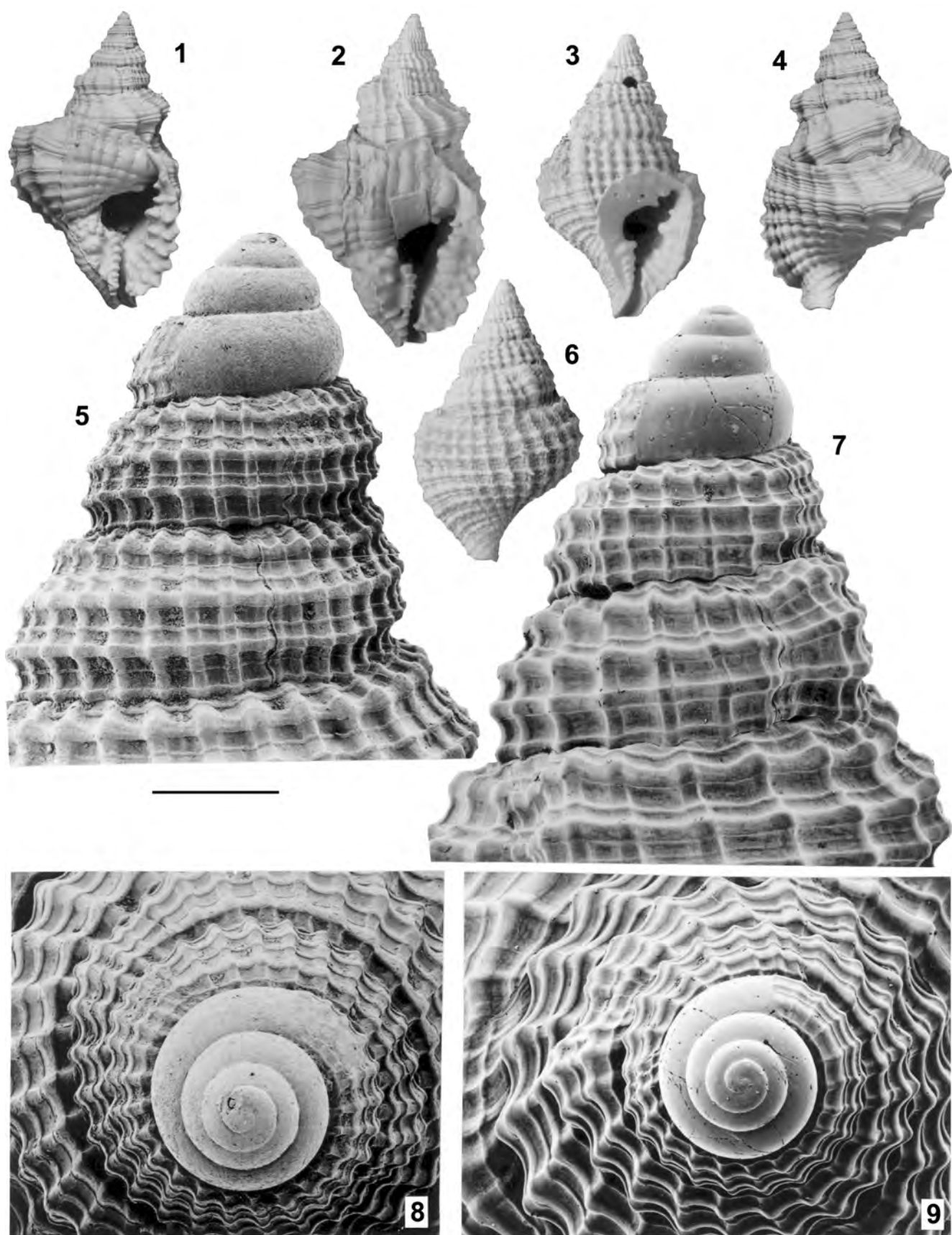
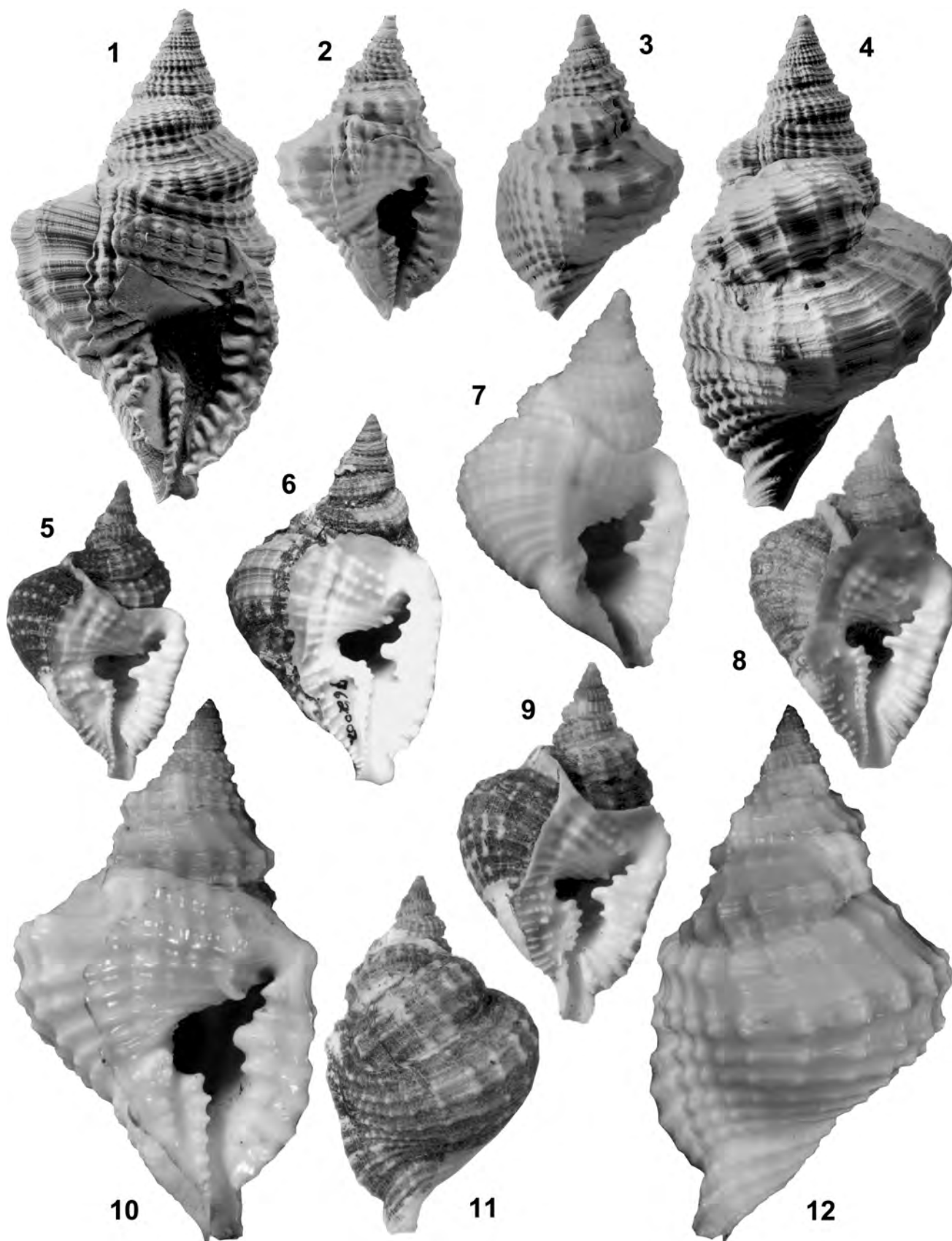


PLATE 18

Figure	Page
1-2, 4-5, 7-9. <i>Distorsio mcgintyi</i> Emerson & Puffer, 1953	92
1, 4. GNS WM16903, Gurabo Fm (Late Miocene/Early Pliocene), loc. TU 1277, Maury's zone F, 2-2.5 km upstream from bridge on Los Quemados-Sabaneta road, Río Gurabo, Dominican Republic; H 35.5 mm.	
2. NMB H 18043, Bowden Shellbed (Late Pliocene), loc. NMB 10635, Bowden, Jamaica; H 39.8 mm.	
5, 8. NMB H 18057, Gurabo Fm (Early Pliocene), loc. NMB 15807, Río Gurabo, Dominican Republic, near center of map of Saunders <i>et al.</i> (1986: text-fig. 4); SEM micrographs of protoconch and spire apex; scale bar = 1 mm for all micrographs.	
7, 9. GNS WM10575, Recent, dredged, 55 m, W of Cedar Key, Florida, USA; SEM micrographs of protoconch and spire apex; scale bar = 1 mm for all micrographs.	
3, 6. <i>Personopsis grasi</i> (Bellardi in D'Ancona, 1872). GNS WM17190, Recent, 300 m, fishermen's traps off Basse Terre, Guadeloupe, West Indies, coll./pres. D. Lamy; H 18.3 mm.	99

PLATE 19

Figure		Page
1, 4.	<i>Distorsio mcgintyi</i> Emerson & Puffer, 1853. NMB H 18339, Gurabo Fm (Late Miocene), loc. NMB 16910, Bluff 1 of Maury, <i>ca.</i> 1 km upstream from Cercado de Mao, Río Mao, Dominican Republic; H 44.8 mm.	92
2-3, 10, 12.	<i>Distorsio minoruohnishii</i> Parth, 1989	94
	2-3. NMB H 17922, Montezuma Fm (Pleistocene), loc. NMB 18161, SE coast of Playa Cocalito, ENE of Montezuma village, Nicoya Peninsula, Pacific Costa Rica; H 27.6 mm.	
	10, 12. BMNH 1990025, holotype, Recent, "Oaxaca, Mexico" [restricted by Emerson & Piech (1992) to off Isla Macapule, Sinaloa, W Mexico]; H 38.3 mm.	
5-9, 11.	<i>Distorsio perdistorta</i> Fulton, 1938	94
	5, 8-9, 11. Specimens in a private collection, Recent, 3 specimens, trawled in 110 m, off of Ambriz, Angola, SE Atlantic; H 54.8 (Fig. 5), 65.1 mm (Fig. 8), 65.9 mm (Figs 9, 11).	
	6. USNM 762002, Recent, "La Rafale" Survey I, Transect 12, sta. 6, 100 m, Gulf of Guinea, West Africa; H 65.3 mm.	
	7. Specimen in collection of D. Lamy, Recent, fishermen's traps in 200 m, Racket Bank, off of St. Barthelemy Island, West Indies; H 45.0 mm.	



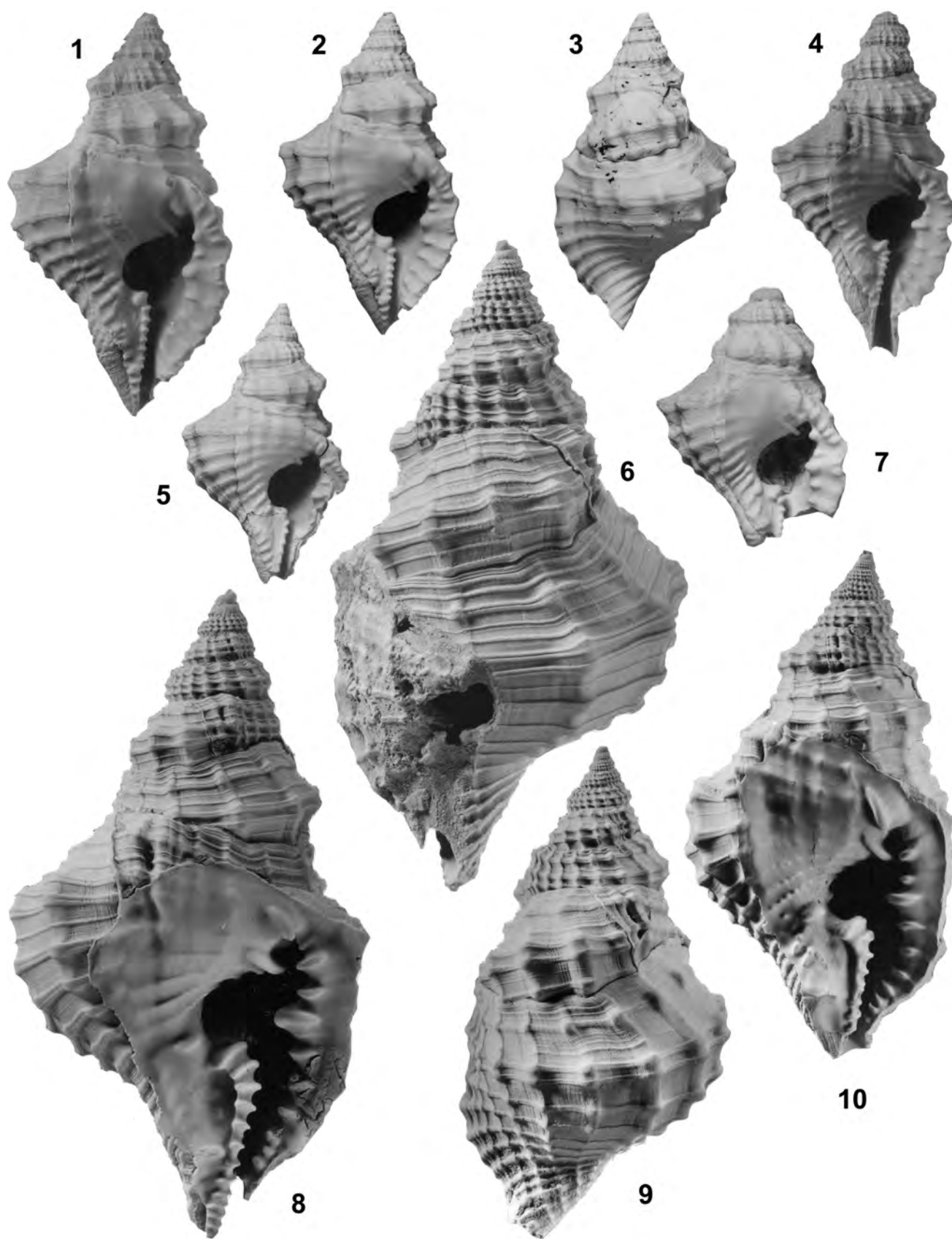
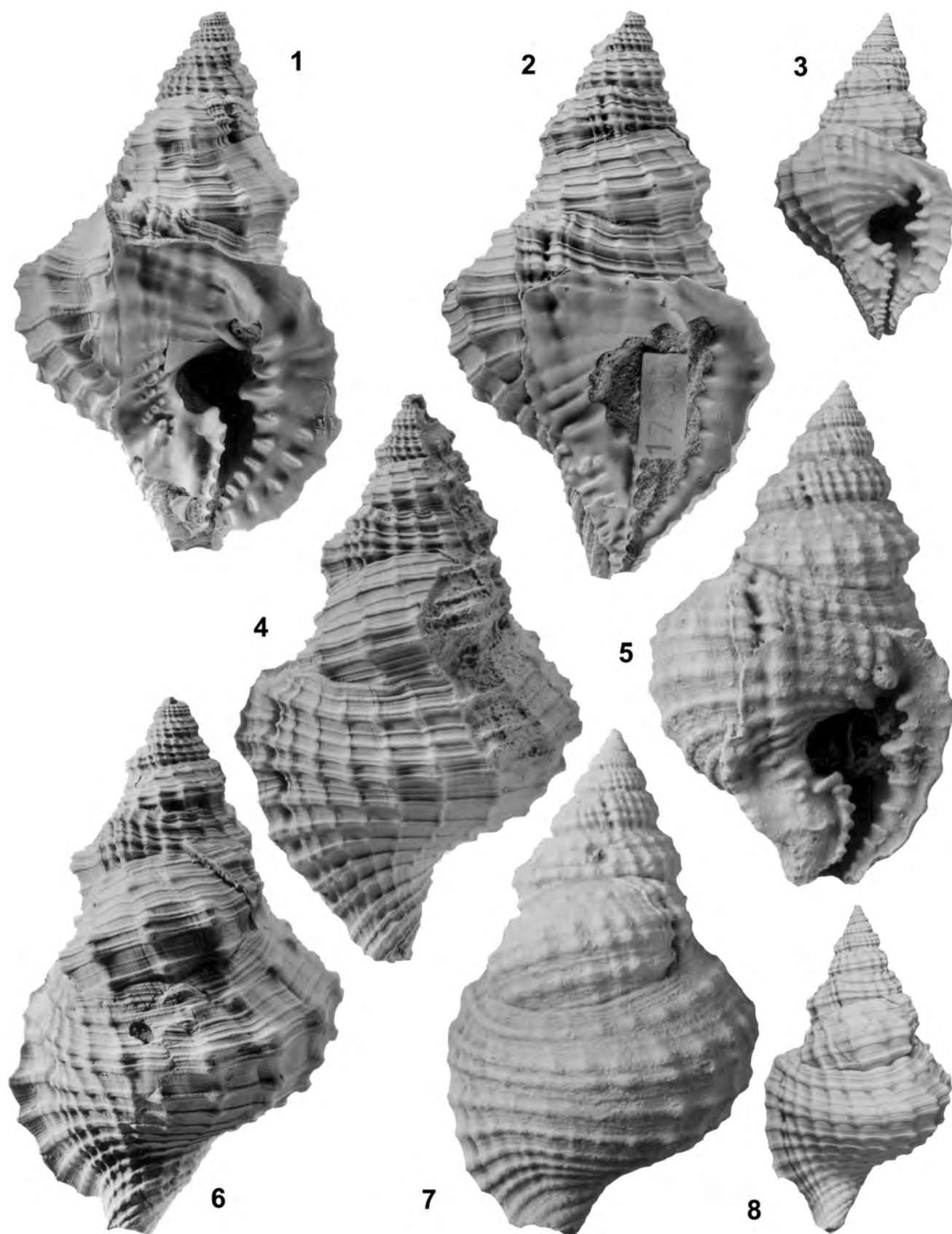


PLATE 20

Figure		Page
1-5, 7.	<i>Distorsio ringens</i> (Philippi, 1887). Formerly at Department of Earth and Planetary Sciences, Purdue University (now at PRI); Navidad Fm (Oligocene-Early Miocene mollusks reworked into Late Miocene- Early Pliocene rocks), coastal cliff N of mouth of Río Rapel, near Navidad, central Chile.	95
	1. W. J. Zinsmeister loc. 145; H 57.5 mm.	
	2-3. W. J. Zinsmeister loc. 145; H 54.8 mm.	
	4. W. J. Zinsmeister loc. 254; H 50.0 mm.	
	5, 7. W. J. Zinsmeister loc. 286; H 53.2 (Fig. 5), 45.8 mm (Fig. 7).	
6, 8-10.	<i>Distorsio simillima</i> (G. B. Sowerby I, 1850)	97
	6, 8. NMB H 17913, Escudo de Veraguas Fm (Pliocene), loc. NMB 18681, 4 easternmost islands at E end of Escudo de Veraguas Island, Bocas del Toro Basin, Atlantic Panama; H 60.2 mm.	
	9-10. NMB H 17915, Gurabo Fm (Early Pliocene), loc. NMB 16869, Río Cana, Dominican Republic; H 61.1 mm.	

PLATE 2 I

Figure		Page
1-8.	<i>Distorsio simillima</i> (G. B. Sowerby I, 1850)	97
	1, 6. NMB H 17911, Gurabo Fm (Late Miocene), loc. NMB 16910, Bluff 1 of Maury, <i>ca.</i> 1 km upstream from Cercado de Mao, Río Mao, Dominican Republic; H 66.1 mm (specimen with unusually complete outer lip).	
	2, 4. NMB H 17912, Escudo de Veraguas Fm (Pliocene), loc. NMB 17836, small island on N coast of Escudo de Veraguas Island, Bocas del Toro Basin, Atlantic Panama; H 51.6 mm.	
	3, 8. GNS WM16913, Gurabo Fm (Early Pliocene), loc. TU 1211, second bluff downstream from bridge on Los Quemados-Sabaneta road, Río Gurabo, Dominican Republic; H 62.1 mm.	
	5, 7. NMB H 17910, El Porvenir beds (early Middle Miocene), loc. NMB 17526, Mesa de Cocodite, Paraguaná Peninsula, Venezuela; H 62.1 mm (calcite neomorph; anterior canal incomplete).	



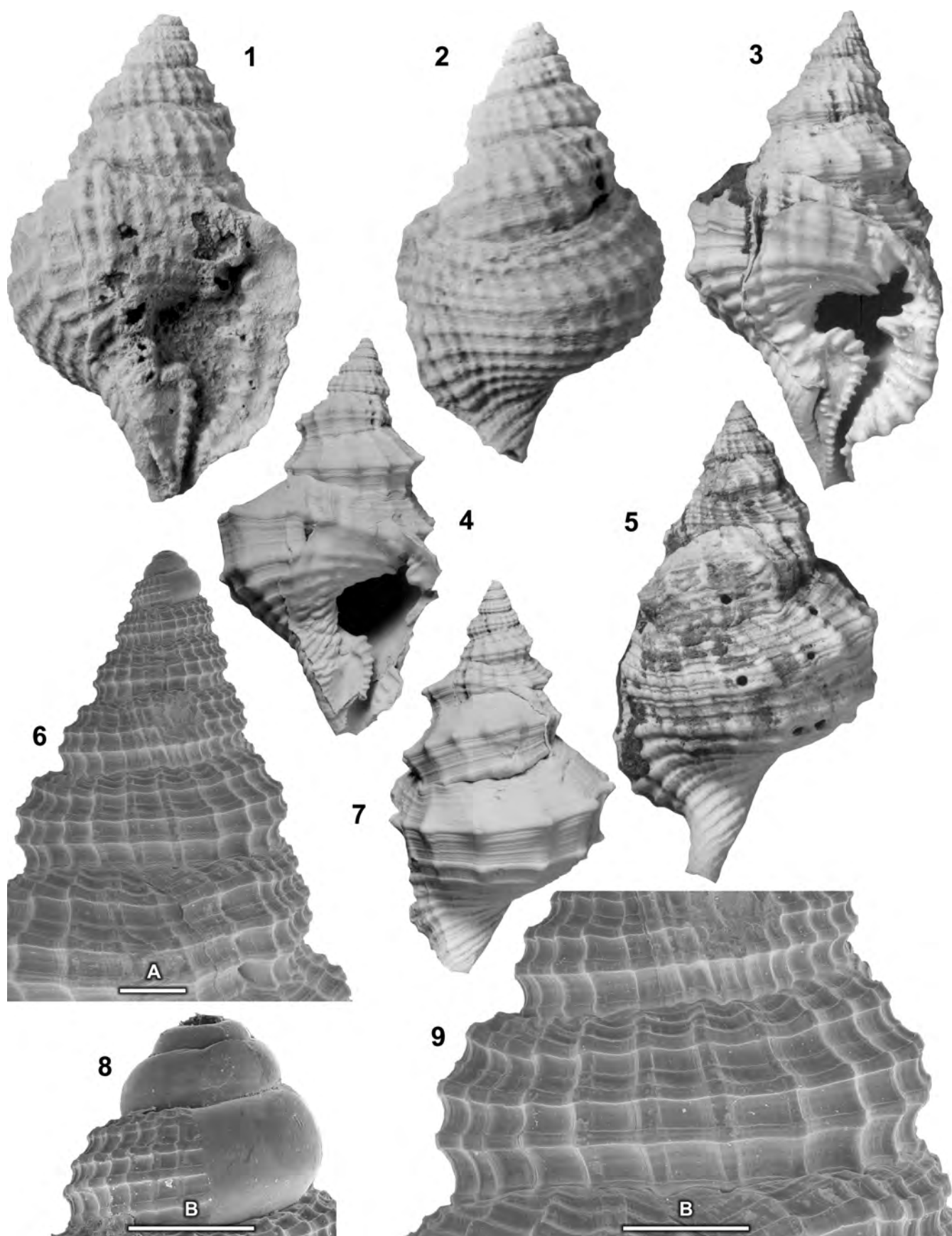
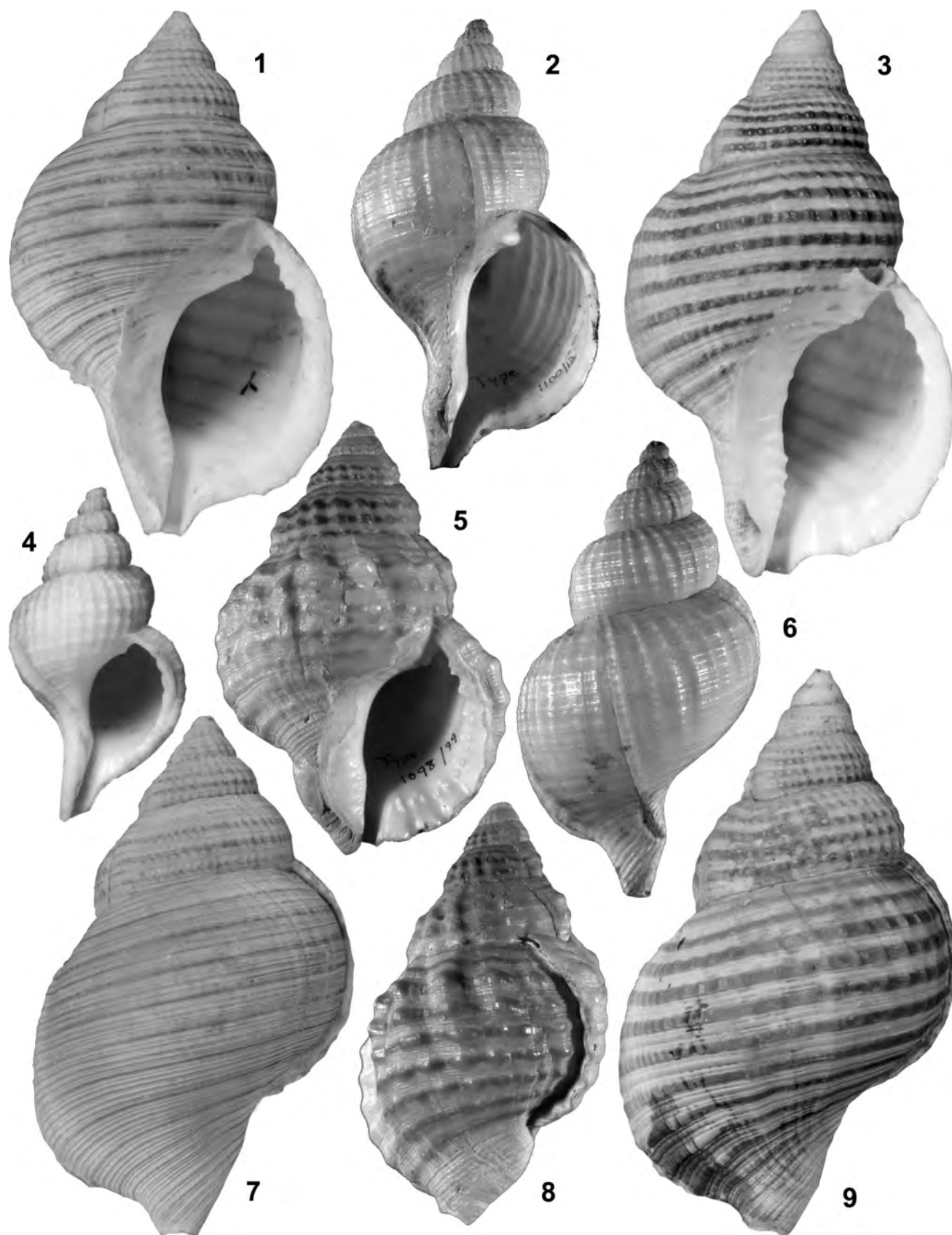


PLATE 22

Figure		Page
1-2, 6, 8-9.	<i>Distorsio simillima</i> (G. B. Sowerby I, 1850)	97
	1-2. NMB H 17909, second specimen from same locality as specimen in Pl. 21, Figs 5, 7; H 52.7 mm.	
	6, 8-9. GNS WM18908, Moín Fm (latest Pliocene-Early Pleistocene), loc. TU 956, hill slope behind Baptist church, between Pueblo Nuevo and Puerto Limón, Atlantic Costa Rica; SEM micrographs of spire apex and protoconch; scale bar A = 2 mm, scale bar B = 1 mm (protoconch apex incomplete, although this was the most complete seen; the distinctive secondary spiral cords can be seen developing on early spire whorls).	
4, 7.	<i>Distorsio biangulata</i> n. sp. UCMP 50022, holotype, Cantaure Fm (late Early Miocene), loc. UCMP S-8360, ca. 300 m S of Casa Cantaure, 10 km W of Pueblo Nuevo, near San José, Paraguaná Peninsula, Falcón, Venezuela; H 73.5 mm.	80
3, 5.	<i>Distorsio smithi</i> (von Maltzan, 1884). ZMC unreg., Recent, GTS <i>Thierry</i> sta. 135/7, 200 m, 6°05'N, 2°15'E, S of Cape Verde Islands and W of Monrovia, Liberia, West Africa; H 87.0 mm.	98

PLATE 23

Figure	Page
1, 3, 5, 7-9. <i>Argobuccinum pustulosum</i> (Lightfoot, 1786)	101
1, 7. BMNH 1973113, one of 3 syntypes of <i>Bursa tumida</i> Dunker, 1862, Recent, New Zealand, ex Cuming collection; H 88.6 mm.	
3, 9. BMNH 1950.11.28.17, one of 3 syntypes of <i>Ranella vexillum</i> G. B. Sowerby I, 1835, Recent, "Chiloé, Concepción," Chile; H 85.0 mm.	
5, 8. MHNG 1098/79, holotype of <i>Ranella polyzonalis</i> Lamarck, 1816, and neotype (designated here) of <i>Buccinum pustulosum</i> Lightfoot, 1786, of <i>Murex argus</i> Gmelin, 1791, and of <i>Tritonium argo-buccinum</i> Röding, 1798, Recent, without locality [South Africa; type locality here designated as Jeffreys Bay]; H 65.9 mm (from a color transparency).	
2, 4, 6. <i>Fusitriton magellanicus</i> (Röding, 1798)	104
2, 6. MHNG 1100/13, lectotype (designated here) of <i>Triton cancellatus</i> Lamarck, 1816, and neotype of <i>Neptunea magellanica</i> Röding, 1798, Recent, without locality [southern South America; type locality here designated as off Maldonado, Uruguay]; H 76.6 mm (from a color transparency).	
4. MNHN unreg., Recent, lobster traps at 600 m, Baie de la Possession, Réunion, Indian Ocean; H 60.5 mm.	



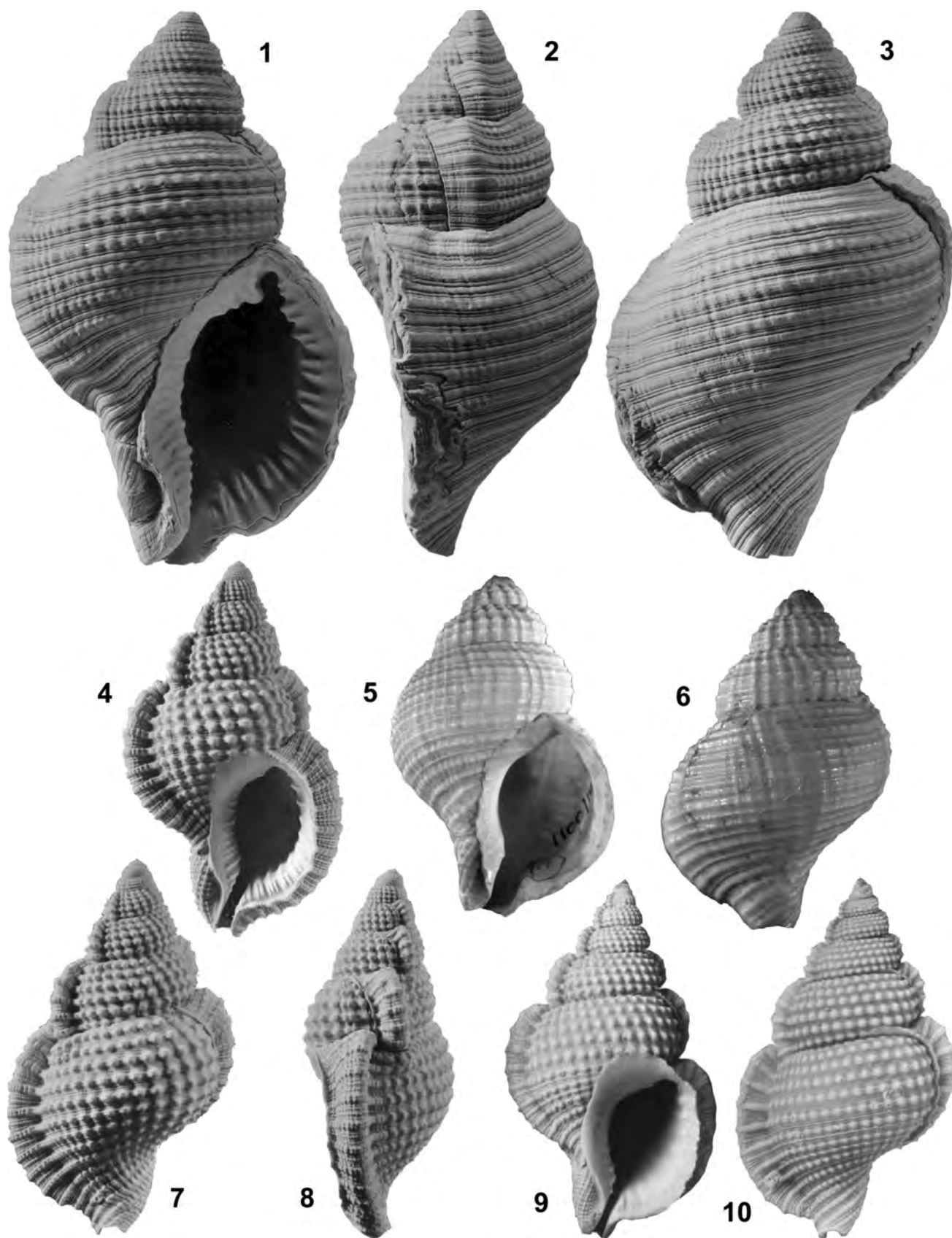
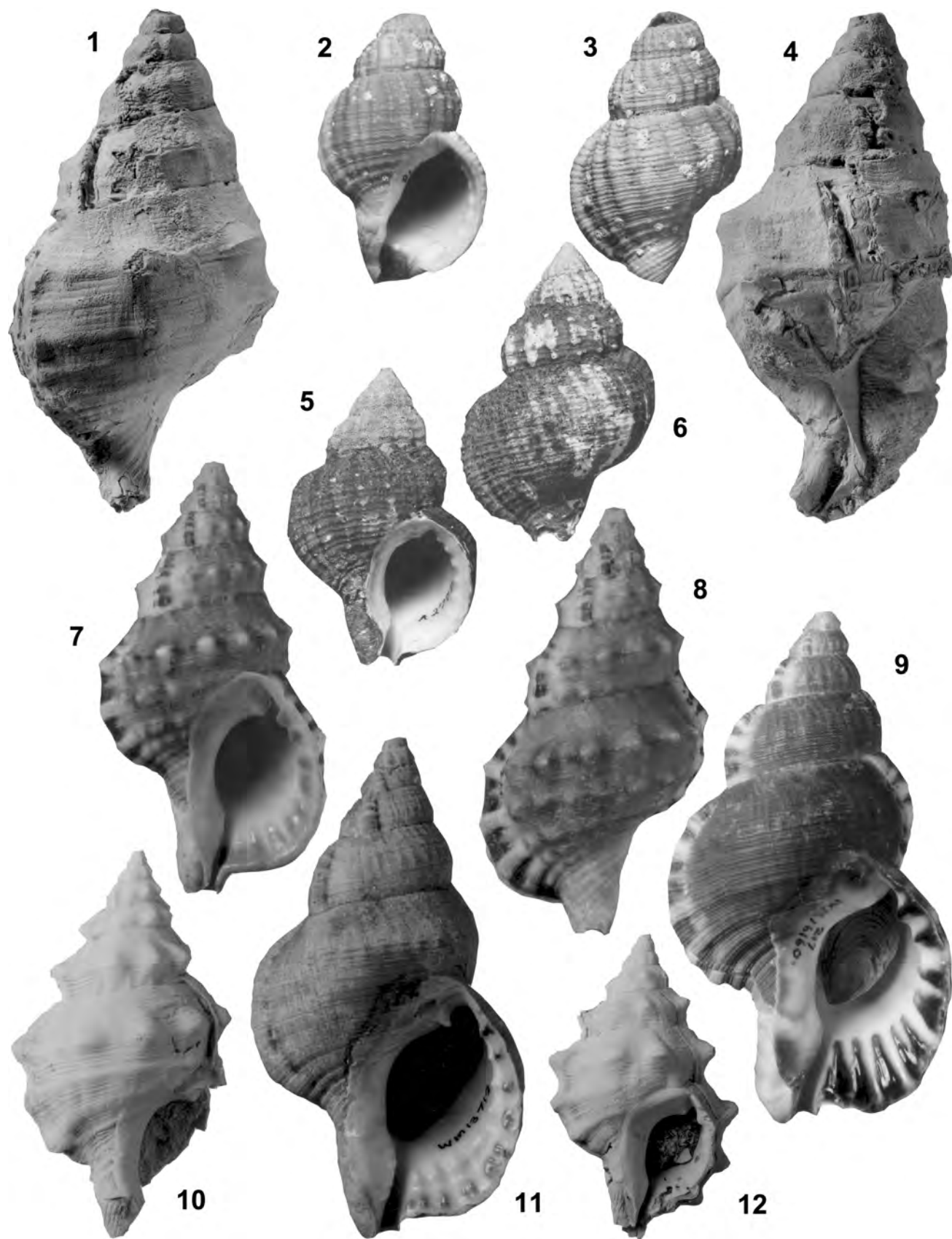


PLATE 24

Figure		Page
1-3.	<i>Argobuccinum pustulosum</i> (Lightfoot, 1786). GNS WM15955, typical South American "ranelliformis" form, Recent, Isla Mocha, 38.5°S, S of Concepción, Chile; H 99.9 mm.	101
4, 7-10.	<i>Halgyrineum louisae</i> (Lewis, 1974)	108
	4, 7-8. NMB H 17923, Moín Fm (latest Pliocene-Early Pleistocene), loc. TU 1240 (= NMB 19008), hill top on Calle King Fish in Barrio Los Corales 2, 1.4 km N of Standard Fruit Company box factory, which is 2 km W of Puerto Limón, Atlantic Costa Rica; H 22.5 mm.	
	9-10. MNHN unreg., Recent, Beryx 2 cruise sta. DW40, 240-300 m, off of southern New Caledonia; H 21.8 mm.	
5-6.	<i>Priene scabrum</i> (King, 1832). MHNG 1100/14/2, paralectotype of <i>Triton cancellatus</i> Lamarck, 1816, Recent, without locality [Chile]; H 57.2 mm (from a color transparency).	109

PLATE 25

Figure	Page
1, 4, 10, 12. <i>Ameranella verruculosa</i> (G. B. Sowerby I, 1846)	117
1, 4. SGO.PI 4827, large incomplete specimen, Capas de Lo Abarca (Late Miocene-Early Pliocene), Lo Abarca, <i>ca.</i> 90 km N of Navidad, SW of Santiago, Chile; H 92.4 mm.	
10, 12. SGO.PI 6449-6450; from Navidad Fm (Late Oligocene-Early Miocene fossils re-worked into Late Miocene-Pliocene rocks), coast N of mouth of Río Rapel, N of Navidad, Chile, coll. Sven Nielsen (Fig. 10, SGO.PI 6450, large incomplete specimen: H 70.0 mm; Fig. 12, SGO.PI 6449, smaller, complete specimen: H 44.5 mm.	
2-3, 5-6. <i>Priene scabrum</i> (King, 1832) LACM 72-78, 2 specimens, Recent, 6-12 m, Isla Chincha Norte, 13°38'S, 76°25'W, Ica Province, Peru (Figs 2-3, specimen commencing as <i>scabrum</i> form, last intervariceal interval is <i>rude</i> form, H 48.3 mm; Figs 5-6, specimen commencing as <i>rude</i> form, last intervariceal interval is <i>scabrum</i> form, H 53.3 mm).	109
7-9, 11. <i>Ranella gemmifera</i> (Euthyme, 1889)	113
7-8. GNS WM17261, Recent, fishermen's nets, 200 m, off of Cabo Frio, Río de Janeiro State, Brazil; H 77.5 mm.	
9. GNS WM16160, Recent, intertidal, Park Rynie, S of Durban, Natal, South Africa; H 92.9 mm.	
11. GNS WM13712, Recent, lobster traps at 40 m, Île Amsterdam, southern Indian Ocean, pres. P. M. Arnaud; H 91.9 mm.	



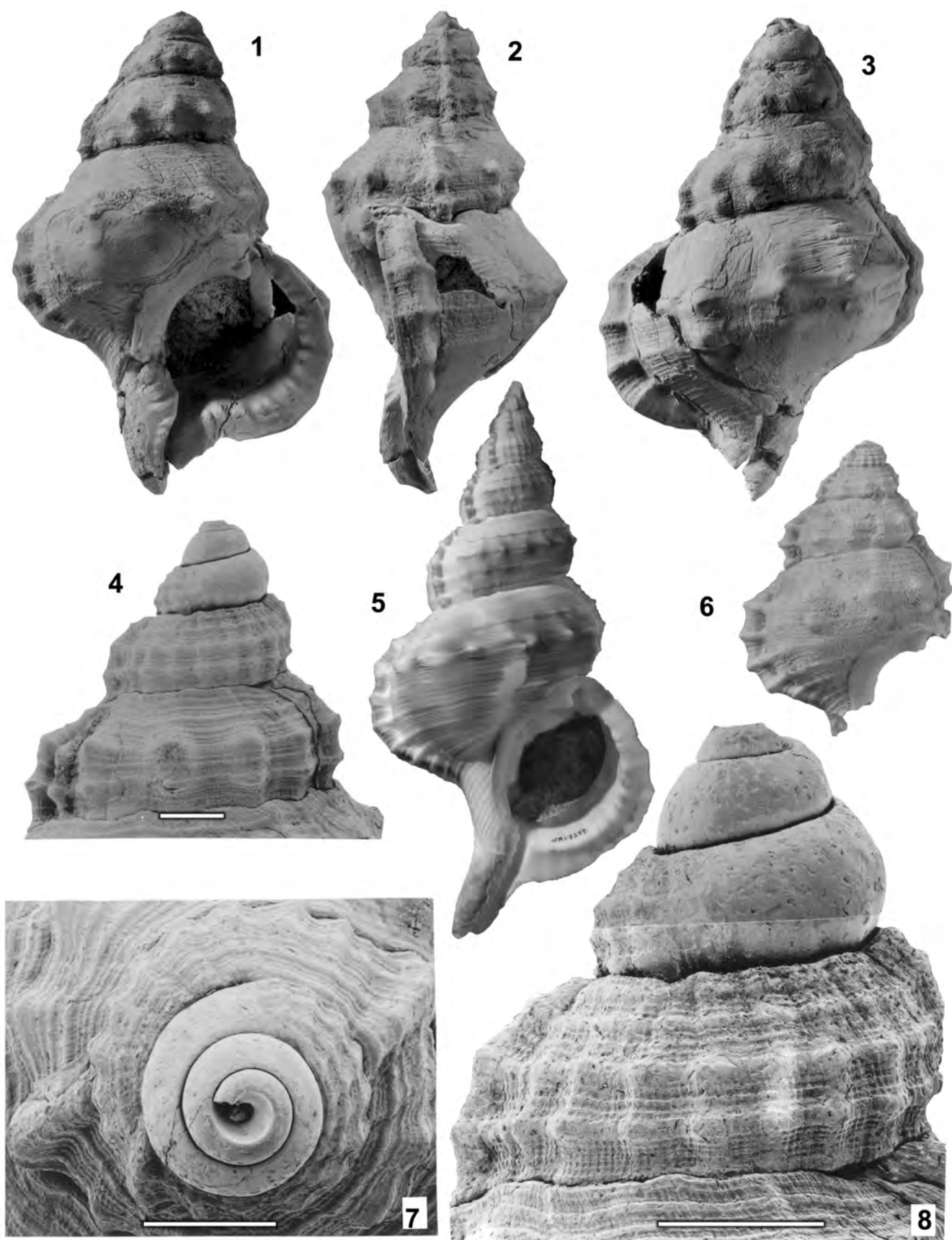


PLATE 26

Figure	Page
1-4, 6-8. <i>Ranella chilena</i> n. sp.	111
1-3. SGO.PI 3706, holotype, Navidad Fm (Late Oligocene-Early Miocene fossils reworked into Late Miocene-Pliocene rocks), Matanzas, 4 km SW of Navidad, SW of Santiago, central Chile; H 87.7 mm.	
4, 7-8. SGO.PI 5838, paratype, locality data same as holotype; SEM micrographs of spire apex and protoconch (all scale bars = 2 mm).	
6. Formerly at Department of Earth and Planetary Sciences, Purdue University, now at PRI, paratype, all locality data same as holotype (W. J. Zinsmeister loc. 245); H 36.2 mm.	
5. <i>Ranella olearium</i> (Linnaeus, 1758). GNS WM17259, Recent, 400 m, 780 km SE of Itajaí, Santa Catarina State, Brazil; H 215 mm.	114

PLATE 27

Figure		Page
1, 3, 5.	<i>Ranella olearium</i> (Linnaeus, 1758)	114
	1. GNS WM11483, Recent, off of Sicily, Mediterranean; H 160.0 mm (see also Pl. 28, Fig. 1).	
	3. Specimen in collection of D. Lamy, Recent, fishermen's traps, 500 m, off of Guadeloupe, West Indies; H 131.6 mm (from a color transparency).	
	5. MNHN unreg., Recent, Cruise MD 32/Réunion, 1982, sta. CP181, 300-410 m, off of Réunion Island, Indian Ocean; H 116.3 mm.	
2, 4, 6.	<i>Ameranella verruculosa</i> (G. B. Sowerby I, 1846). Formerly at Department of Earth and Planetary Sciences, Purdue University, now at PRI; Navidad Fm (Late Oligocene-Early Miocene fossils reworked into Late Miocene-Pliocene rocks), coastal cliff N of mouth of Río Rapel, near Navidad, central Chile.	117
	2, 6. W. J. Zinsmeister loc. 286; H 46.9 mm.	
	4. W. J. Zinsmeister loc. 332; H 37.2 mm.	

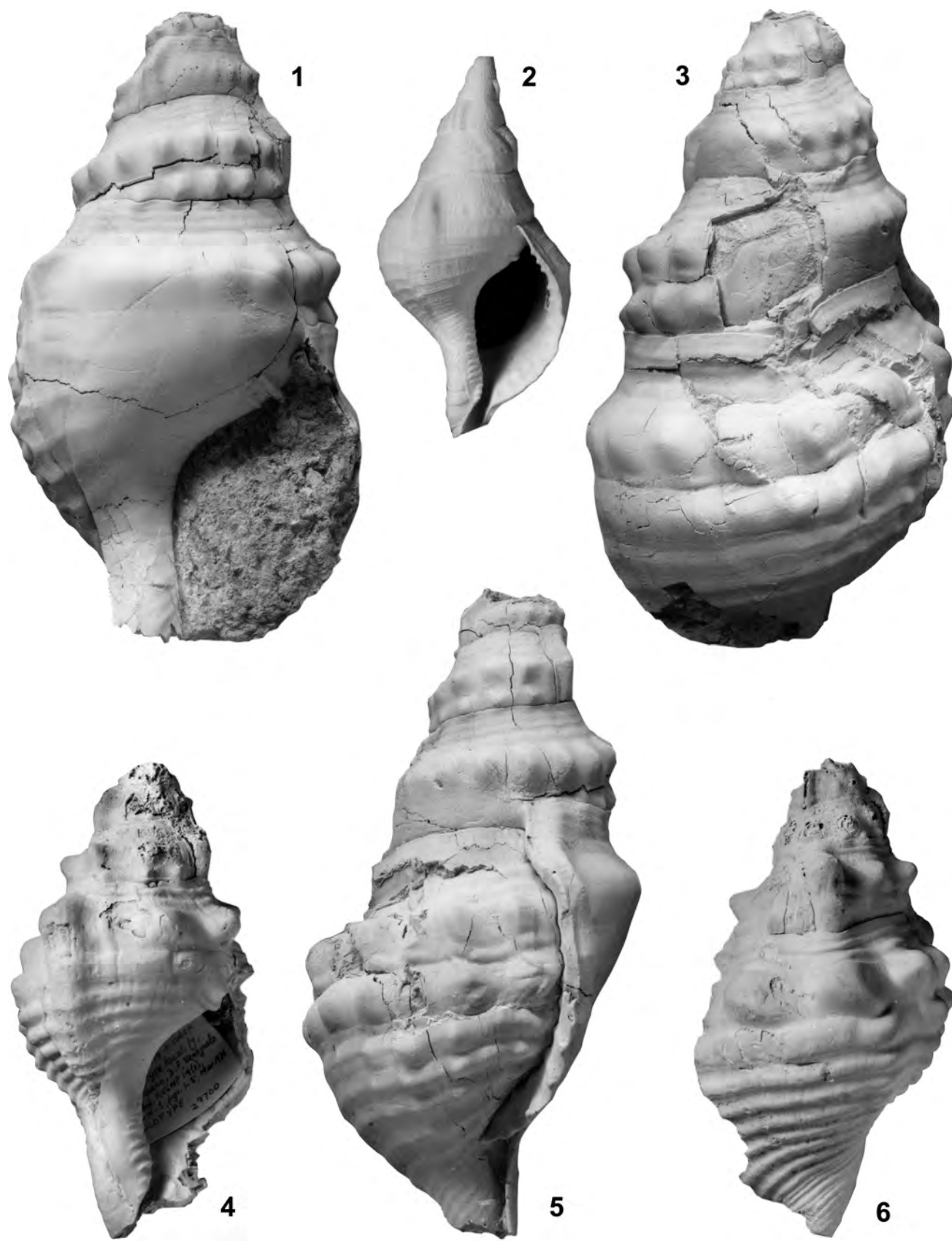




PLATE 28

Figure		Page
1, 3, 7.	<i>Ranella olearium</i> (Linnaeus, 1758)	114
	1. GNS WM12444, Recent, trawled off of Zululand, South Africa; H 162 mm.	
	3, 7. USNM 709826, paratype of <i>Bursa barcellosi</i> Matthews, Rios & Coelho, 1973, Recent, 100 m, off of Albardão, Río Grande do Sul, Brazil; H 115.7 mm.	
2, 4, 6.	<i>Ameranella verruculosa</i> (G. B. Sowerby I, 1846). Formerly at Department of Earth and Planetary Sciences, Purdue University, now at PRI ; Navidad Fm (Late Oligocene-Early Miocene fos- sils reworked into Late Miocene-Pliocene rocks), W. J. Zinsmeister loc. 332, coastal cliff N of mouth of Río Rapel, near Navidad, central Chile (Figs 2, 4, H 25.6 mm; Fig. 6, H 38.5 mm). .	117
5, 8.	<i>Cabestana felipponei</i> (Ihering, 1907). MNRJ 6162, Recent, Punta del Este, Maldonado, Uruguay; H 40.1 mm.	119

PLATE 29		
Figure		Page
1-6.	<i>Charonia lampas</i> (Linnaeus, 1758)	120
	1, 3, 5. BMNH Palaeontology Department, GG20379, Miocene-Pliocene, “Miocene, Yaque River, Santo Domingo” [late Early Miocene, Baitoa Fm, or Early Pliocene, Gurabo Fm?], from original T. S. Heneken collection, <i>ca.</i> 1848; H 174 mm.	
	2. USNM 398480, Plio-Pleistocene, Florida, USA, unlocalised, ex A. A. Olsson collection; H 68.1 mm.	
	4, 6. PRI 29700, holotype of <i>Charonia lampas weisbordi</i> Gibson-Smith, 1976, Mare Fm (Late Pliocene), Cabo Blanco, Venezuela; H 131.3 mm.	



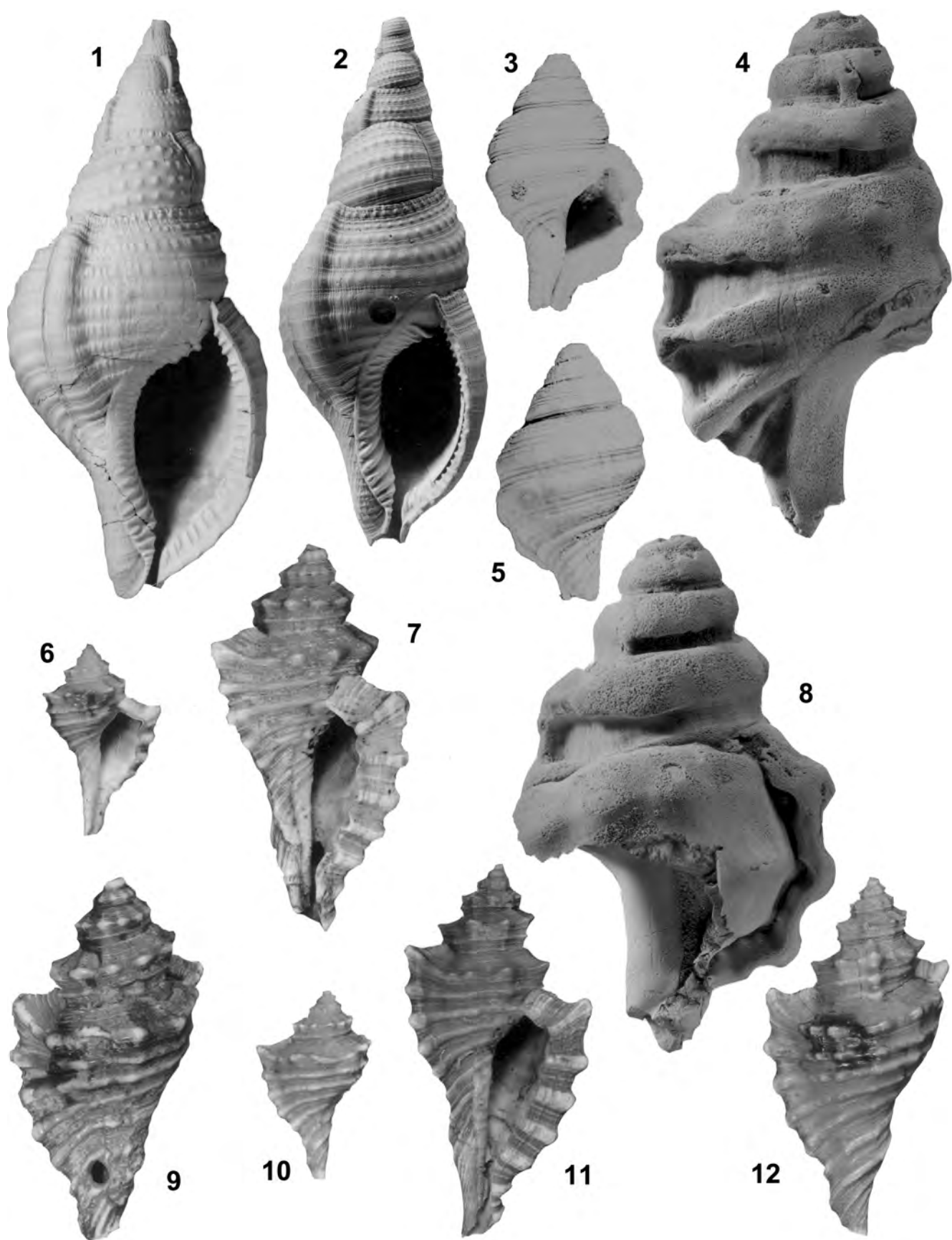


PLATE 30

Figure		Page
1-2.	<i>Charonia variegata</i> (Lamarck, 1816)	126
	1. USNM unreg., Gurabo Fm (Early Pliocene), loc. USGS 8544, bluff no. 3, 150 m upstream from middle ford at Gurabo Adentro, Río Gurabo, Dominican Republic; H 105.2 mm.	
	2. NMB H 17924, Moín Fm (latest Pliocene-Early Pleistocene), loc. TU 1240 (= NMB 19008), hill top on Calle King Fish in Barrio Los Corales 2, 1.4 km N of Standard Fruit Company box factory, which is 2 km W of Puerto Limón, Atlantic Costa Rica; H 64.0 mm.	
3-5, 8.	<i>Crassicymatium crassicordatum</i> n. gen., n. sp.	129
	3, 5. SGO.PI 5841, juvenile paratype, all data same as holotype; H 23.4 mm (S. N. Nielsen photographs).	
	4, 8. SGO.PI 5839, holotype, Navidad Fm (Late Oligocene-Early Miocene fossils reworked into Late Miocene-Pliocene rocks), Matanzas, 4 km SW of Navidad, SW of Santiago, central Chile; H 64.8 mm.	
6, 7, 9-12.	<i>Cymatium femorale</i> (Linnaeus, 1758). Linnean Society of London collection, lectotype of <i>Murex femorale</i> Linnaeus and neotype of <i>Lotorium lotor</i> Montfort, 1810, and <i>Septa triangularis</i> Perry, 1811 (Figs 11-12), with 2 paralectotypes of <i>Murex femorale</i> in Linnaeus' collection, Recent, without locality [western Atlantic; type locality designated as Jamaica by Clench & Turner (1957)] (BMNH photographs; Figs 6, 10, H 32.0 mm; Figs 7, 9, H 62.2 mm; Figs 11, 12, H 60.0 mm).	131

PLATE 3 I

Figure		Page
1, 4.	<i>Cymatium raderi</i> D'Attilio & Myers, 1984. GNS WM13595, Recent, 2 specimens, trawled, 45 m, off of NE Honduras, Gulf of Mexico (Fig. 1, H 136.5 mm; Fig. 4, H 131.7 mm).	133
2, 5-7.	<i>Cymatium femorale</i> (Linnaeus, 1758)	131
	2, 5. GNS WM16214, Recent, 1.3 m of water, Green Turtle Cay, Abaco, Bahamas; H 114.0 mm.	
	6-7. NMB H 17925, Mare Fm (Late Pliocene), loc. NMB 17512, Cabo Blanco, Venezuela; H 78.7 mm.	
3.	<i>Cymatium praefemorale</i> (Maury, 1917). NMB H 17926, Cayo Agua Fm (Pliocene), loc. NMB 17829, 1.2 km SE of Punta de Tiburón, E coast of Cayo Agua, Bocas del Toro Basin, Atlantic Panama; H 96.2 mm.	132



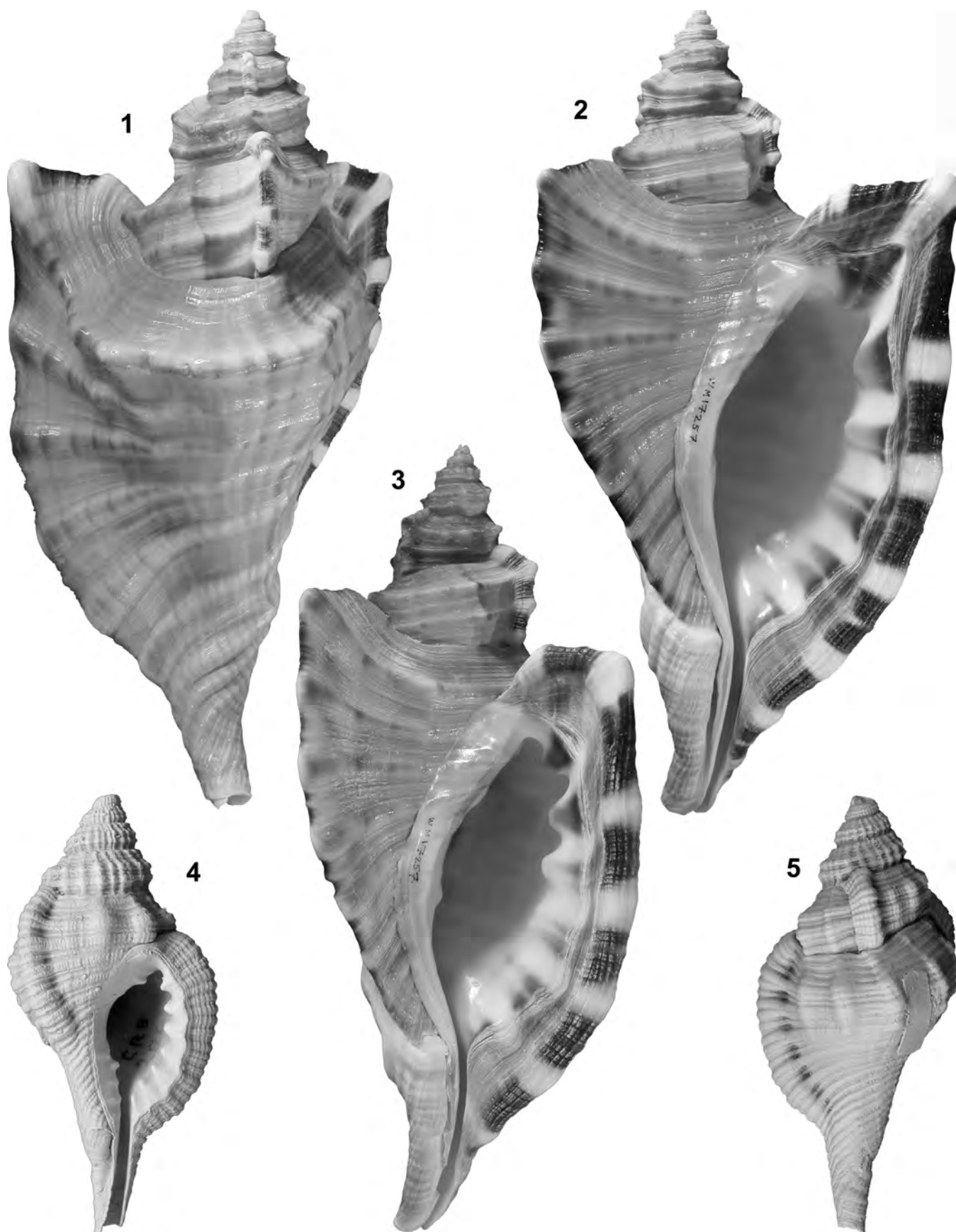
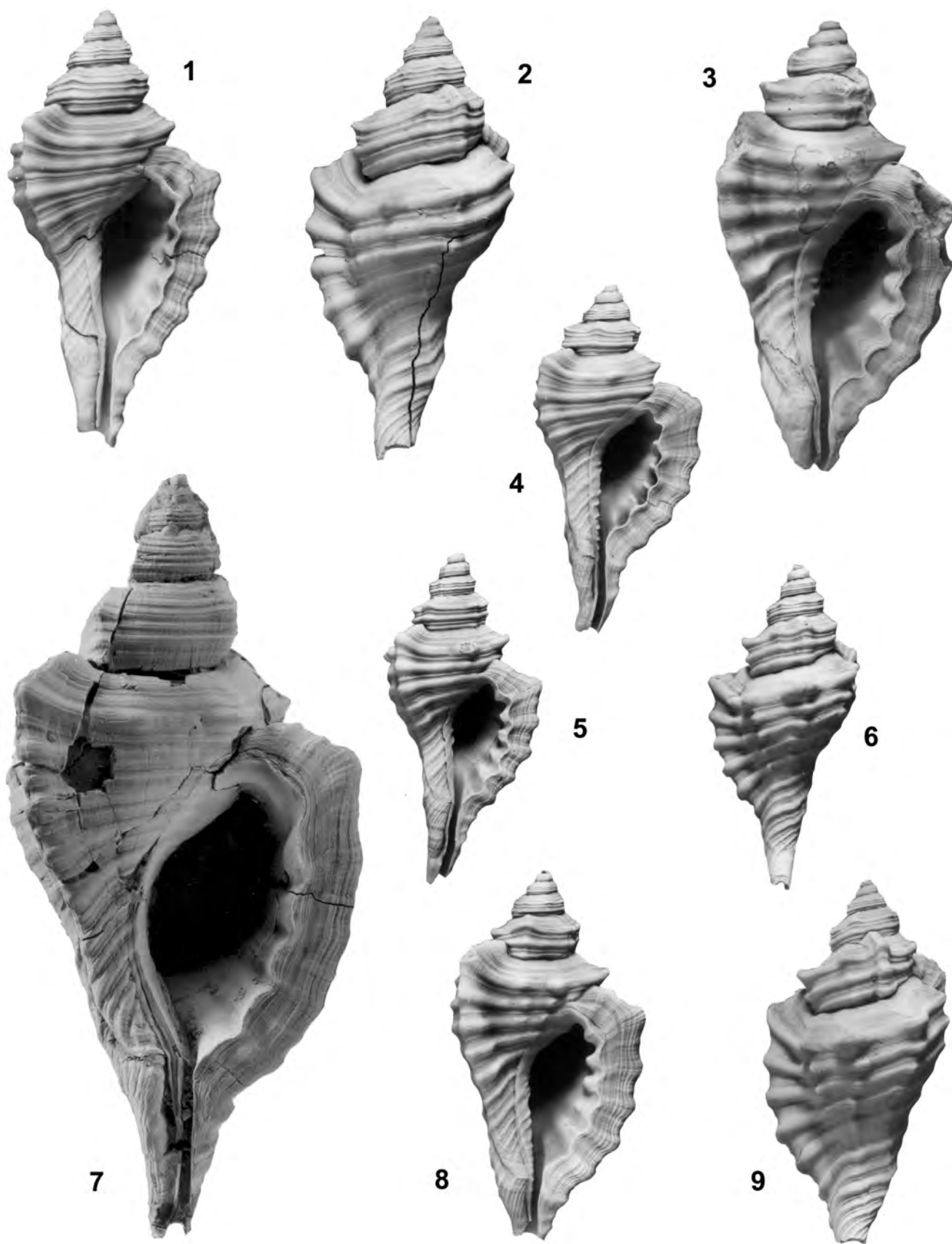


PLATE 32

Figure		Page
1-3.	<i>Cymatium raderi</i> D'Attilio & Myers, 1984. GNS WM17257, 2 specimens, Recent, lobster divers on coral reef, 10-20 m, Rio de Fogo, North Natal, Rio Grande do Norte, Brazil (Figs 1-2, H 224.4 mm; Fig. 3, H 219.2 mm).	133
4-5.	<i>Monoplex amictus</i> (Reeve, 1844). BMNH Palaeontology Department unreg., Onzole Fm (Early Pliocene), loc. CRB 284, Quebrada Camarones, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town, Ecuador; H 35.8 mm.	143

PLATE 33

Figure		Page
1-9.	<i>Cymatium praeemorale</i> (Maury, 1917)	132
	1-2. NMB H 18324, Gurabo Fm (Late Miocene), loc. NMB 19014 (= TU 1280), bluff on W side Río Mao 1 km N of Cercado de Mao, Dominican Republic; H 79.6 mm.	
	3. NMB H 18325, Late Miocene/Early Pliocene, loc. NMB 19006 (= TU 1231), "float" near ford on Los Quemados-Sabaneta road, Río Gurabo, Dominican Republic; H 92.4 mm.	
	4. NMB H 18326, all data same as in Fig. 3; H 63.5 mm.	
	5-6. NMB H 18329, Cercado Fm (Late Miocene), loc. NMB 16838, toward upper end of major horseshoe bend, Río Cana, Dominican Republic; H 58.0 mm.	
	7. NMB H 17927, Gurabo Fm (Late Miocene/Early Pliocene), loc. TU 1455 (= NMB 19023), E side Río Guanajuma, long platform <i>ca.</i> 1 km upstream from trail at Higuerito Penueles, Dominican Republic; H 143.0 mm.	
	8-9. NMB H 18328, Gurabo Fm (Early Pliocene), loc. NMB 18579 (= TU 1210), first bluff downstream from bridge on Los Quemados-Sabaneta road, Río Gurabo, Dominican Republic; H 66.9 mm.	



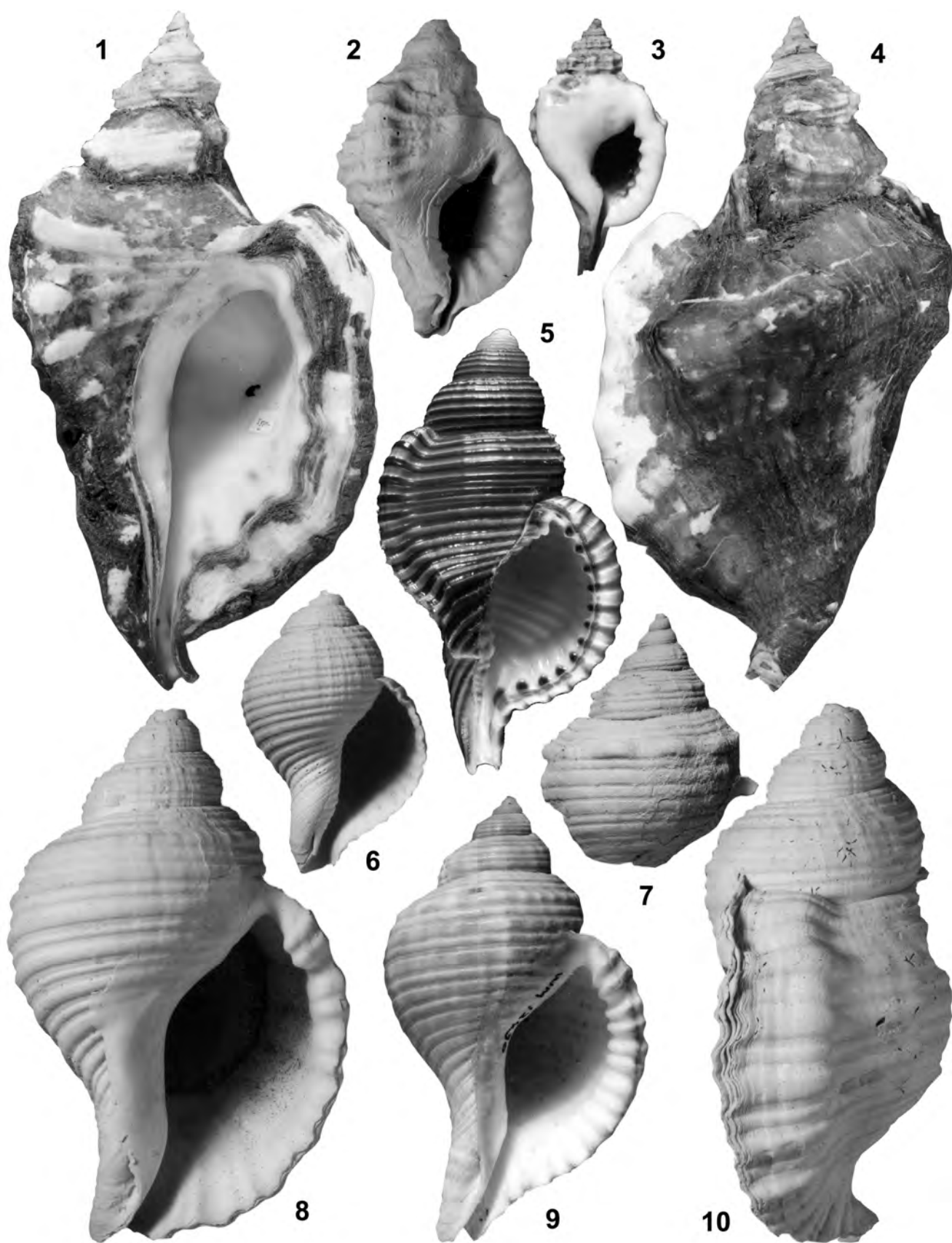
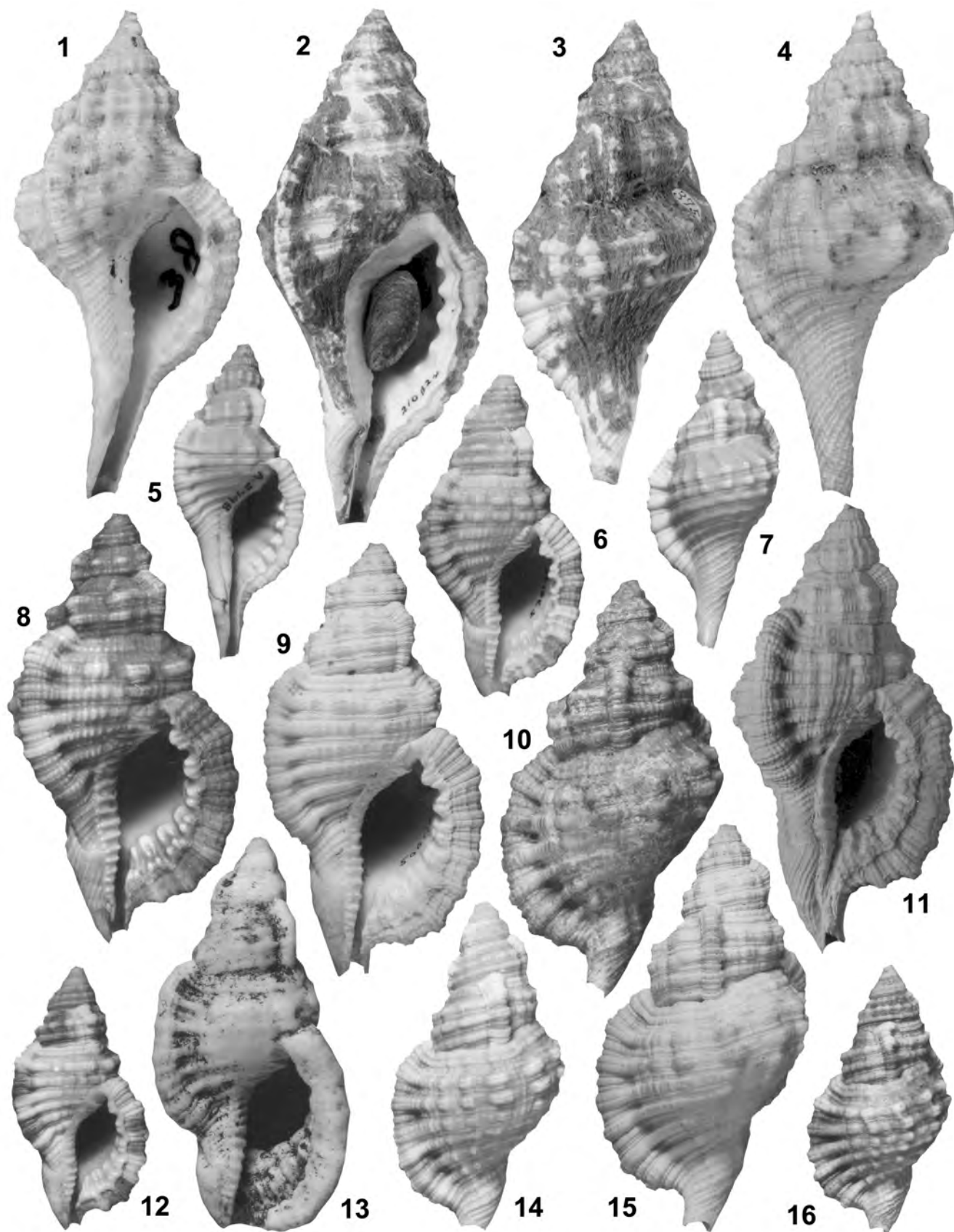


PLATE 34

Figure		Page
1, 4.	<i>Cymatium tigrinum</i> (Broderip, 1833). BMNH 1950.8.28.21, lectotype (designated here), Recent, "Guacomayo" [type locality designated here as Corinto, Nicaragua], ex Cuming collection; H 166.2 mm.	135
2-3.	<i>Guttarium muricinum</i> (Röding, 1798)	138
	2. NMB H 18051, Coral Rock (Pleistocene), loc. NMB 10118, pit in garden at Kenilworth, Barbados; H 38.5 mm.	
	3. MNHN unreg., Recent, "Îles du Cap Vert," coll. Bouvier, ex H. Fischer collection; H 46.2 mm.	
5.	<i>Gelagna succincta</i> (Linnaeus, 1771). Specimen in collection of D. Lamy, Recent, Guadeloupe, West Indies; H 49.6 mm (from a color transparency).	137
6-10.	<i>Linatella caudata</i> (Gmelin, 1791)	140
	6. USNM 370465, holotype of <i>Cymatium</i> (<i>Linatella</i>) <i>floridanum</i> Mansfield, 1930, Jackson Bluff Fm, Choctawhatchee Group (Pliocene), loc. USGS 11732, borrow pit near Jackson Bluff, Leon County, Florida, USA; H 25.0 mm.	
	7. UCMP unreg., Cubagua Fm (Pliocene), UCMP loc. S122, Cubagua Island, Venezuela; H 44.8 mm.	
	8, 10. USNM unreg., Pinecrest Fm (middle Pliocene), loc. USGS 26552, 4.8 km W of Indian Prairie Canal, NW of Lake Okeechobee, Elderberry, Florida, USA; H 96.7 mm (largest specimen seen).	
	9. GNS WM12430, Recent, Sulu Sea, Philippine Islands; H 82.5 mm.	

PLATE 35

Figure		Page
1-5, 7.	<i>Monoplex amictus</i> (Reeve, 1844)	143
	1, 4. BMNH 1967650, holotype, Recent, "Philippine Islands" [wrong, eastern Pacific; type locality designated here as Isla San José, Perlas Islands, Panama Bay], ex Cuming collection; H 35.0 mm.	
	2-3. USNM 210824, holotype of <i>Cymatium corrugatum</i> var. <i>tremperi</i> Dall, 1907, Recent, 77 m, off of San Pedro, California, USA; H 83.8 mm.	
	5, 7. LACM 55054, Recent, Perlas Islands, Panama; H 57.8 mm.	
6, 8-16.	<i>Monoplex aquatilis</i> (Reeve, 1844)	145
	6, 14. USNM 530190, Recent, St. Thomas, West Indies; H 60.0 mm.	
	8, 10. BMNH 1854.10.4.408, paralectotype of <i>Triton martinianum</i> d'Orbigny, 1841, Recent, "Cuba, St. Lucia," West Indies; H 76.4 mm.	
	9, 15. USNM 500116, Recent, Barbados, West Indies; H 79.3 mm.	
	11. NMB H 18049, Coral Rock (Pleistocene), loc. NMB 10118, Barbados, West Indies; H 64.8 mm.	
	12, 16. MNHN unreg., one of 2 specimens, Recent, "Îles du Cap Vert," ex H. Fischer collection; H 49.4 mm (see also Pl. 36, Fig. 2).	
	13. AMNH 107015, Recent, Wafer Bay, Cocos Island, Costa Rica; H 72.3 mm.	



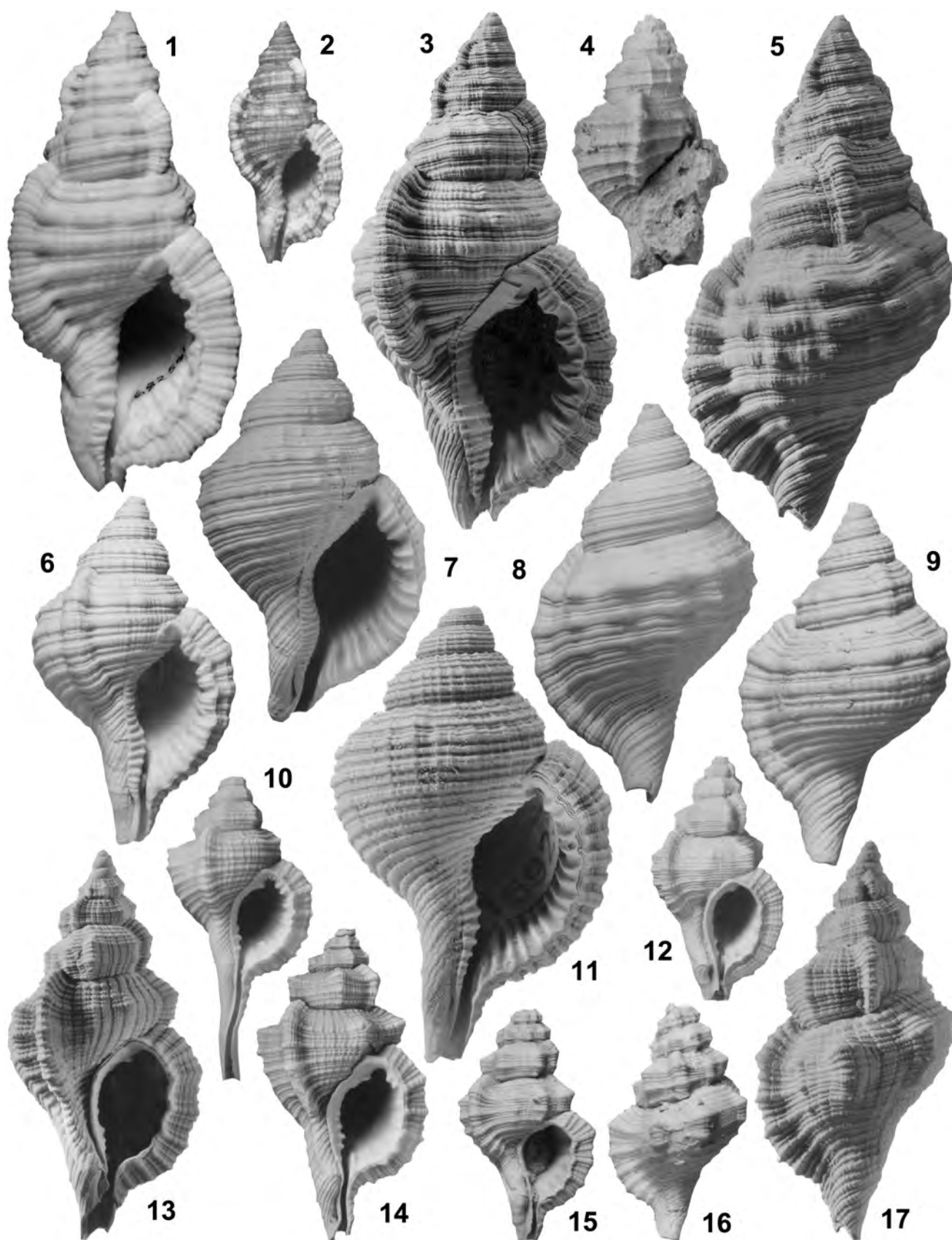
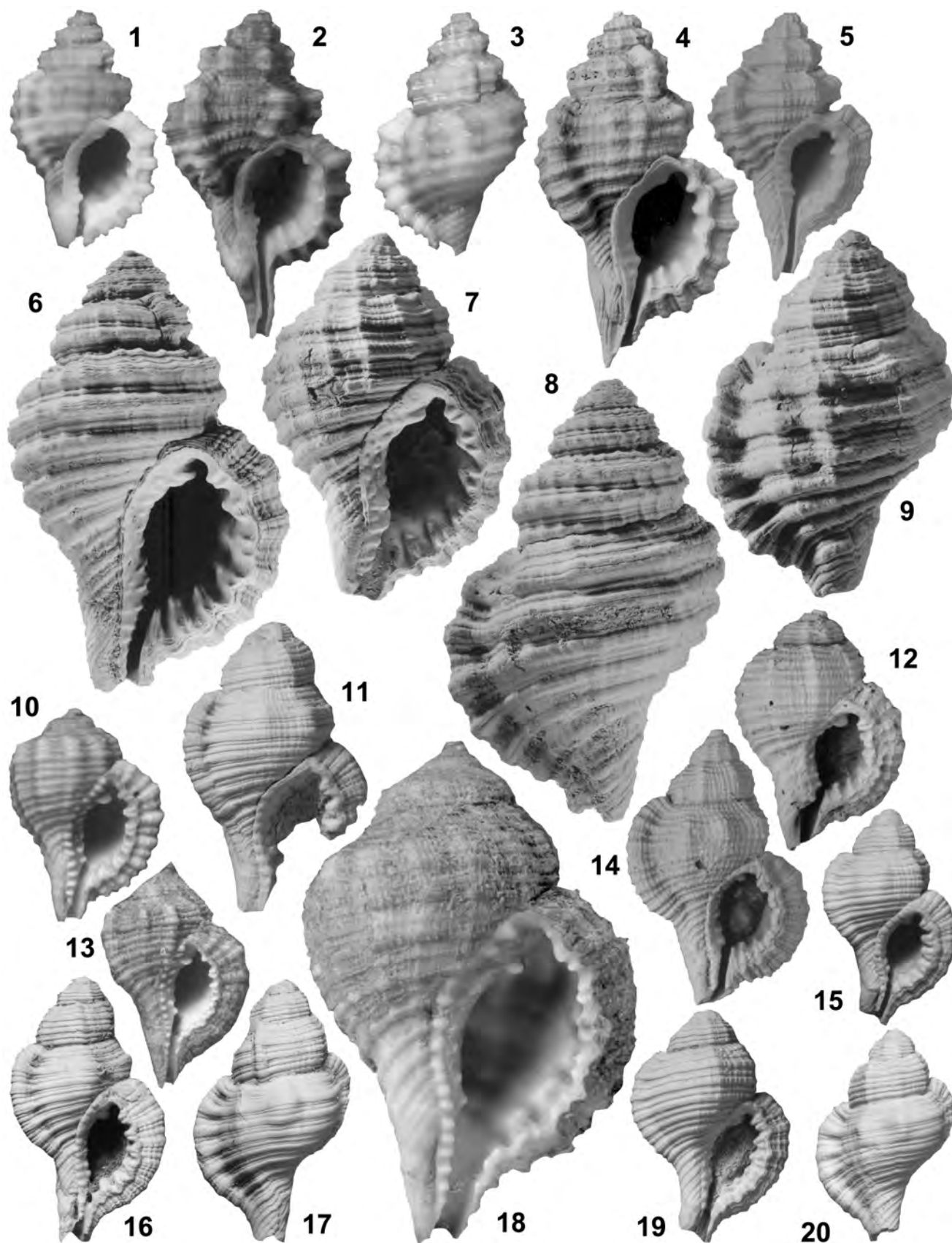


PLATE 36

Figure		Page
1-2.	<i>Monoplex aquatilis</i> (Reeve, 1844)	145
	1. USNM 682591, Recent, off of Cocoa Point, Barbuda, West Indies; H 87.2 mm.	
	2. MNHN, unreg., Recent, “Îles du Cap Vert,” second specimen in same lot as specimen in Pl. 35, Figs 12, 16; H 45.5 mm.	
3, 5.	<i>Monoplex longispira</i> n. sp. NMB H 71929, holotype, Gurabo Fm (Late Miocene/Early Pliocene), loc. TU 1250 (= NMB 18558), just above ford, S bank Río Verde, 10 km N of La Vega, Dominican Republic; H 92.9 mm.	161
4.	<i>Monoplex cecilianus</i> (Dall, 1916). USNM 166727, holotype, Flint River Fm (Late Oligocene), loc. USGS 7074, Hale landing, Flint River, 11 km S of Bainbridge, Decatur County, Georgia, USA; H 25 mm.	147
6-9, 11.	<i>Monoplex cercadicus</i> (Maury, 1917)	148
	6, 9. PRI 28758, holotype, Cercado Fm (Late Miocene), Cercado de Mao, Río Mao, Dominican Republic; H 44.3 mm.	
	7-8. Specimen in collection of Bernard Landau, Gurabo Fm (Late Miocene), loc. TU 1379, 100 m on either side of mouth of Arroyo Bajón, Río Mao, Dominican Republic; H 57.4 mm.	
	11. NMB H 17930, Gurabo Fm (Late Miocene), loc. NMB 16923, ca. 50 m upstream from mouth of Arroyo Bajón, Río Mao, Dominican Republic; H 28.0 mm (the common immature form).	
10, 14.	<i>Monoplex comptus</i> (A. Adams, 1855)	149
	10. MNHN unreg., Recent, <i>Lagon</i> sta. 1163, 48 m, Secteur de Belep, New Caledonia; H 27.0 mm.	
	14. MNHN unreg., Recent, <i>Corail</i> 2 sta. DW99, 52 m, Chesterfield Plateau, Coral Sea; H 28.5 mm.	
12-13, 15-17.	<i>Monoplex gurabonicus</i> (Maury, 1917)	154
	12. USNM unreg., Gurabo Fm (Early Pliocene), loc. USGS 8547, Río Gurabo above Gurabo Adentro, Dominican Republic; H 28.9 mm.	
	13, 17. NMB H 17931, Gurabo Fm (Early Pliocene), loc. TU 1210 (= NMB 18579), first bluff downstream from ford on Los Quemados-Sabaneta road, Río Gurabo, Dominican Republic; H 23.7 mm.	
	15-16. PRI 28764, holotype, Gurabo Fm (Early Pliocene), Maury's Zone D (= TU 1215), from bridge on Los Quemados-Sabaneta road to 1 km upstream, Río Gurabo, Dominican Republic; H 21.7 mm.	

PLATE 37

Figure	Page
1-4. <i>Monoplex exaratus</i> (Reeve, 1844)	151
1, 3. Bernice P. Bishop Museum, Honolulu, BPBM 62160, Recent, Midway Island, Hawaiian Islands; H 29.3 mm.	
2. Specimen in collection of E. Wils; Recent, Lotus Bay, N of Safaga, Egyptian Red Sea coast; H 40.0 mm.	
4. Specimen in collection of E. Wils; Recent, Golden Beach, Hurghada, Egyptian Red Sea coast; H 43.3 mm.	
5. <i>Monoplex heptagonus</i> (Brocchi, 1814). SMF unreg., forma <i>wimmeri</i> Hoernes & Auinger, 1879, from its type locality, Badenian (Middle Miocene), Kosteï, near Lapugy, western Romania; H 32.3 mm.	153
6-9. <i>Monoplex jackwinorum</i> n. sp.	155
6, 8. NMB H 17932, holotype, lower shellbed, Cantaure Fm (late Early Miocene), loc. NMB 17516, Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; H 40.7 mm.	
7, 9. NMB H 17933, paratype, all data same as holotype; H 33.1 mm.	
10, 12-14, 18. <i>Monoplex lignarius</i> (Broderip, 1833)	160
10, 13. National Museum of Wales, NMW a4.23, 2 specimens, Recent, "St. Helena" [wrong; = Cabo Santa Elena, Costa Rica or, more probably, Bahia Santa Elena, Ecuador] (Fig. 10, H 26.1 mm; Fig. 13, H 27.1 mm).	
12. NMB H 6169, holotype of <i>Cymatium</i> (<i>Ranularia</i>) <i>kugleri</i> Rutsch, 1942, Springvale Fm (Early Pliocene), Springvale Quarry, Trinidad; H 21.7 mm.	
14. NMB H 17948, Mataruca Member, Caujarao Fm (Late Miocene), loc. NMB 13112, Cementario de Carrizal, E of La Vela, N Venezuela; H 24.3 mm.	
18. BMNH 1968528a, lectotype, Recent, type locality here designated as Pacific Panama, ex Cuming collection; H 32.1 mm.	
11, 15-17, 19-20. <i>Monoplex gatunicus</i> n. sp. Paratypes, from Gatun Fm (Late Miocene), Atlantic Panama.	153
11. USNM 542200, loc. USGS 22016, 100 m N of Transisthmian Highway and 75 m W of refinery road, immediately E of Cativa, Colon; H 25.9 mm.	
15, 20. California Academy of Sciences Geology, CAS 60189, 1.5 km NW of Sabanita, Colon; H 25.6 mm.	
16-17. California Academy of Sciences Geology, CAS 70835, loc. 9A-B2-407, hill due N of Sabanita, Colon; H 31.4 mm.	
19. USNM 542201, loc. USGS 22019, top of hill NE of refinery gate, Isla Payardi, Colon; H 20.5 mm.	



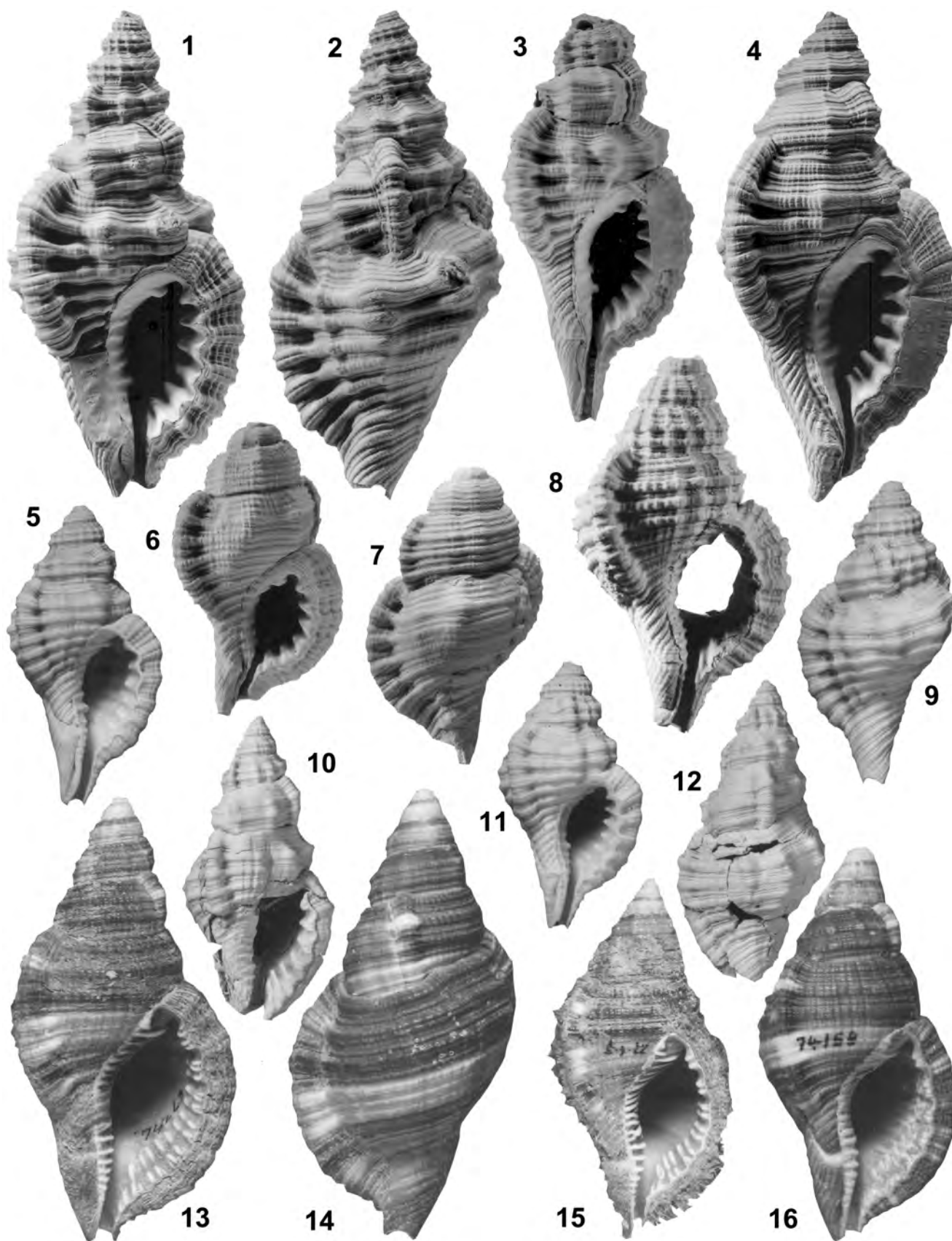


PLATE 38

Figure	Page
1-5, 8-12. <i>Monoplex krebssii</i> (Mörch, 1877)	157
1-3. NMB H 17938-17939, 2 specimens, Moín Fm (latest Pliocene-Early Pleistocene), loc. TU 1240 (= NMB 19008), hill top on Calle King Fish in Barrio los Corales 2, 1.4 km N of Standard Fruit Company box factory, which is 2 km W of Puerto Limón, Atlantic Costa Rica (Figs 1-2, H 58.8 mm; Fig. 3, H 49.8 mm).	
4. NMB H 17937, Gurabo Fm (Late Miocene/Early Pliocene), loc. TU 1231 (= NMB 19006), float near ford on Los Quemados-Sabaneta road, Río Gurabo, Dominican Republic; H 59.4 mm.	
5, 9, 11. USNM 518535, 2 specimens, Recent, Chaguaramas Bay, Trinidad (the common, immature form; Figs 5,9, H 37.3 mm; Fig. 11, H 33.0 mm).	
8. NMB H 17940, Chipola Fm (late Early Miocene), loc. TU 951 (= NMB 17594), Tenmile Creek, Chipola River, Florida, USA; H 22.5 mm (<i>M. cf. krebssii</i> , incomplete juvenile).	
10, 12. USNM 562584, holotype of <i>Cymatium pileare benicum</i> Woodring, 1959, Gatun Fm (Middle or Late Miocene), Stanford University loc. 2611, Transisthmian Highway, Atlantic Panama; H 53.7 mm.	
6-7. <i>Monoplex gatunicus</i> n. sp. NMB H 17941, paratype, Gatun Fm (Late Miocene), loc. NMB 17643, 100 m SE of refinery gates, Isla Payardi, Colon, Atlantic Panama; H 26.9 mm.	153
13-16. <i>Monoplex macrodon</i> (Valenciennes, 1832)	162
13-14. AMNH 74263, neotype, Recent, Puritan Expedition sta. 35, Isla San Juanito, Islas Tres Marias, Nayarit, Mexico; H 81.3 mm.	
15. LACM 72-63, Recent, 8-12 m, N side of Isla del Caño, Puntarenas Province, Pacific Costa Rica; H 64.6 mm.	
16. AMNH 74158, Recent, Puritan Expedition sta. 27, Isla Maria Madre, Islas Tres Marias, Nayarit, Mexico; H 71.0 mm.	

PLATE 39

Figure	Page
1-13, 15, 18. <i>Monoplex pilearis</i> (Linnaeus, 1758)	169
1-2. NMB H 17943, Gurabo Fm (Early Pliocene), loc. NMB 15844, bluff 150 m upstream from small side stream, Río Gurabo, Dominican Republic; H 42.9 mm.	
3-4. NMB H 17942, Gurabo Fm (Early Pliocene), loc. TU 1212 (= NMB 19004), third bluff below ford on Los Quemados-Sabaneta road, Río Gurabo, Dominican Republic; H 37.2 mm.	
5, 10. BMNH 1854.10.4.409, lectotype of <i>Triton martinianum</i> d'Orbigny, 1841, Recent, "Cuba, St Lucia, Guadeloupe," West Indies; H 36.0 mm.	
6-7, 12, 15. USNM 530190, 3 specimens, Recent, St. Thomas, West Indies (Figs 6-7, H 50.0 mm; Fig. 12, H 50.3 mm; Fig. 15, H 72.4 mm).	
8. USNM 767929, Recent, Freeport area, Monrovia, Liberia, West Africa; H 47.8 mm.	
9, 13. BMNH Palaeontology Department, G10928, 2 specimens, Coral Rock (Pleistocene), Barbados (Fig. 9, H 54.5 mm; Fig. 13, H 45.9 mm).	
11. USNM 94367a, Recent, Bermuda; H 41.9 mm.	
18. NMB H 18044, Holocene, loc. NMB 10663, Simpsons Point, near Point-a-Pierre, Trinidad; H 72.5 mm.	
14, 16-17. <i>Monoplex mundus</i> (Gould, 1849)	162
14. MNHN unreg., Recent, Expédition Montrouzier sta. 1237, Baie de Touho, New Caledonia; H 22.4 mm (see also Pl. 41, Fig. 5).	
16-17. Specimen in collection of K. Sunderland, Recent, 180-360 m, off of Key West, S of Dry Tortugas, Florida, USA; H 39.0 mm.	

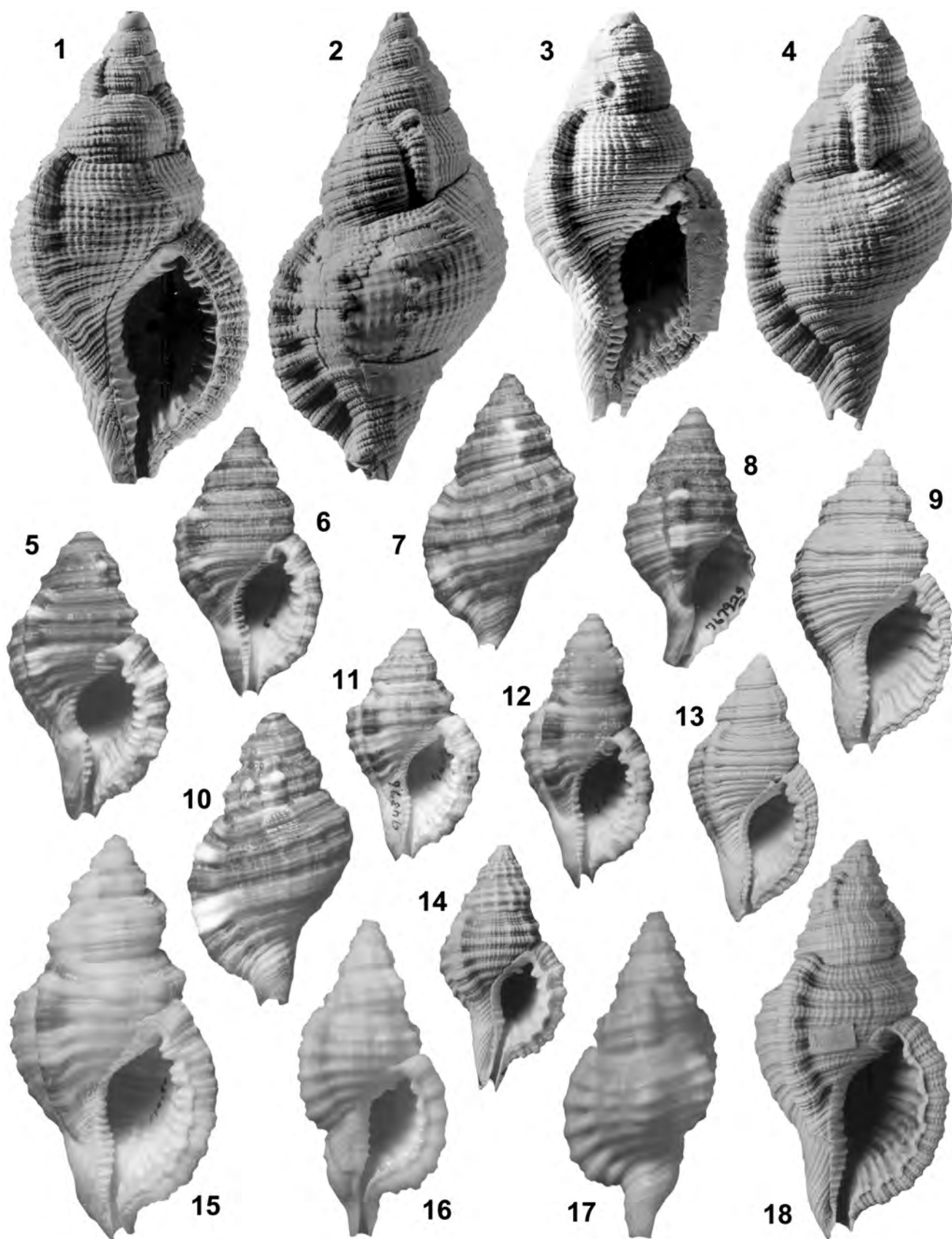




PLATE 40

Figure		Page
1, 3, 5, 7.	<i>Monoplex panamensis</i> n. sp.	165
	1, 3. NMB H 17944, holotype, Tuirá Fm (Late Miocene), loc. NMB 18503, Río Chico, 2 km below confluence with Río Cubilele, Darien, Pacific Panama; H 65.0 mm.	
	5, 7. NMB H 17945, paratype, Tuirá Fm (Late Miocene), loc. NMB 18502, Río Chico, 1 km downstream from confluence with Río Cubilele, Darien, Pacific Panama; H 44.8 mm.	
2, 8-9.	<i>Monoplex parthenopeus</i> (von Salis Marschlins, 1793)	166
	2. NMB H 17950, Mao Adentro Limestone (Early Pliocene), loc. TU 1281 (= NMB 19012), road metal quarry S side Río Yaque del Norte, Mao-Guayubin Road 1 km E of Guayubin, Dominican Republic; H 33.4 mm.	
	8. NMB H 17949, Bowden Shellbed (Late Pliocene), loc. NMB 10635, Bowden, Jamaica; H 36.3 mm.	
	9. Specimen in collection of D. Lamy, Recent, Guadeloupe, West Indies; H 173.2 mm.	
4, 6.	<i>Monoplex mundus</i> (Gould, 1849)	162
	4. USNM unreg., late Pleistocene terrace, loc. USGS 18381, near airport, Pine, Barbados, West Indies; H 20.0 mm.	
	6. GNS WM 15552, Recent, Tryon Island, Capricorn Group, Queensland, Australia; H 47.3 mm.	

PLATE 4I

Figure		Page
1, 5.	<i>Monoplex mundus</i> (Gould, 1849)	162
	1. GNS WM15228, Recent, S end of Lake Worth, Florida, USA, ex D'Attilio collection; H 24.8 mm.	
	5. MNHN unreg., Expédition Montrouzier sta. 1237, Baie de Touho, New Caledonia; H 26.9 mm (see also Pl. 39, Fig. 14).	
2, 4.	<i>Monoplex parthenopeus</i> (von Salis Marschlins, 1793)	166
	2. USNM 644661, holotype of <i>Cymatium (Linatella) valentinei</i> Olsson & Petit, 1964, Pinecrest Fm (middle Pliocene), Slough Ditch, N of Hwy 10, Brighton, Highlands County, Florida, USA; H 119.8 mm.	
	4. BMNH 1854.12.4.525a, lectotype of <i>Triton americanum</i> d'Orbigny, 1841, Recent, Río de Janeiro, Brazil; H 94.5 mm (specimen nearest to d'Orbigny's figure, but not agreeing in detail).	
3, 6-7.	<i>Monoplex keenae</i> (Beu, 1970). LACM 74-6, 2 specimens, Recent, 1.5-9 m, Isla Lobos de Afuera, Peru (Fig. 3, H 91.5 mm; Figs 6-7, H 127.8 mm).	156



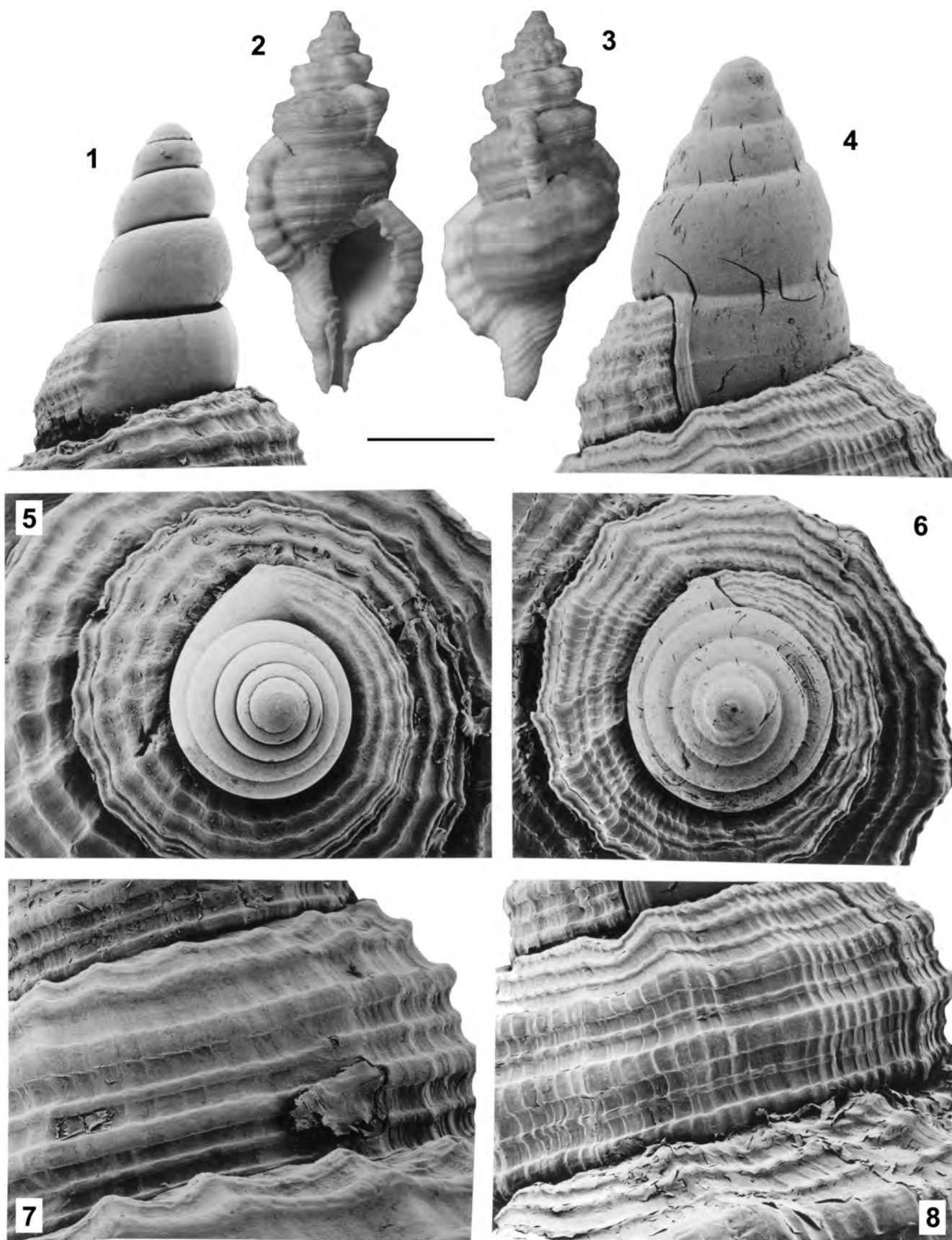
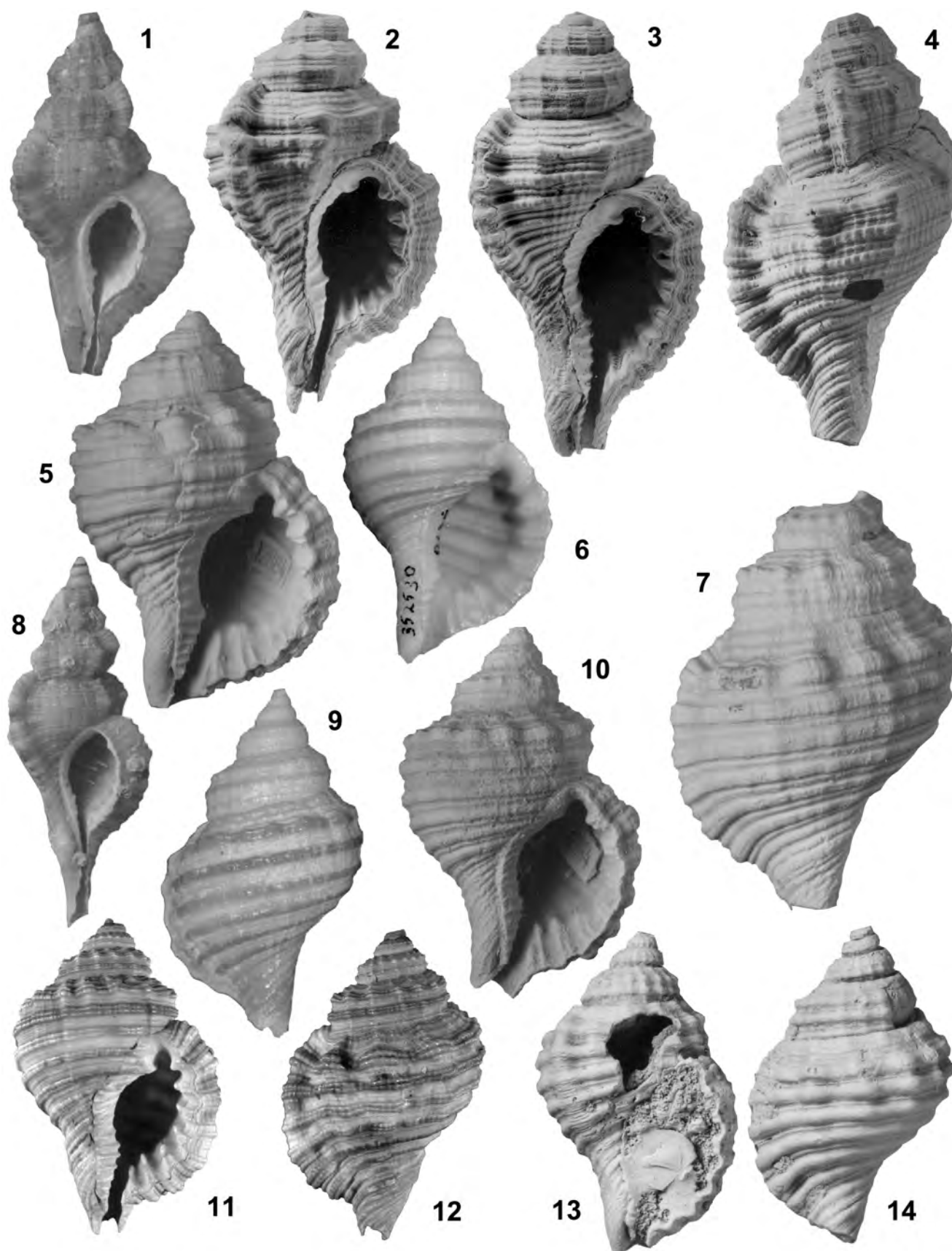


PLATE 42

Figure	Page
1, 5, 7. <i>Monoplex parthenopeus</i> (von Salis Marschlins, 1793). GNS WM11102, Recent, beach, Boydtown, Twofold Bay, S New South Wales, Australia; SEM micrographs of spire apex and protoconch; scale bar = 1 mm (applies to all photomicrographs).	166
2-4, 6, 8. <i>Monoplex turtoni</i> (E. A. Smith, 1890)	176
2-3. BMNH 1889.10.1.2435, lectotype, Recent, St. Helena, South Atlantic; H 47.0 mm.	
4, 6, 8. BMNH 1889.10.1.2439, juvenile paralectotype, Recent, St. Helena; SEM micrographs of protoconch and spire apex; scale bar = 1 mm (applies to all photomicrographs).	

PLATE 43

Figure	Page
1, 8. <i>Turritriton tenuiliratus</i> (Lischke, 1873)	197
1. USNM 94887, holotype of <i>Lampusia? pharcidum</i> Dall, 1908, Recent, <i>Blake</i> sta. 293, 150 m, off of Barbados, West Indies; H 23.6 mm.	
8. RMNH unreg., Recent, <i>Luymes</i> Guyana Shelf Expedition sta. 1, 130-104 m, 7°10'N, 53°35'W, off of Suriname; H 26.1 mm.	
2-4. <i>Monoplex ritteri</i> (Schmelz, 1989). NMB H 17951-17952, 2 specimens, lower shellbed, Cantaure Fm (late Early Miocene), loc. NMB 17516, near Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela (Fig. 2, H 36.6 mm; Figs 3-4, H 39.4 mm).	172
5-7, 9-14. <i>Monoplex tranquebaricus</i> (Lamarck, 1816)	173
5, 7, 10. NMB H 18046-18048, 3 specimens, Castillo de Araya Fm (Pleistocene), loc. NMB 12884, Quebrada Araya, Araya Peninsula, Venezuela (Fig. 5, H 47.5 mm; Fig. 7, H 50.2 mm; Fig. 10, H 44.8 mm).	
6, 9. ANSP 352530, Recent, shrimp net, 48 m, NW of Loggerhead Light, Dry Tortugas, Florida, USA; H 52.1 mm.	
11-12. MHNG 979/332, holotype, Recent, "Oc. Indien" [= West Africa; type locality designated here as Île Gorée, Sénégal]; H 39.8 mm (from a color transparency).	
13-14. USNM unreg., "Miocene" (Plio-Pleistocene?), loc. USGS 11520, limestone scarp <i>ca.</i> 1.5 miles NW of Las Perdices, Departamento de Atlantico, Colombia; H 38.7 mm.	



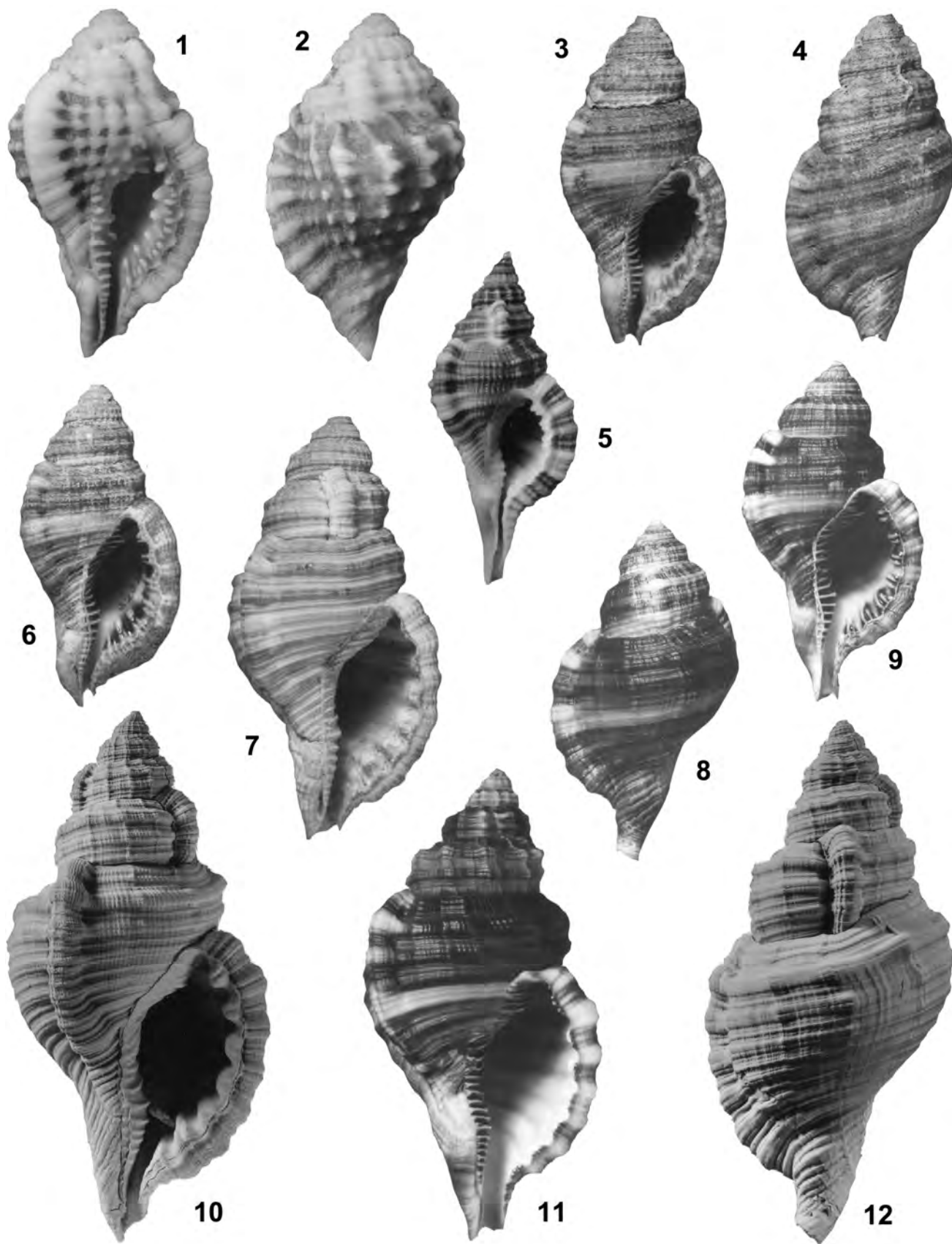
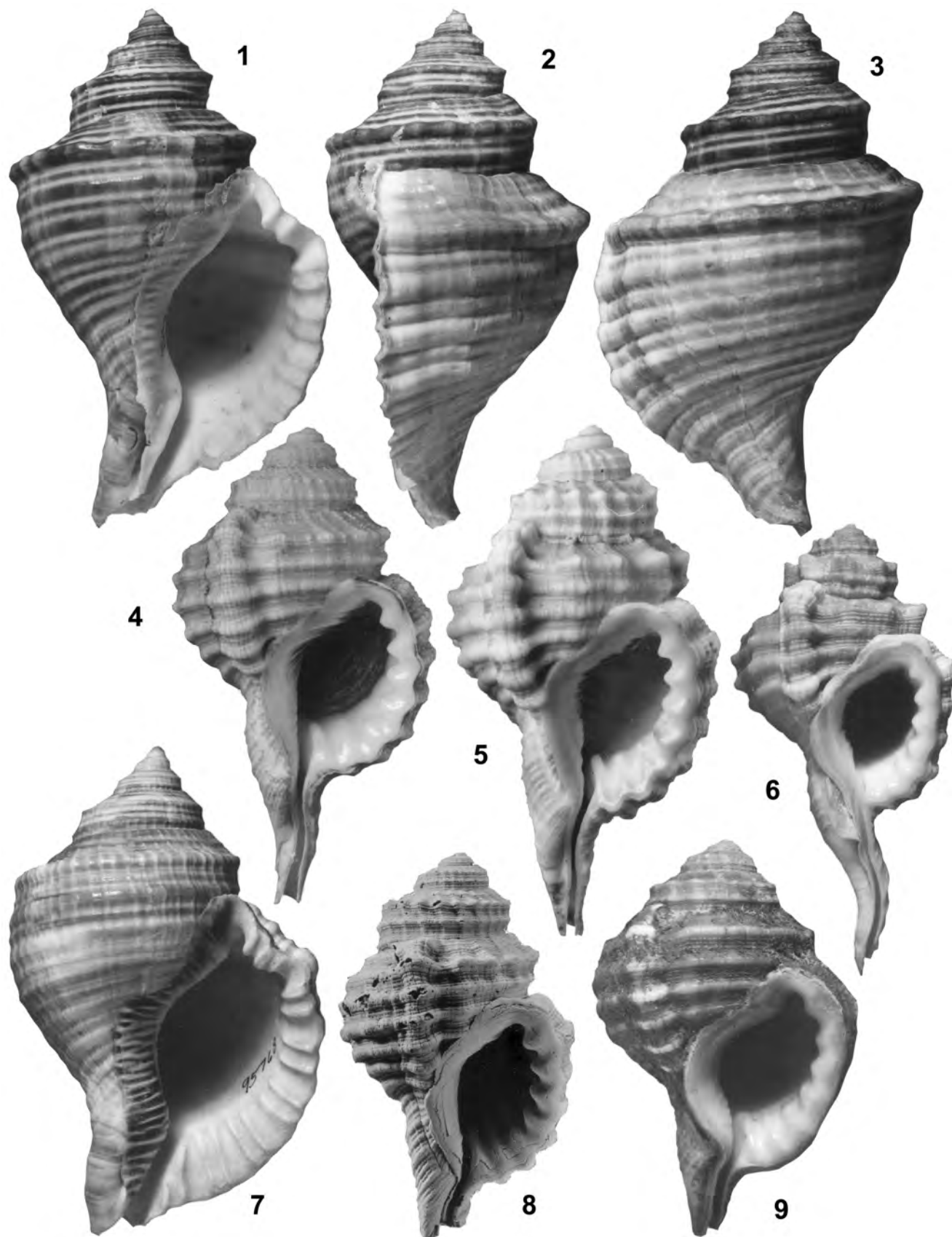


PLATE 44

Figure		Page
1-2.	<i>Monoplex trigonus</i> (Gmelin, 1791). BMNH 1983099, specimen illustrated by F. J. & W. Gibson-Smith (1970), Recent, beach, Camuri Grande, Distrito Federal, Venezuela; H 42 mm.	175
3-4, 6-12.	<i>Monoplex vestitus</i> (Hinds, 1844)	178
	3-4. Neotype of <i>Triton vestitum</i> Hinds and of <i>T. vestitum</i> var. <i>senior</i> C. B. Adams, 1852, USNM 32329, Recent, Islas Tres Marias, Nayarit, Mexico, ex Stearns collection; H 59.7 mm.	
	6. USNM 32330, Recent, W coast of Panama, ex Stearns collection; H 58.4 mm.	
	7. USNM 36631, Recent, W coast of Panama; H 75.9 mm.	
	8-9. Specimen formerly in collection of S. D. Kaicher [present location unknown, not at ANSP], Recent, Pedro Gonzales Island, Perlas Islands, Pacific Panama; H 62.0 mm.	
	10, 12. NMB H 17928, Armuelles Fm (Pleistocene), loc. NMB 17441, float, Rio Rabo de Puerco, W of Puerto Armuelles, Pacific Panama; H 95.5 mm.	
	11. GNS WM13828, Recent, Pedro Gonzales Island, Perlas Islands, Pacific Panama; H 85.1 mm.	
5.	<i>Monoplex vespaceus</i> (Lamarck, 1822), specimen in collection of B. J. Piech (now owned by K. Piech), Recent, Roatan Island, Atlantic Honduras; H 41 mm.	176

PLATE 45

Figure	Page
1-3, 7. <i>Monoplex wiegmanni</i> (Anton, 1838)	179
1-3. LACM 23202, Recent, western Panama; H 94.5 mm.	
7. LACM 95768, Recent, Changame Island, Panama Bay; H 87.0 mm.	
4-6, 8-9. <i>Ranularia cynocephalum</i> (Lamarck, 1816)	181
4. BMNH 1967632/1, one of 3 syntypes of <i>Triton moritinctus</i> Reeve, 1844, Recent, "Philippines" [wrong, East Africa or western Atlantic; type locality here designated as Bahia, Brazil]; H 69.2 mm (smallest syntype, nearest to Reeve's figure, although none matches it exactly).	
5. Specimen in collection of D. Lamy, Recent, Martinique, West Indies; H 93.1 mm.	
6. Specimen in collection of D. Peled, Recent, off of Mombassa, Kenya, East Africa; H 82.5 mm.	
8. NMB H 17953, El Manglillo Fm (Pleistocene), loc. NMB 17563, El Manglillo, S coast of Isla Margarita, Venezuela; H 70.0 mm.	
9. Specimen in collection of D. Peled, Recent, fishermen's nets off of Somalia, East Africa; H 72.2 mm ("smooth form").	



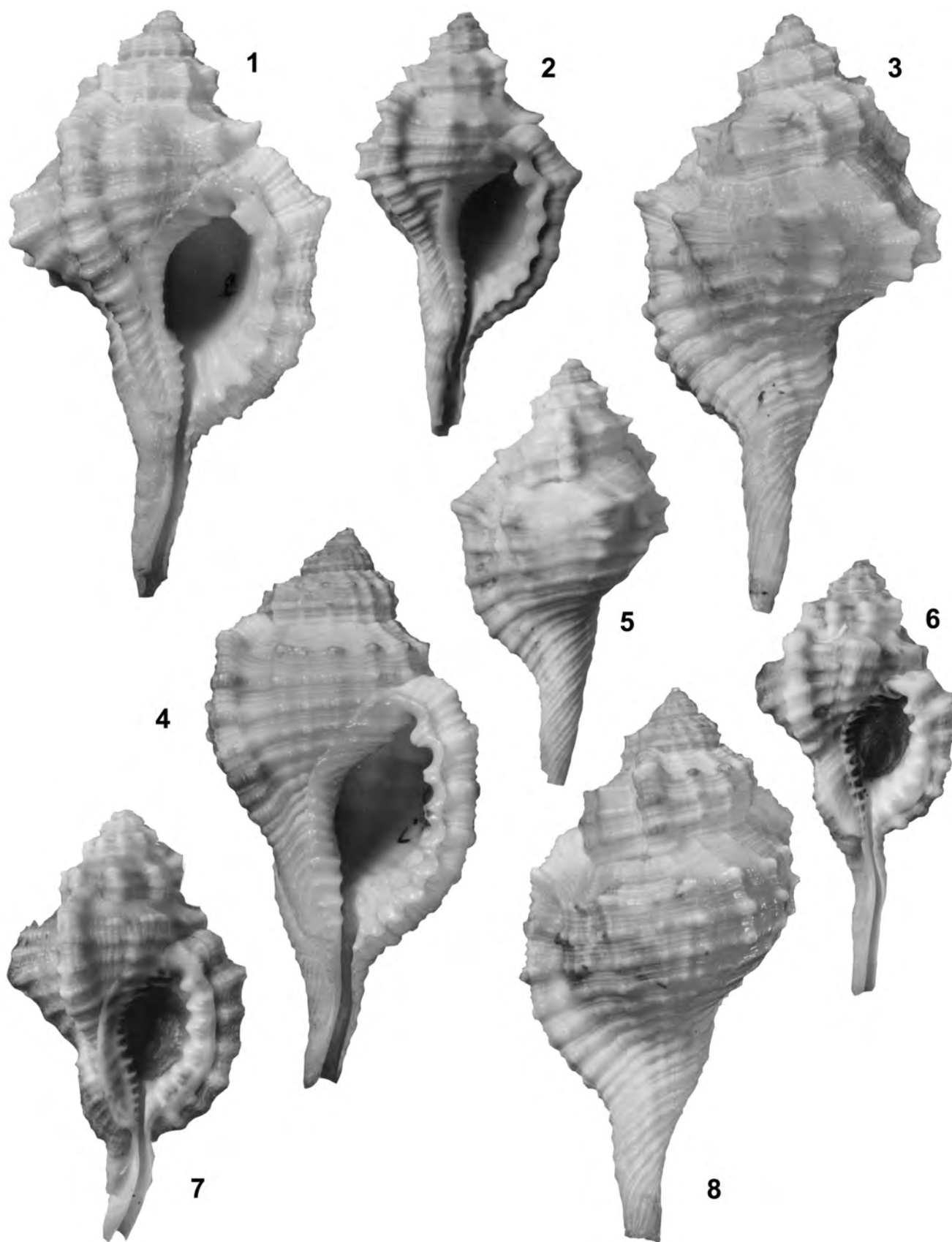
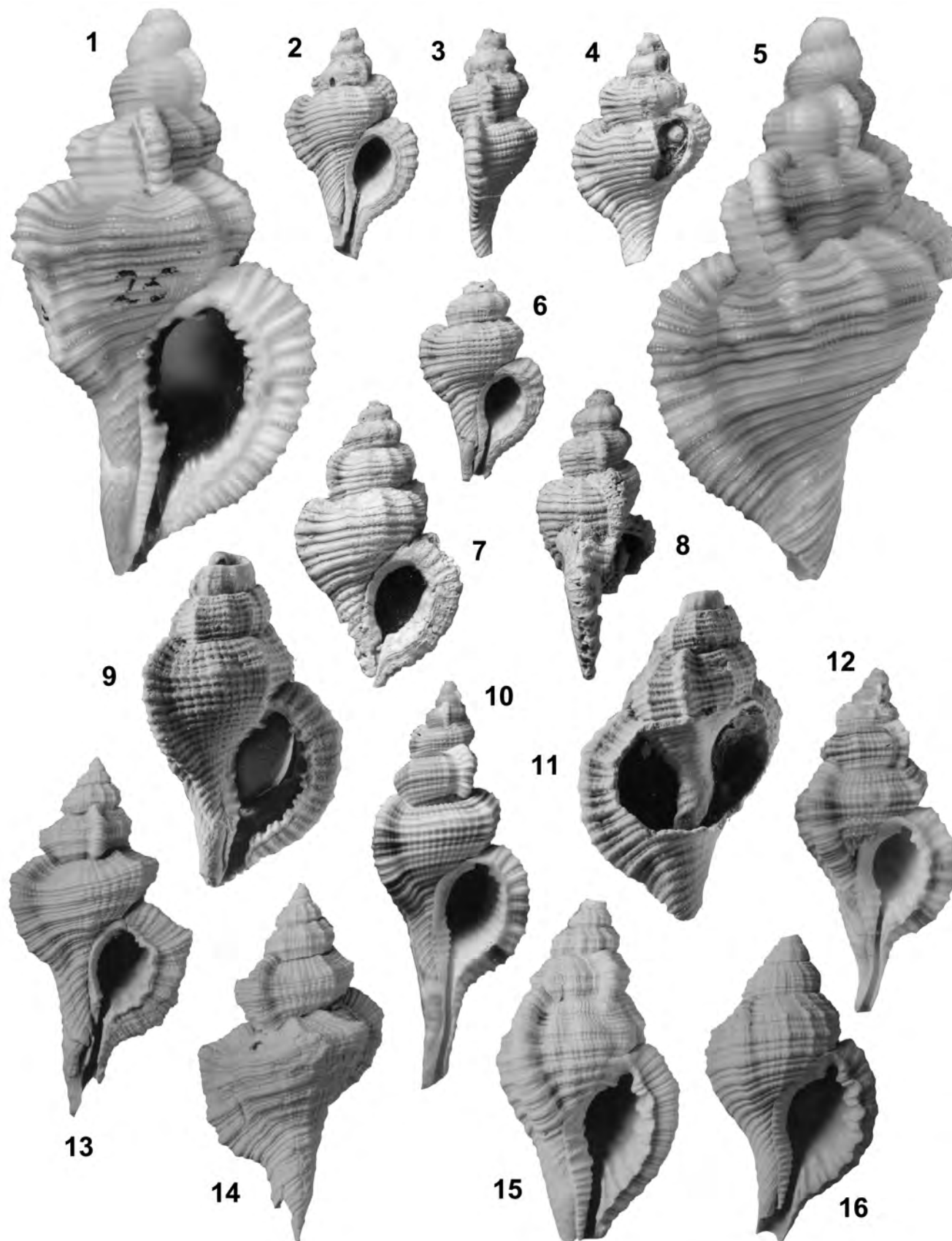


PLATE 46

Figure		Page
1-5, 8.	<i>Ranularia gallinago</i> (Reeve, 1844)	183
	1, 3. BMNH 1967593, lectotype, Recent, "Cagayan, Province of Misamis, Island of Mindanao, Philippines" [wrong, W Indian Ocean; type locality here designated as Mauritius], ex Cuming collection; H 60.0 mm.	
	2, 5. Specimen in collection of B. J. Piech [now owned by K. Piech], Recent, Todos Santos Bay, Salvador, Bahia, Brazil; H 61.5 mm.	
	4, 8. BMNH 1967628, lectotype of <i>Triton aegrotus</i> Reeve, 1844, Recent, "China" [wrong, W Indian Ocean; type locality here designated as Mauritius], ex Cuming collection; H 48.0 mm.	
6-7.	<i>Ranularia rehderi</i> (Verrill, 1950). Two specimens in collection of D. Lamy, collected together, Recent, Guadeloupe, West Indies (Fig. 6, male, H 62.6 mm; Fig. 7, female, H 62.7 mm). . . .	184

PLATE 47

Figure		Page
1, 5.	<i>Reticutriton lineatus</i> (Broderip, 1833). BMNH 1968526, one of 2 syntypes, Recent, Galápagos Islands, ex Cuming collection; H 57.1 mm.	187
2-4, 6-8.	<i>Reticutriton elsmereensis</i> (English, 1914). LACM IP unreg., 3 specimens, San Diego Fm (Pliocene), loc. LACM IP 305, Alpha oil field, 100 m from Mexican border fence, K Ranch, Tijuana River basin, San Diego County, California, USA (Figs 2-4, H 27.3 mm; Fig. 6, H 23.9 mm; Figs 7-8, H 36.0 mm).	186
9, 11.	<i>Reticutriton</i> n. sp.? NMB H 17954, upper shellbed, Cantaure Fm (late Early Miocene), loc. NMB 17520, near Casa Cantaure, Paraguaná Peninsula, Venezuela; H 15.2 mm.	188
10, 12.	<i>Reticutriton pfeifferianus</i> (Reeve, 1844)	187
	10. GNS WM13877, Recent, trawled, Gulf of Carpentaria, N Australia, H 73.7 mm.	
	12. GNS WM13844, Recent, shrimp nets, 60 m, off of Tanabe, Wakayama Prefecture, Japan; H 61.3 mm.	
13-14.	<i>Turritriton gibbosus</i> (Broderip, 1833). BMNH Palaeontology Department, GG22584, lower Gatun Fm (Middle Miocene), quarry floor, Los Lomos Suites, Cativa, Colon, Atlantic Panama, coll. J. Todd, 1999; H 32.4 mm.	194
15.	<i>Monoplex krebsii</i> (Mörch, 1877). BMNH Palaeontology Department, GG22582, lower Gatun Fm (Middle Miocene), "Sand Dollar hill," Sabanita, Colon, Atlantic Panama, coll. J. Todd, 1999; H 31.0 mm.	157
16.	<i>Monoplex cercadicus</i> (Maury, 1917). BMNH Palaeontology Department, GG22580, lower Gatun Fm (Middle Miocene), <i>ex situ</i> , Los Lomos Suites, Cativa, Colon, Atlantic Panama; H 45.5 mm.	148



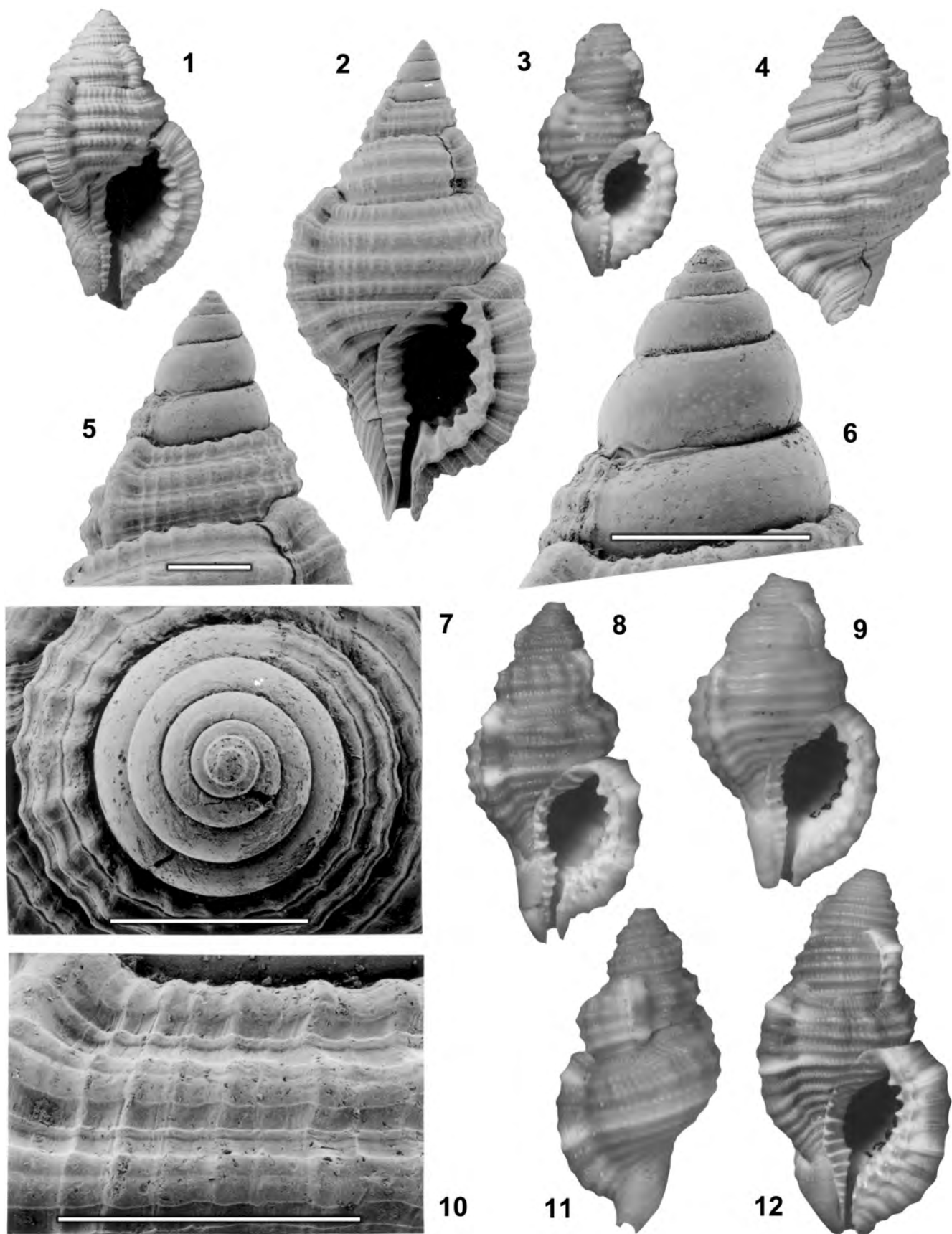
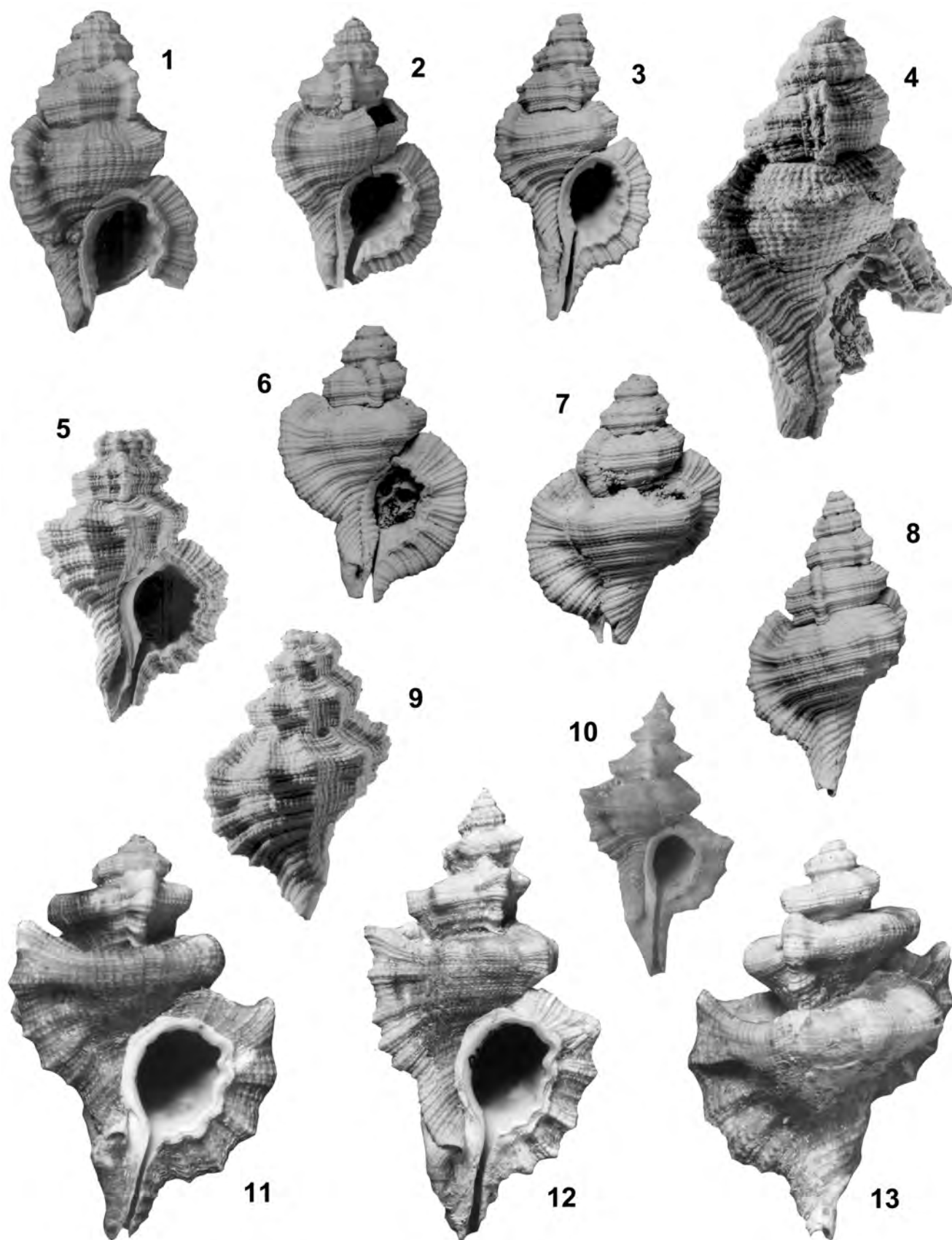


PLATE 48

Figure	Page
1, 2, 4-7, 10. <i>Septa landaui</i> n. sp.	189
1, 4. NMB H 17955, holotype, Gurabo Fm (Early Pliocene), loc. TU 1214 (= NMB 19005), fifth to eighth bluffs downstream from ford on Los Quemados-Sabaneta road, Río Gurabo, Dominican Republic; H 37.1 mm.	
2, 5-7, 10. NMB H 17956, paratype, Baitoa Fm (late Early Miocene), loc. TU 1364 (= NMB 18560), downstream from waterfall in Arroyo Hondo, Boca de los Rios, downstream from Baitoa, Río Yaque del Norte, Dominican Republic; SEM micrographs of entire specimen (Fig. 2, H 20.6 mm), protoconch and spire apex, and sculpture of first teleoconch whorl; all scale bars = 1 mm.	
3, 8-9, 11-12. <i>Septa occidentalis</i> (Mörch, 1877)	190
3. USNM 417842, Recent, Cable House, Guantanamo, Cuba; H 31.0 mm.	
8, 11. TFM C 520, Recent, La Palma, Canary Islands; H 41.0 mm.	
9. AMS C.60662, holotype of <i>Septa? blacketi</i> Iredale, 1936, Recent, Nielsen Park, Watson's Bay, Sydney Harbor, Australia; H 38.8 mm.	
12. GNS WM13668, Recent, Samar Island, Philippines; H 45.8 mm.	

PLATE 49

Figure		Page
1-4, 8.	<i>Turritriton domingensis</i> (Gabb, 1873)	193
	1. ANSPIP 3226, lectotype, Late Miocene or Early Pliocene, Cibao Valley, Dominican Republic, ex W. M. Gabb collection; H 29.0 mm.	
	2. ANSPIP 79195, paralectotype, all data same as lectotype; H 25.0 mm.	
	3, 8. NMB H 18054, Cercado Fm (Late Miocene), loc. NMB 16916, mouth of Arroyo Bajón, upper Río Mao, Dominican Republic; H 27.8 mm.	
	4. NMB H 17962, Mataruca Member, Caujarao Fm (Late Miocene), loc. NMB 17530, Cemeterio de Carrizal, E of La Vela, Falcón, Venezuela; H 25.9 mm.	
5, 9.	<i>Turritriton labiosus</i> (Wood, 1828). NMB H 17963, Moín Fm (latest Pliocene-Early Pleistocene), loc. TU 1240 (= NMB 19008), hill top on Calle King Fish in Barrio Los Corales 2, 1.4 km N of Standard Fruit Company box factory, which is 2 km W of Puerto Limón, Atlantic Costa Rica; H 17.5 mm.	195
6-7.	<i>Turritriton</i> cf. <i>gibbosus</i> (Broderip, 1833). UCMP loc. S-71, Pliocene(?), <i>Turritella</i> bed above Point Canoas, Departamento de Bolívar, Caribbean coast of Colombia; H 24.6 mm.	194
10-13.	<i>Turritriton gibbosus</i> (Broderip, 1833)	194
	10. USNM 214103, holotype of <i>Cymatium adairense</i> Dall, 1910, Recent, U. S. Fish Commission sta. 3023, 18 m, Adair Bay, N Gulf of California, Mexico; H 32.7 mm.	
	11, 13. LACM 66-28, Recent, Partida Bay, between Isla Partida and Islas Espiritu Santo, Baja California Sur, Mexico; H 48.5 mm.	
	12. LACM 67-18, Recent, Punta Tormenta, Isla Tiburón, Sonora, Mexico; H 54.5 mm.	



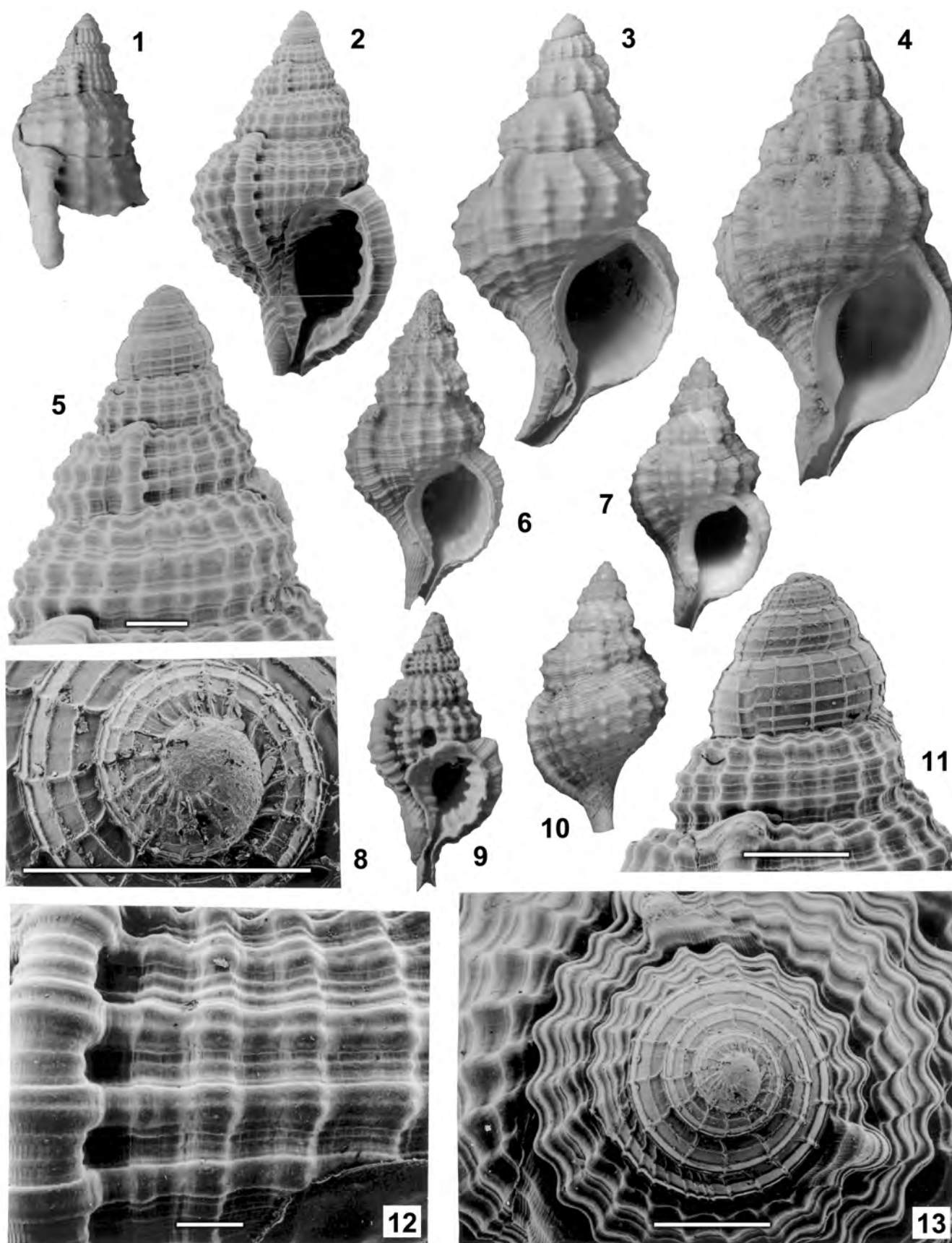
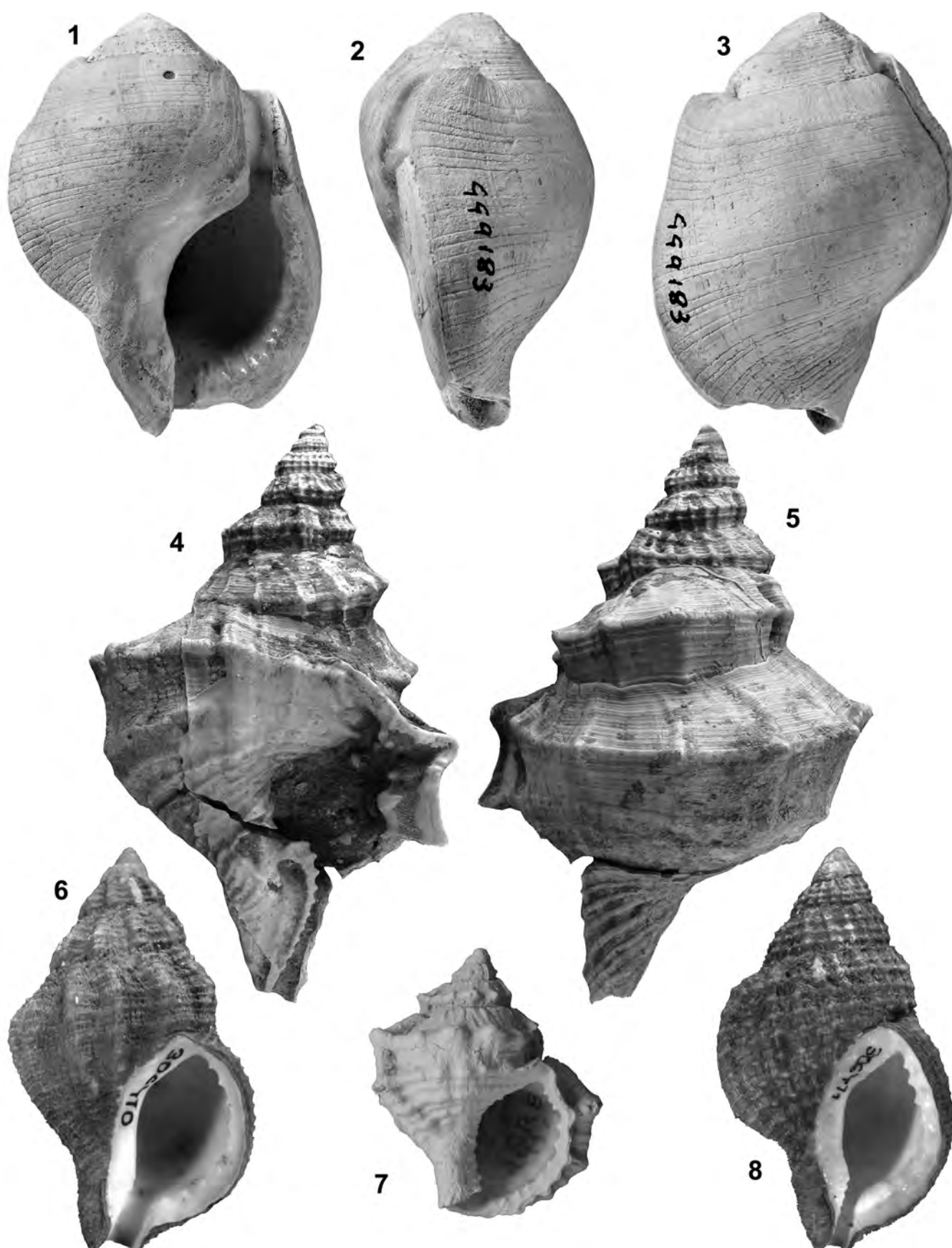


PLATE 50

Figure		Page
1.	<i>Sassia</i> cf. <i>apenninica</i> (Sassi, 1827). NMB H 18042, fragment, Kendace Siltstone Member, Belmont Fm (Middle Miocene), loc. NMB 13759, Kendace Point, Carriacou Island, Grenadine Islands, West Indies; H 25.6 mm.	199
2, 5, 8, 11-13.	<i>Sassia warreni</i> n. sp. NMB H 17964, holotype, Gurabo Fm (Early Pliocene), loc. TU 1215 (= NMB 18581), Maury's zone D, bluffs for 1 km above bridge at Los Quemados, Río Gurabo, Dominican Republic; SEM micrographs of entire specimen (Fig. 2, H 15.2 mm), spire apex and protoconch (Fig. 8 showing distinct protoconchs I and II), and sculpture of last whorl above aperture (all scale bars = 1 mm).	200
3-4.	<i>Sassia kampyla</i> (Watson, 1885)	202
	3. BMNH 1887.2.9.1246/1, lectotype, Recent, HMS <i>Challenger</i> sta. 164B, 750 m, off of Sydney, E Australia; H 39.0 mm.	
	4. BMNH 1994145, holotype of <i>Cymatona tomlini</i> Powell, 1955, Recent, BANZARE sta. 83, 69 m, Lusitania Bay, Macquarie Island; H 36.7 mm.	
6-7, 10.	<i>Sassia philomelae</i> (Watson, 1880)	204
	6. BMNH 1887.2.9.1188, one of 2 BMNH syntypes, Recent, HMS <i>Challenger</i> , 300 m, off of Nightingale Island, Tristan da Cunha Group, South Atlantic; H 29.0 mm.	
	7, 10. USNM 118764, syntype, all data same as for Fig. 6; H 24.6 mm.	
9.	<i>Sassia lewisi</i> Harasewych & Petuch, 1980. Specimen in collection of B. J. Piech [now owned by K. Piech], Recent, fish traps in 100 m, off Sandy Lane, Barbados, West Indies; H 17.0 mm.	200

PLATE 5 I

Figure		Page
1-3.	<i>Aspa marginata</i> (Gmelin, 1791). BMNH Palaeontology Department, GG9183a, neotype (designated here) of <i>Murex marginatus</i> Gmelin, 1791, of <i>Ranella laevigata</i> Lamarck, 1822, and of <i>Eione inflata</i> Risso, 1826, Asti sand beds (late Zanclean-early Piacenzian, Pliocene), Valle Andona, near Torino, Italy; H 39.6 mm.	66
4-5.	<i>Distorsio biangulata</i> n. sp. Paratype in collection of Bernard Landau, Cantaure Fm (late Early Miocene), near Casa Cantaure, Paraguana Peninsula, Falcón, Venezuela; H 71.0 mm.	80
6, 8.	<i>Priene scabrum</i> (King, 1832) 109 6. SMF 306410/1, probable syntype of <i>Triton rudis</i> Broderip, 1833, Recent, Peru, ex Cuming collection; H 35.2 mm. 8. SMF 306411/1, probable syntype, Recent, Valparaíso, Chile, ex Cuming collection; H 47.4 mm.	
7.	<i>Crossata ventricosa</i> (Broderip, 1833). BMNH Palaeontology Department unreg., Onzole Fm (Early Pliocene), loc. CRB 291, Quebrada Camarones, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town, Ecuador; H 23.4 mm.	68



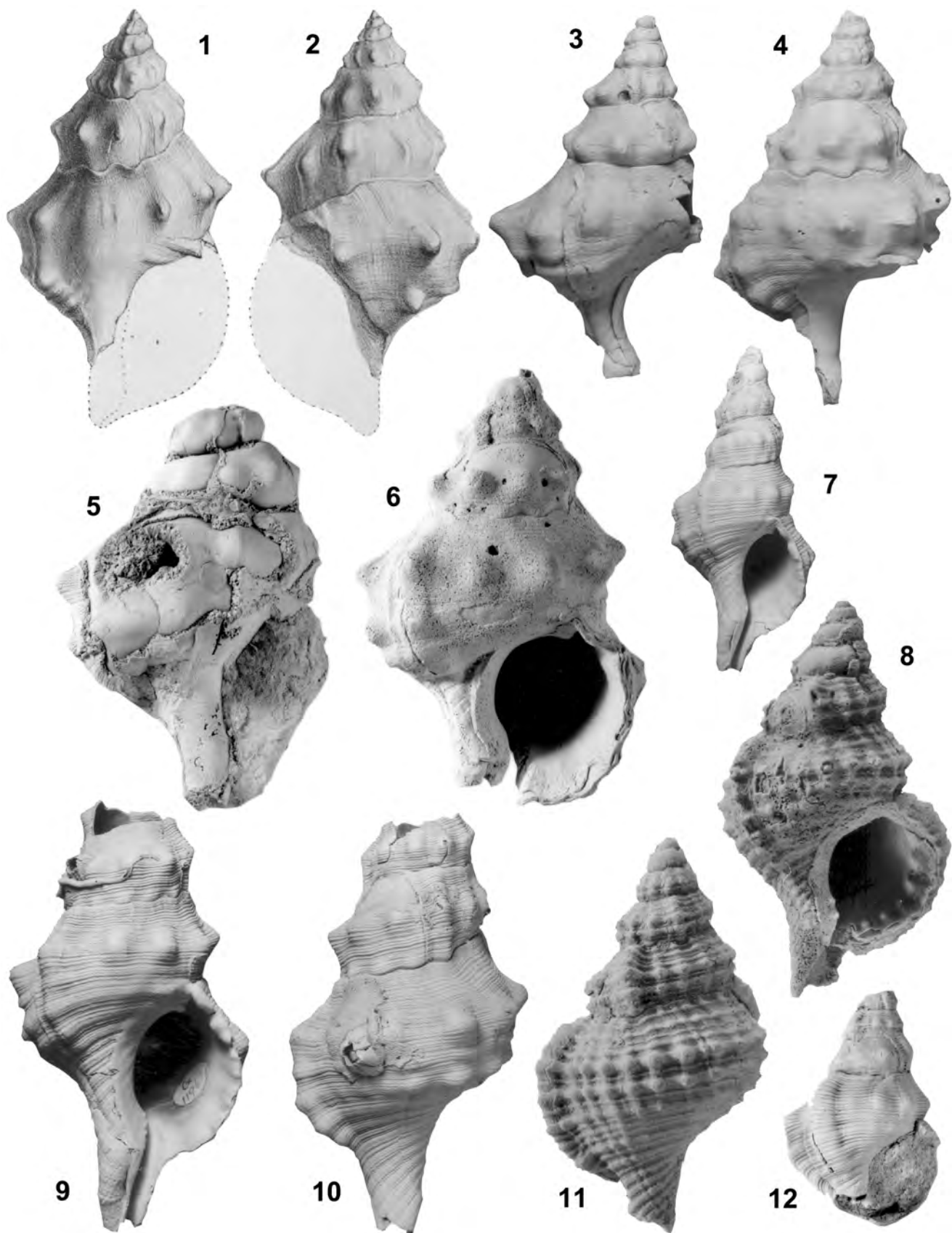
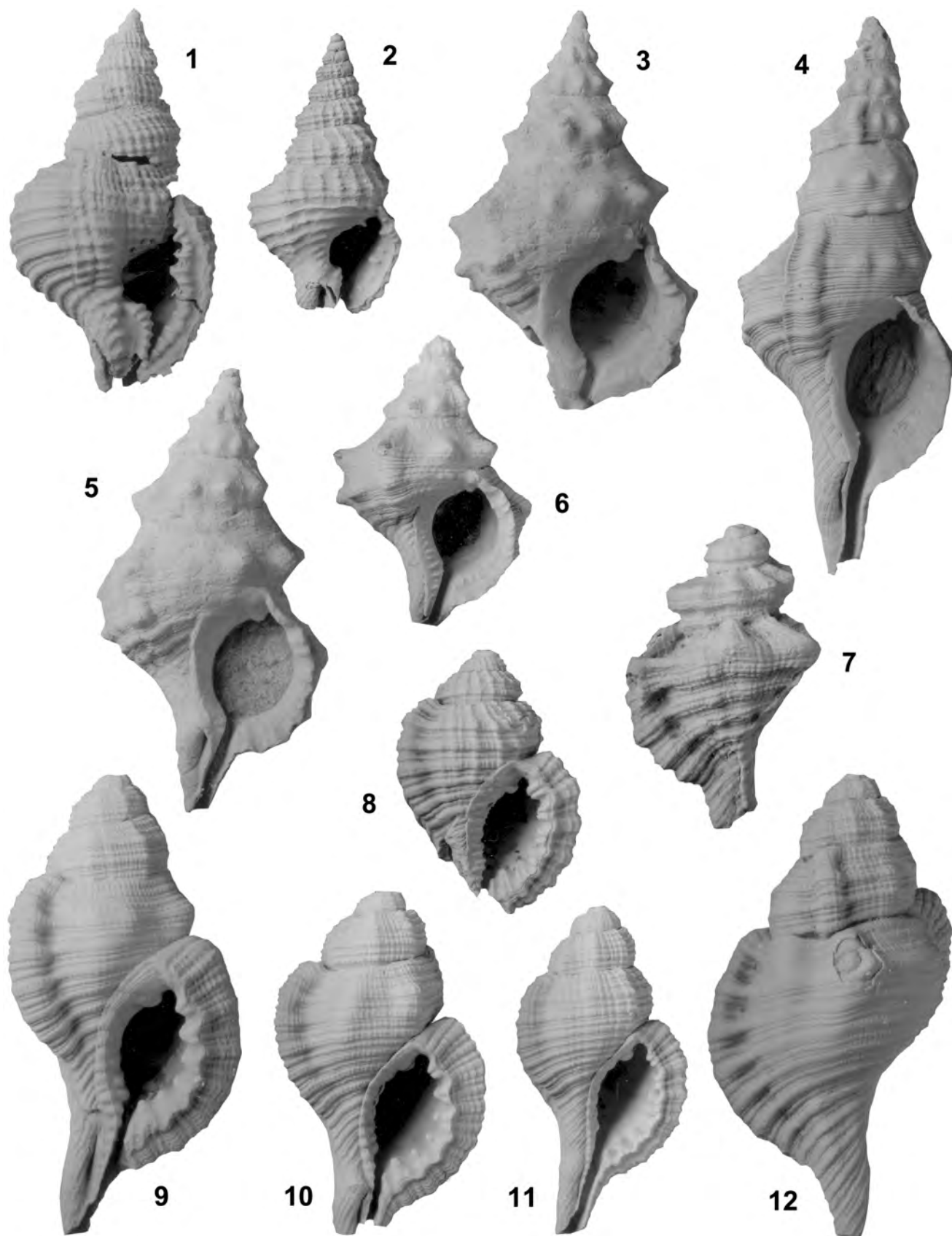


PLATE 52

Figure	Page
1-6, 12. <i>Sassia armata</i> (Hupé, 1854)	205
1-2. Hupé's (1854: Conquiliogia pl. 3, fig. 1) original illustration of <i>Triton armatus</i> , from "Coquimbo," Pliocene [actually from Navidad Fm (Late Oligocene-Early Miocene fossils reworked into Late Miocene-Early Pliocene rocks), near Navidad, Chile]; H 65.1 mm (specimen in Département de l'Histoire de la Terre, MNHN, Gg2001/21).	
3-4. Formerly at Department of Earth and Atmospheric Sciences, Purdue University, now at PRI, PU.P 675a, b, specimens mentioned and illustrated (PU.P 675a; Fig. 4) by Ortmann (1902: 206, pl. 33, fig. 15), Mount Entrance Member, Monte Leon Fm (Late Oligocene/Early Miocene), bluff on S side of Santa Cruz River a short distance upstream from the mouth, Patagonia, Argentina (Fig. 3, H 67.9 mm; Fig. 4, H 74.8 mm).	
5. MACN, Ihering type collection 845a, holotype of <i>Siphonalia matthewsi</i> Ihering, 1914, Chenque Fm (Late Oligocene/Early Miocene), Golfo San Jorge, Patagonia, Argentina; H 74.1 mm (photo M. Griffin).	
6. MACN, Ihering type collection 790, holotype of <i>Tritonium bicegoi</i> Ihering, 1897, Mount Entrance Member, Monte Leon Fm (Late Oligocene/Early Miocene), bluff on S side of Santa Cruz River a short distance upstream from the mouth, Patagonia, Argentina; H 78.9 mm (photo M. Griffin).	
12. MACN, Ihering type collection 790, paratype of <i>Tritonium bicegoi</i> , same data as for holotype; H 42.9 mm (photo M. Griffin).	
7, 9-10. <i>Sassia morgani</i> (Ortmann, 1900)	206
7. Formerly at Department of Earth and Planetary Sciences, Purdue University, now at PRI, PU.P 676, holotype, Monte Leon Fm (Late Oligocene/Early Miocene), "mouth of the Santa Cruz River," Patagonia, Argentina [probably actually from Monte Leon Beach, 40 km further south]; H 62.3 mm.	
9-10. BMNH Palaeontology Department, G11963, Monte Leon Fm (Late Oligocene/Early Miocene), Monte Leon Beach, 40 km S of Santa Cruz River mouth, Patagonia, Argentina; H 77.4 mm.	
8, 11. <i>Sassia leucostomoides</i> (G. B. Sowerby I, 1846). GNS WM15954, Pliocene, Estero Tres Calles Bay, Isla Guafo, S Chile; H 24.4 mm.	207

PLATE 53

Figure	Page
1. <i>Distorsio</i> n. sp.? A. NMB H 18037, Onzole Fm (Pliocene), loc. NMB 19084, downstream from Picaderos village, Río Santiago, Borbón, Esmeraldas Province, Ecuador; H 69.0 mm.	88
2. <i>Distorsio</i> n. sp.? B. SGO.PI 6450, from Navidad Fm (Late Oligocene-Early Miocene fossils reworked into Late Miocene-Pliocene rocks), S. Nielsen's loc. PPN, sandy facies on coast just S of Punta Perro, S of mouth of Río Rapel, Navidad, Chile; H 33.4 mm.	96
3, 5-6. <i>Sassia armata</i> (Hupé, 1854). SGO.PI 6447-6448, from Navidad Fm (Late Oligocene-Early Miocene fossils reworked into Late Miocene-Pliocene rocks), S. Nielsen loc. RAP, N of mouth of Río Rapel, N of Navidad, Chile (Figs 3, 5, SGO.IP 6447; Fig. 3, H 72.3 mm; Fig. 5, H 80.1 mm; Fig. 6, SGO.PI 6448, juvenile, H 23.3 mm).	205
4. <i>Sassia morgani</i> (Ortmann, 1900). GNS WM15880, Monte Leon Fm (Late Oligocene/Early Miocene), Monte Leon Beach, 40 km S of mouth of Santa Cruz River, Argentina, coll. M. Griffin; H 100.3 mm.	207
7. <i>Turritriton labiosus</i> (Wood, 1828). NMB H 18306, Pleistocene shellbed, loc. NMB 19149, road cuts 5 km from Manta on road to Montecristi, Manabi Province, Ecuador; H 27.3 mm.	195
8. <i>Monoplex</i> n. sp. B. BMNH, Palaeontology Department, GG22583, lower Gatun Fm (Middle Miocene), <i>ex situ</i> , Los Lomos Suites, Cativa, Colon, Atlantic Panama; H 31.5 mm.	181
9-12. <i>Monoplex gatunicus</i> n. sp.	153
9, 12. BMNH, Palaeontology Department, GG22578, holotype, lower Gatun Fm (Middle Miocene), quarry floor, Los Lomos Suites, Cativa, Colon, Atlantic Panama; H 42.0 mm.	
10-11. BMNH, Palaeontology Department, GG22577 and GG22579, 2 paratypes, lower Gatun Fm (Middle Miocene), Los Lomos Suites, Cativa, Colon, Atlantic Panama (Fig. 10, H 31.5; Fig. 11, H 29.5 mm).	



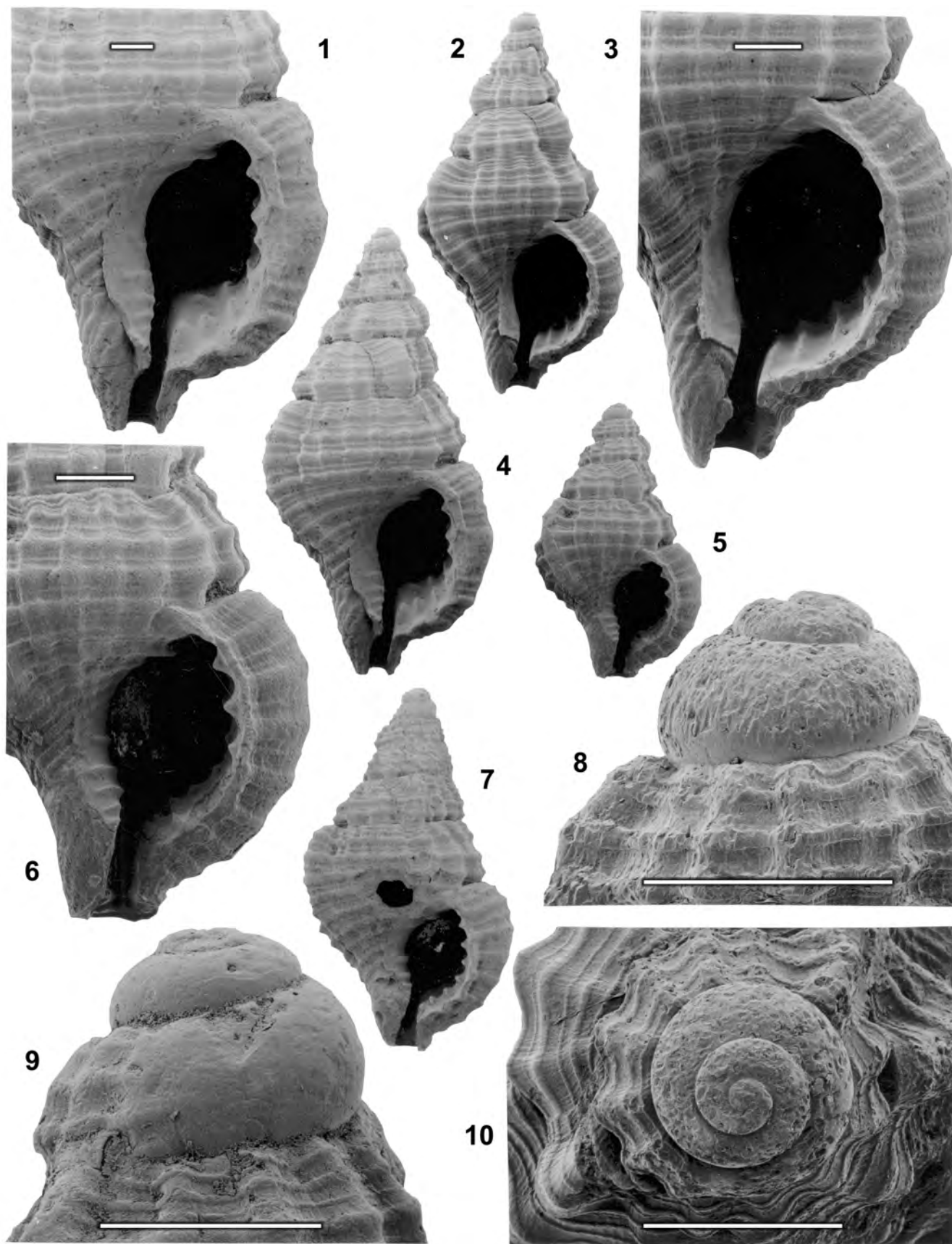
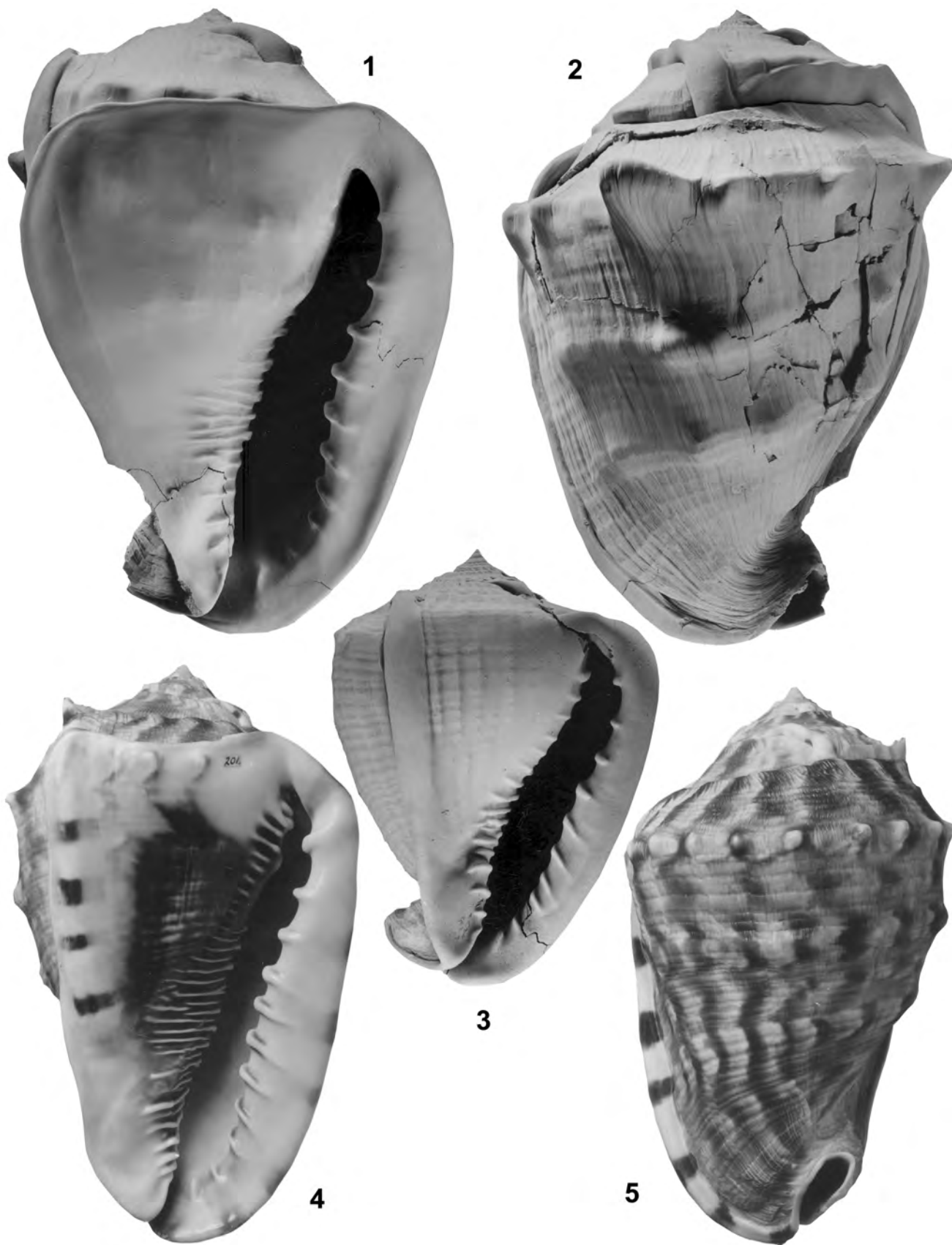


PLATE 54

Figure		Page
1-10.	<i>Cymatiella vokesorum</i> n. sp. All scale bars = 1 mm.	209
	1, 4, 9. NMB H 17967, holotype, unnamed formation (Middle Miocene), loc. TU 1249 (= NMB 19010), road cut on road to Bani, 8.6 km W of plaza at San Cristobal, S Dominican Republic; SEM micrographs of aperture and siphonal canal (Fig. 1), entire specimen (Fig. 4, H 14.0 mm), and protoconch (Fig. 9).	
	2-3. NMB H 17968, paratype, all data same as for holotype; SEM micrographs of entire specimen (Fig. 2, H 12.2 mm) and aperture and siphonal canal (Fig. 3).	
	7. NMB H 17970, paratype, Baitoa Fm (late Early Miocene), loc. TU 1364 (= NMB 18560), downstream from waterfall in Arroyo Hondo, Boca de los Rios, downstream from Baitoa, Río Yaque del Norte, Dominican Republic; SEM micrograph of entire specimen, H 11.6 mm.	
	5-6, 8, 10. USNM unreg., small specimen, Brasso Fm (Miocene), loc. USGS 9219, Guaico-Tamana Road, Trinidad; SEM micrographs of entire specimen (Fig. 5, H 7.9 mm), aperture and siphonal canal (Fig. 6), and protoconch (Figs 8, 10).	

PLATE 55

Figure		Page
1-3.	<i>Cassis altispira</i> n. sp.	212
	1-2. NMB H 17972, holotype, Cayo Agua Fm (Late Pliocene), loc. NMB 18734, 300 m WNW of Punta Piedra Roja, Cayo Agua, Bocas del Toro Basin, Atlantic Panama; H 155.2 mm.	
	3. NMB H 17973, immature paratype, all data same as for holotype; H 73.2 mm (see also Pl. 56, Fig. 7).	
4-5.	<i>Cassis norai</i> Prati-Musetti, 1995. RMNH 3762, Recent, Curaçao, Caribbean, 1956, ex C. A. van der Peijl collection; H 163.7 mm.	221



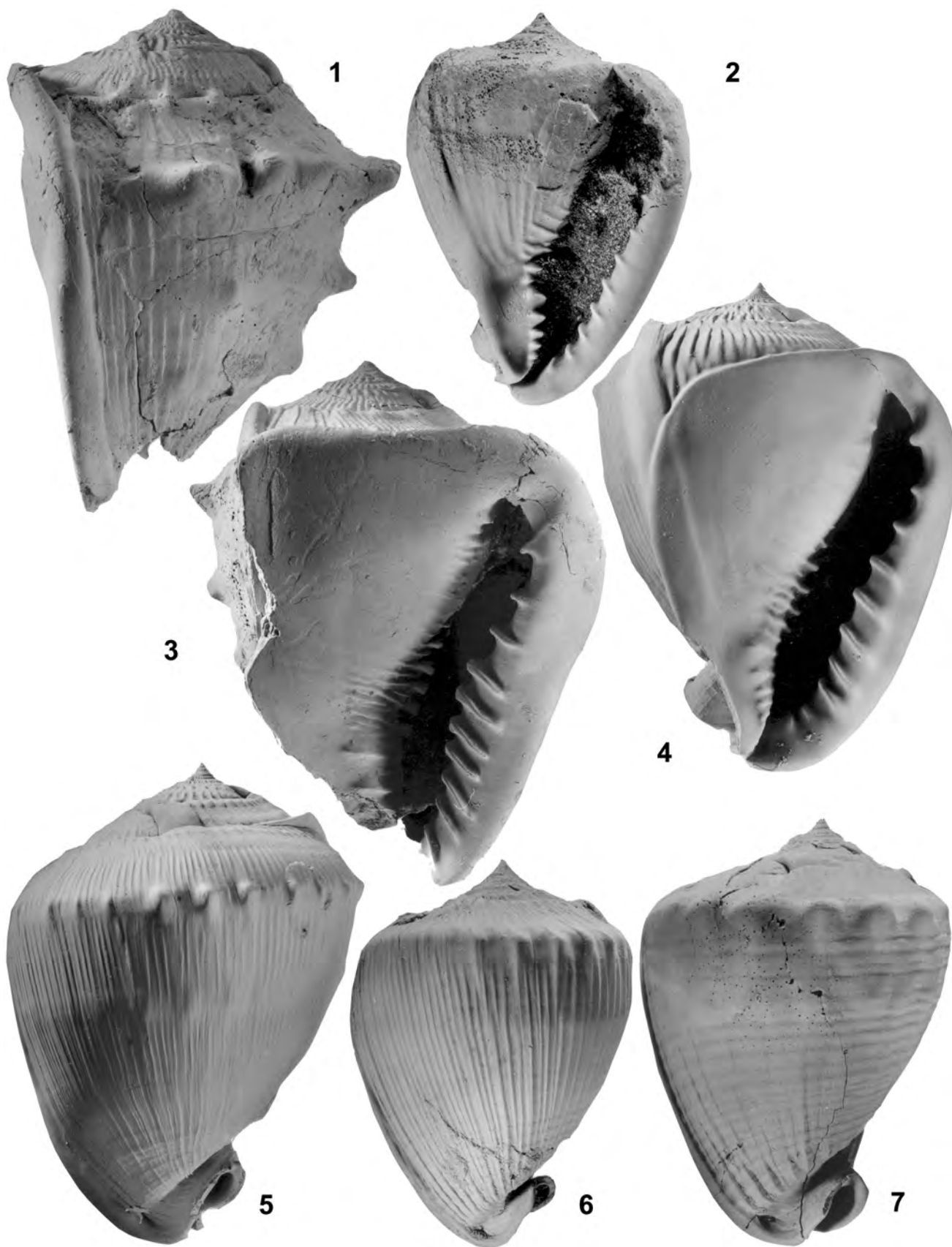


PLATE 56

Figure		Page
1, 3, 7.	<i>Cassis altispira</i> n. sp.	212
	1, 3. NMB H 17981, Gurabo Fm (Early Pliocene), loc. NMB 16824, bluff at upstream end of major bends around Cañada de Zamba, E bank Río Cana, Dominican Republic; H 142 mm.	
	7. NMB H 17973, dorsal view of immature paratype in Pl. 55, Fig. 3; H 73.2 mm.	
2, 4-6.	<i>Cassis costulifera</i> n. sp.	214
	2, 6. NMB H 17977, immature paratype, Escudo de Veraguas Fm (Pliocene), loc. NMB 18668, N coast of Escudo de Veraguas Island, Bocas del Toro Basin, Atlantic Panama; H 47.7 mm.	
	4-5. NMB H 17967, holotype, all data same as for paratype; H 89.0 mm.	

PLATE 57

Figure		Page
1, 4.	<i>Cassis ketteri</i> Parodiz & Tripp, 1992. Small specimen in collection of Bernard Landau, unit 10, Pinecrest Fm (middle Pliocene), Quality Aggregates phase 6 quarry, Sarasota, Florida, USA; H 145 mm (photo Bernard Landau).	219
2-3.	<i>Cassis floridensis</i> Tucker & Wilson, 1932. Specimen in collection of Bernard Landau, Bermont Fm (early Pleistocene), Palm Beach Rock quarry, 3 km W of Loxahatchee on Hwy 441, Palm Beach County, Florida, USA; H 146 mm (photo Bernard Landau).	218

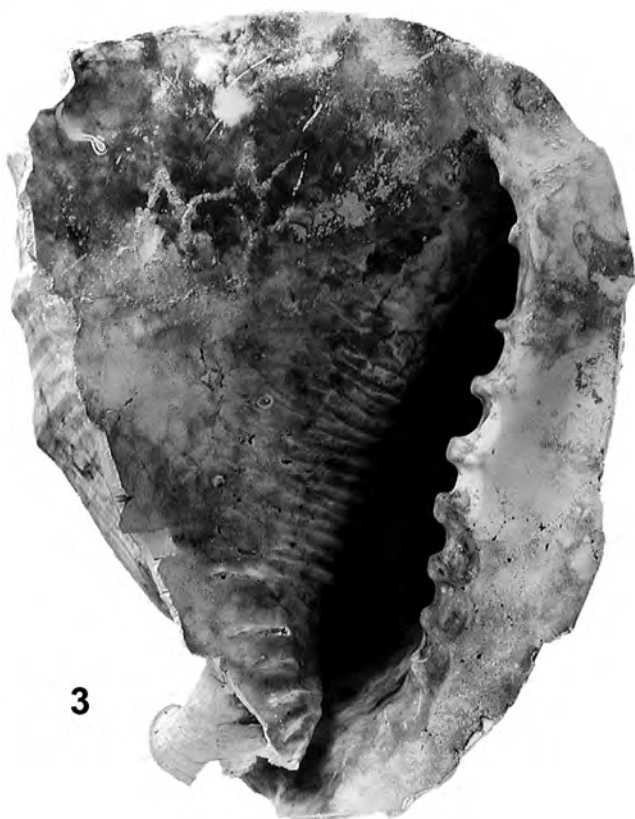
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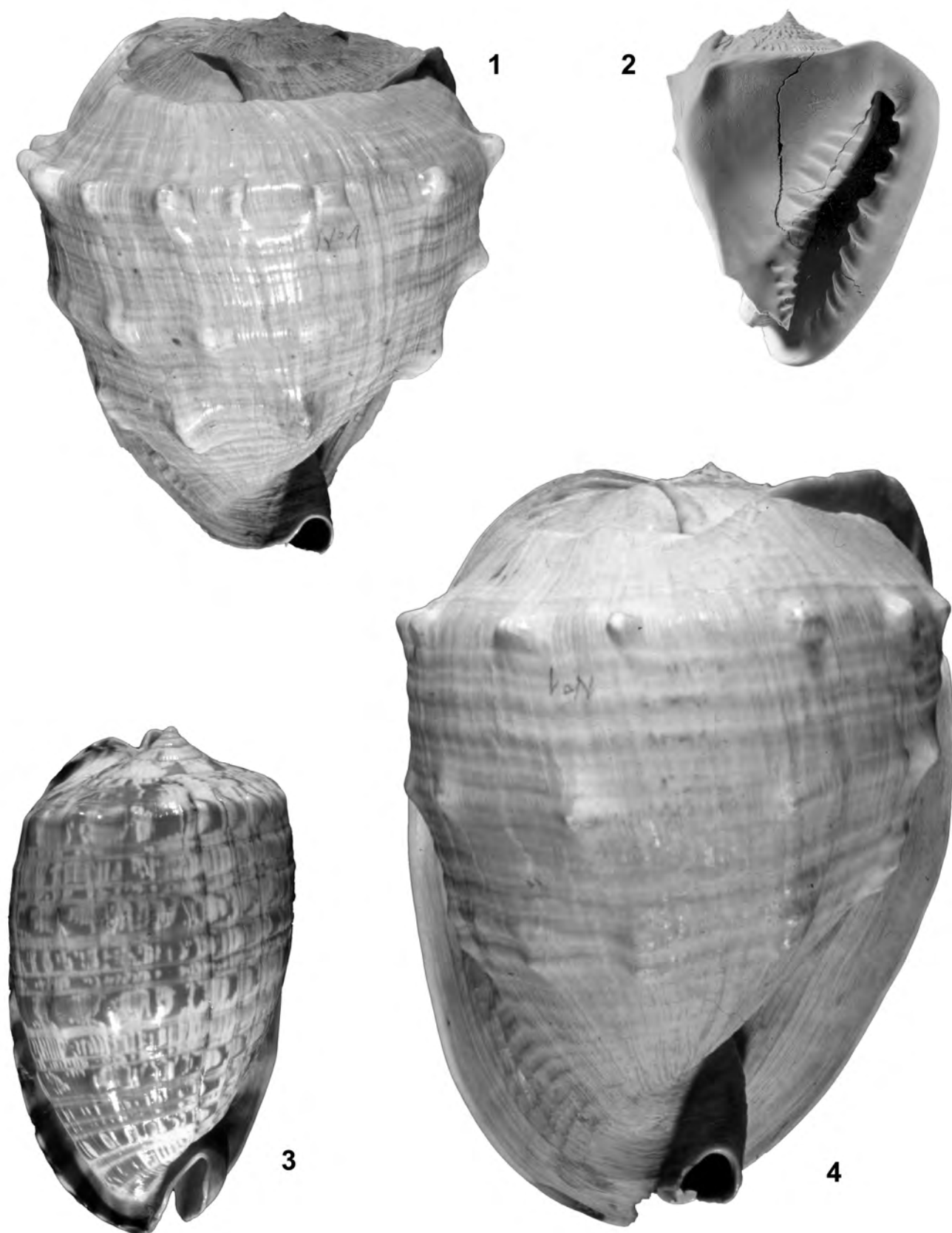


PLATE 58

Figure		Page
1, 5.	<i>Cassis madagascariensis</i> Lamarck, 1822. MHNG 1100/77-78, lectotype (Fig. 5) and paralectotype, Recent, western Atlantic [type locality here designated as Beaufort, North Carolina] (Fig. 1, H 201 mm; Fig. 5, H 283 mm; see also Pl. 59, Figs 1, 4) (from a color transparency).	219
2-3.	<i>Cypraecassis chipolana</i> Duerr, 2001. NMB H 17984, incomplete specimen, Chipola Fm (late Early Miocene), loc. TU 820 (= NMB 17597), Chipola River, Farley Creek, at bridge of Florida Highway 275, Calhoun County, Florida, USA; H 45.9 mm.	226
4.	<i>Cypraecassis tenuis</i> (Wood, 1828). MHNG 1152/37, holotype of <i>Cassis massenae</i> Kiener, 1835, and neotype of <i>C. tenuis</i> , Recent, Galápagos Islands; H 92.5 mm (see also Pl. 59, Fig. 3) (from a color transparency).	227

PLATE 59

Figure		Page
1, 4.	<i>Cassis madagascariensis</i> Lamarck, 1822. MHNG 100/77-78, dorsal views of lectotype (Fig. 4, H 283 mm) and paralectotype (Fig. 1, H 201 mm) shown in Pl. 58, Figs 1, 5 (from a color transparency).	219
2.	<i>Cassis sulcifera</i> G. B. Sowerby I, 1850. NMB H 17982, Gurabo Fm (Early Pliocene), loc. NMB 16808, mouth of side stream at minor bend, Río Gurabo, Dominican Republic; H 63.4 mm (see also Pl. 60, Fig. 5).	221
3.	<i>Cypraecassis tenuis</i> (Wood, 1828). MHNG 1152/37, holotype of <i>Cassis massenae</i> Kiener, 1835 and neotype of <i>C. tenuis</i> , dorsal view of specimen shown in Pl. 58, Fig. 4; H 92.5 mm (from a color transparency).	227



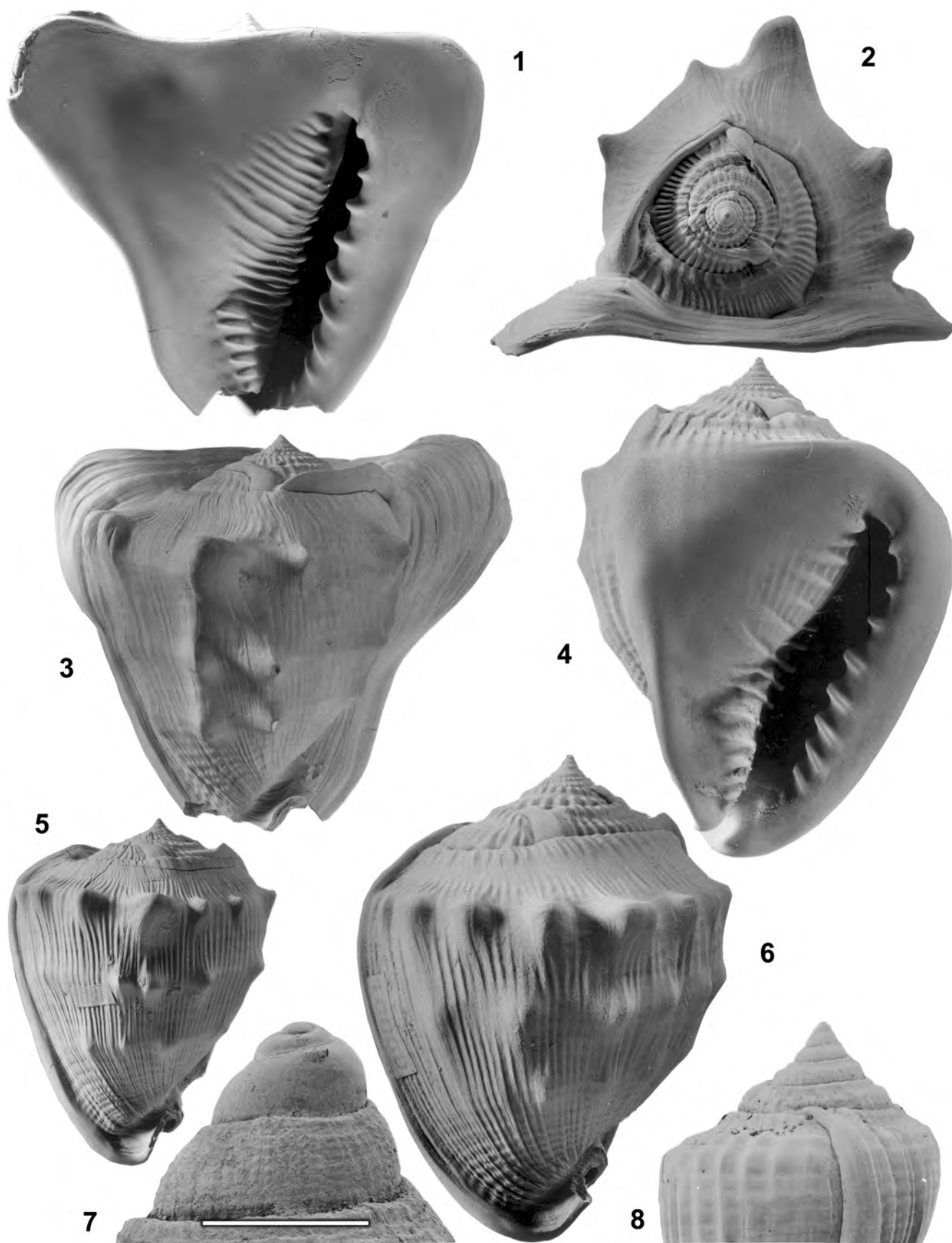
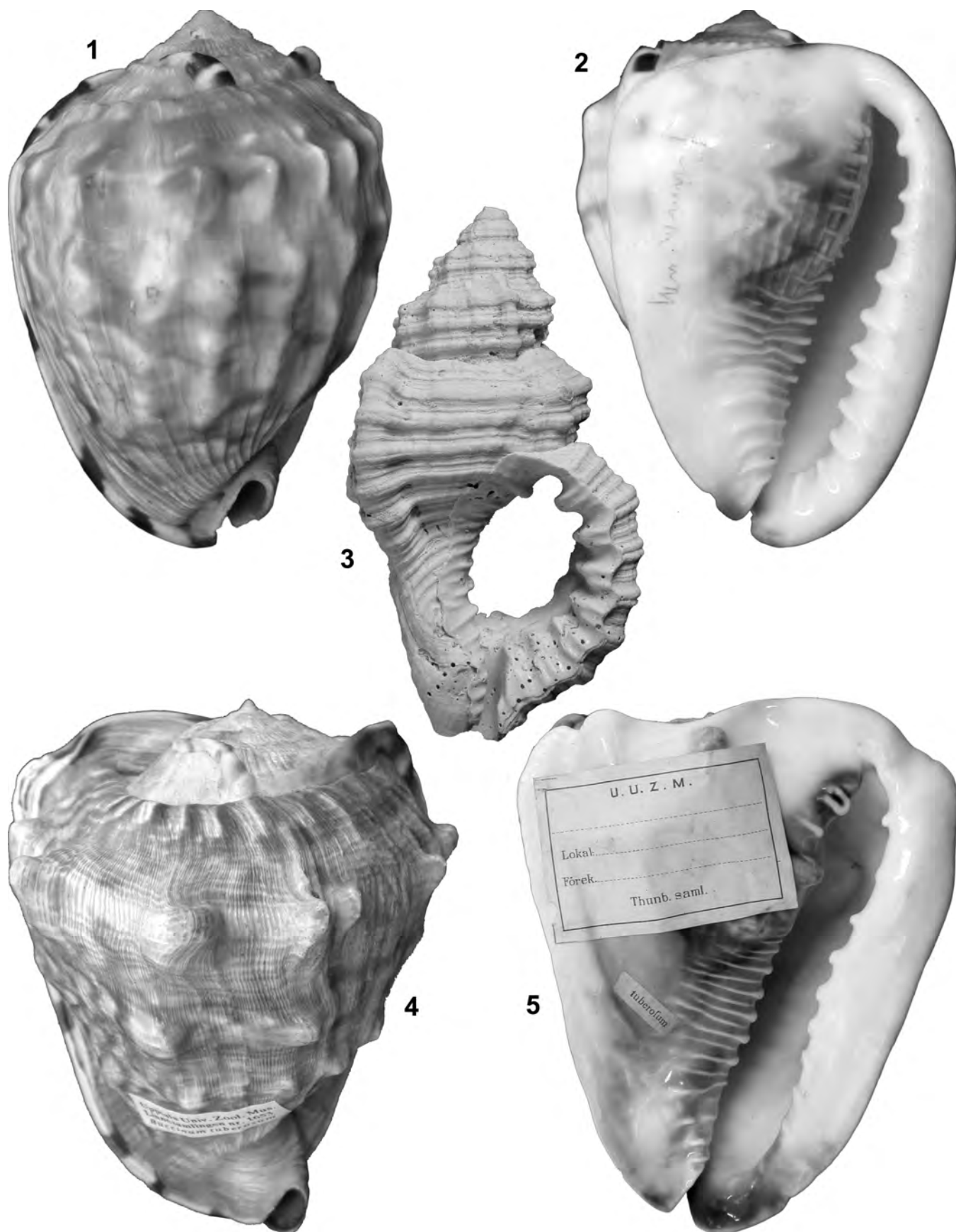


PLATE 60

Figure		Page
1-8.	<i>Cassis sulcifera</i> G. B. Sowerby I, 1850	221
	1-3. NMB H 17980, large (male?) adult, Gurabo Fm (Late Miocene), loc. NMB 16916, mouth of Arroyo Bajón, upper Río Mao, Dominican Republic; H 72.8 mm.	
	4, 6. NMB H 17983, juvenile specimen, Gurabo Fm (Early Pliocene), loc. NMB 16869, Río Cana, Dominican Republic; H 46.0 mm.	
	5. NMB H 17982, dorsal view of specimen in Pl. 59, Fig. 2; H 63.4 mm.	
	7-8. NMB H 18016, Gurabo Fm (Early Pliocene), loc. NMB 16883, Río Gurabo, Dominican Republic (immediately above center of map of Saunders <i>et al.</i> , 1986: text-fig. 15); SEM micrographs of protoconch and early teleoconch whorls (Fig. 7, scale bar = 1 mm) and posterior part of small juvenile (Fig. 8, D 13.1mm).	

PLATE 61

Figure		Page
1-2.	<i>Cassis flammea</i> (Linnaeus, 1758). UUZM 931, lectotype (designated here) , ex collection of Queen Ludovica Ulrica, without locality [type locality here designated as Grand Bahama Island]; H 90.4 mm (UUZM photos by Olle Israelsson).	216
3.	<i>Monoplex</i> n. sp. A. Specimen in collection of Bernard Landau, Chipola Fm (late Early Miocene), loc. TU 826, Farley Creek, Chipola River, Calhoun County, Florida, USA; H 49.7 mm.	180
4-5.	<i>Cassistuberosa</i> (Linnaeus, 1758). UUZM 1653, lectotype (designated here) , ex collection of Queen Ludovica Ulrica, without locality [type locality here designated as Puerto Plata, Dominican Republic]; H 154.0 mm (UUZM photos by Olle Israelsson).	223



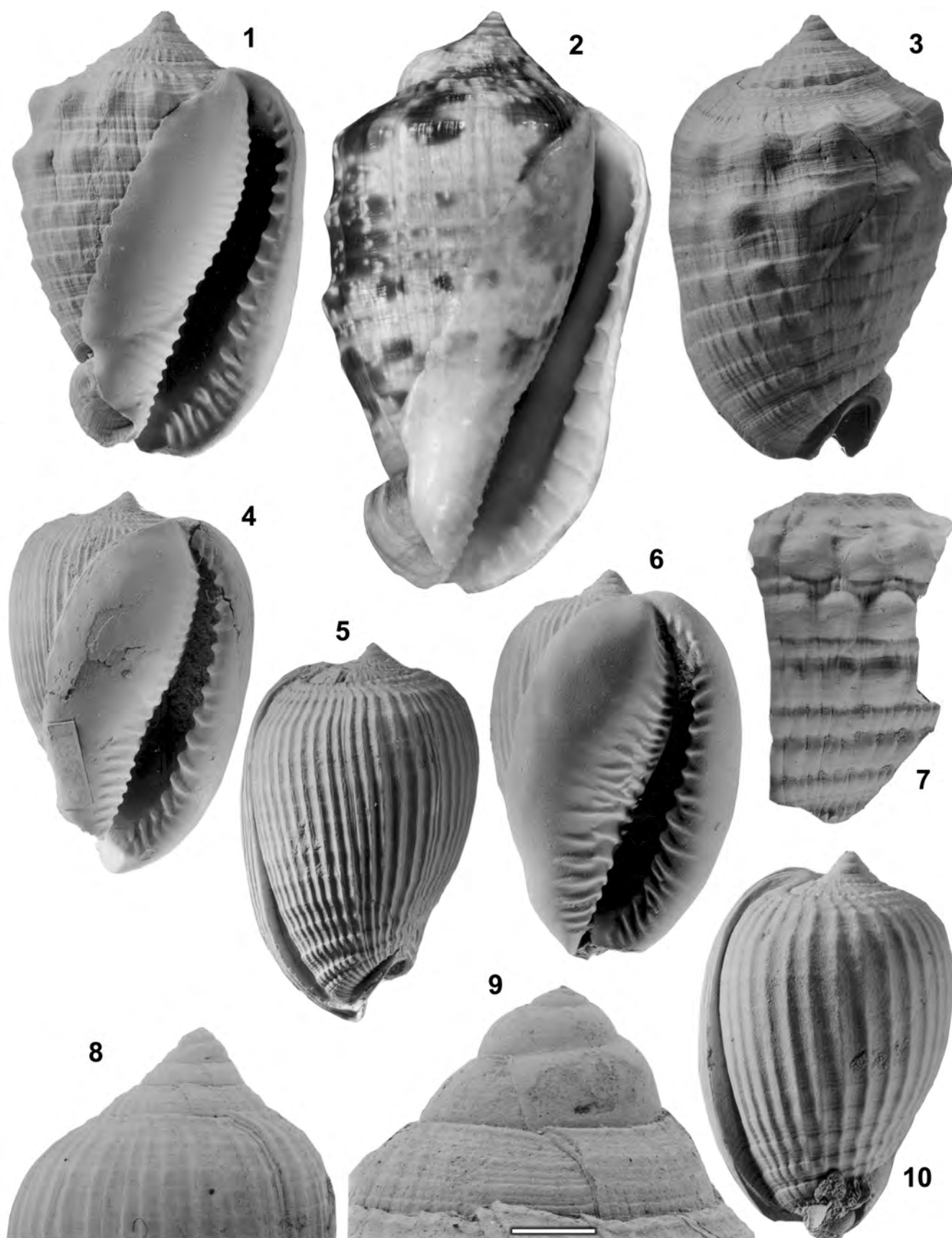
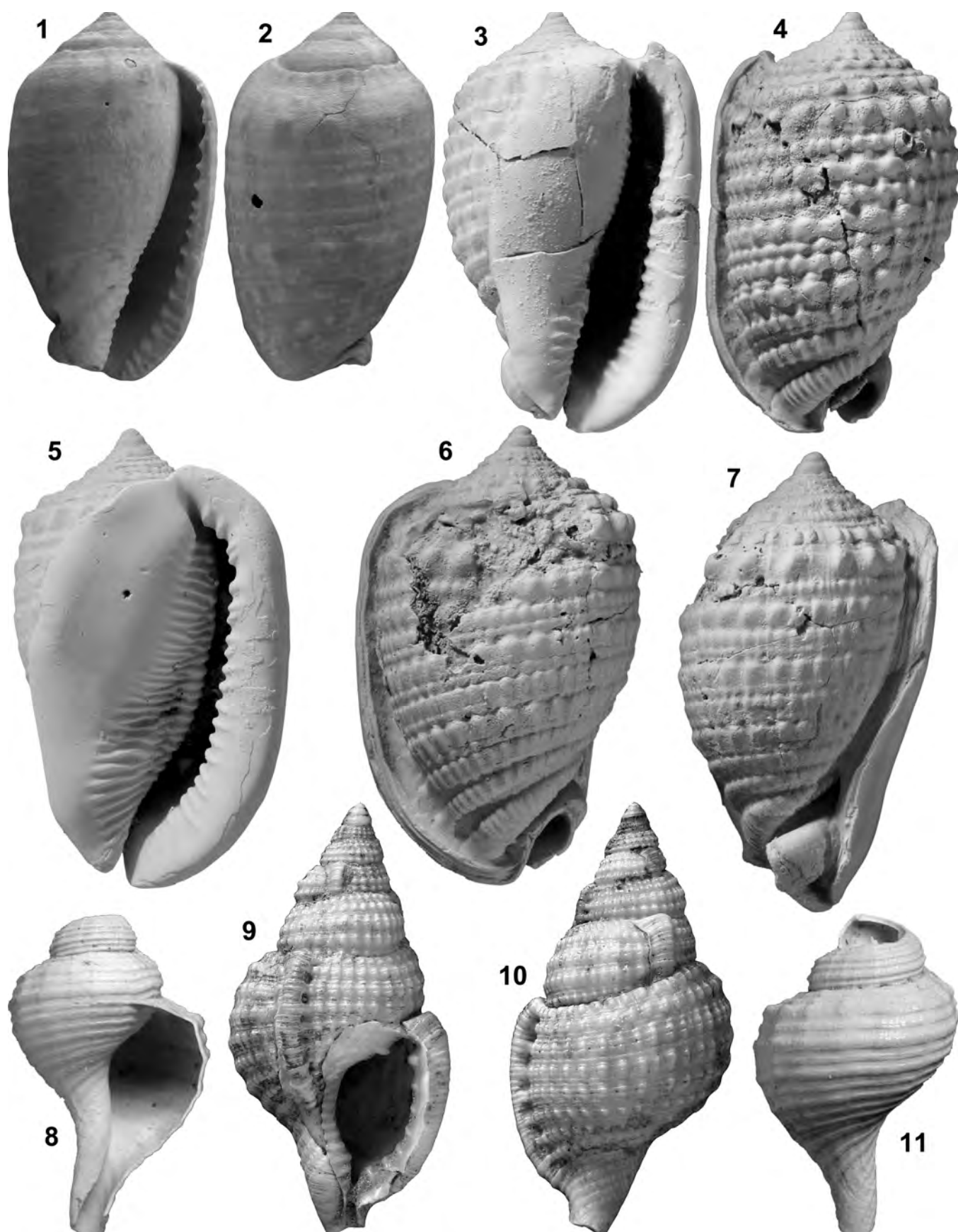


PLATE 62

Figure		Page
1, 3.	<i>Cypraecassis wilmae</i> Kreipl & Alf, 2000. NMB H 17989, Armuelles Fm (Pleistocene), loc. NMB 18306, S of Quebrada Corotú, 3.3 km S of Puerto Limones, Burica Peninsula, Pacific Panama; H 41.0 mm.	230
2.	<i>Cypraecassis coarctata</i> (G. B. Sowerby I, 1825). BMNH 1967673, holotype, Recent, without locality [type locality designated as Acapulco, Mexico, by Abbott (1968)]; H 71.3 mm.	227
4-6, 8-10.	<i>Cypraecassis testiculus</i> (Linnaeus, 1758)	228
	4-5. NMB H 17987, Gurabo Fm (Early Pliocene), loc. TU 1354 (= NMB 18585), Cañada de Zamba, tributary on W side Río Cana, Dominican Republic; H 45.0 mm.	
	6, 10. NMB H 17986, strongly callused specimen, Gurabo Fm (Early Pliocene), loc. NMB 16828, Río Cana, Dominican Republic; H 34.8 mm.	
	8-9. NMB H 17988, juvenile specimen, all data same as for Figs 4-5; SEM micrographs of spire and posterior part of last whorl (Fig. 8, D 14.5 mm) and protoconch and first teleoconch whorl (Fig. 9, scale bar = 1 mm).	
7.	<i>Cypraecassis chipolana</i> Duerr, 2001. NMB H 17985, fragment, Chipola Fm (late Early Miocene), loc. TU 830 (= NMB 17588), Tenmile Creek, 1.6 km W of Chipola River, Florida, USA; H 37 mm.	226

PLATE 63

Figure		Page
1-2.	<i>Cypraecassis coarctata</i> (G. B. Sowerby I, 1825). Specimen in collection of Bernard Landau, Mulegé Terrace cover beds (late Middle Pleistocene, oxygen isotope stage 5e), Bahia Santa Inéz, near Mulegé, Baja California Sur, Mexico; H 68.6 mm.	227
3-7.	<i>Cypraecassis cantaurana</i> n. sp.	225
	3-4. Paratype in collection of Bernard Landau, dorsal and ventral views, all data same as for holotype; H 52.4 mm.	
	5-7. BMNH Palaeontology Department, GG22902, holotype, ventral, dorsal and right lateral views, Cantaure Fm (late Early Miocene), near Casa Cantaure, Paraguana Peninsula, Falcón, Venezuela, ex Bernard Landau collection; H 57.6 mm.	
8, 11.	<i>Linatella caudata</i> (Gmelin, 1791). NMB H18343, Armuelles Fm (Pleistocene), loc. NMB 17442, blue silts, Río Rabo de Puerco, W of Puerto Armuelles, Burica Peninsula, Pacific Panama (one of 5 juvenile specimens in sample); H 9.4 mm.	140
9-10.	<i>Sassia warreni</i> n. sp. Largest paratype, in collection of Bernard Landau, Gurabo Fm (Early Pliocene), loc. TU 1215, Maury's zone D, bluffs for 1 km above ford on Los Quemados-Sabaneta road, Río Gurabo, Dominican Republic; H 37.4 mm.	200



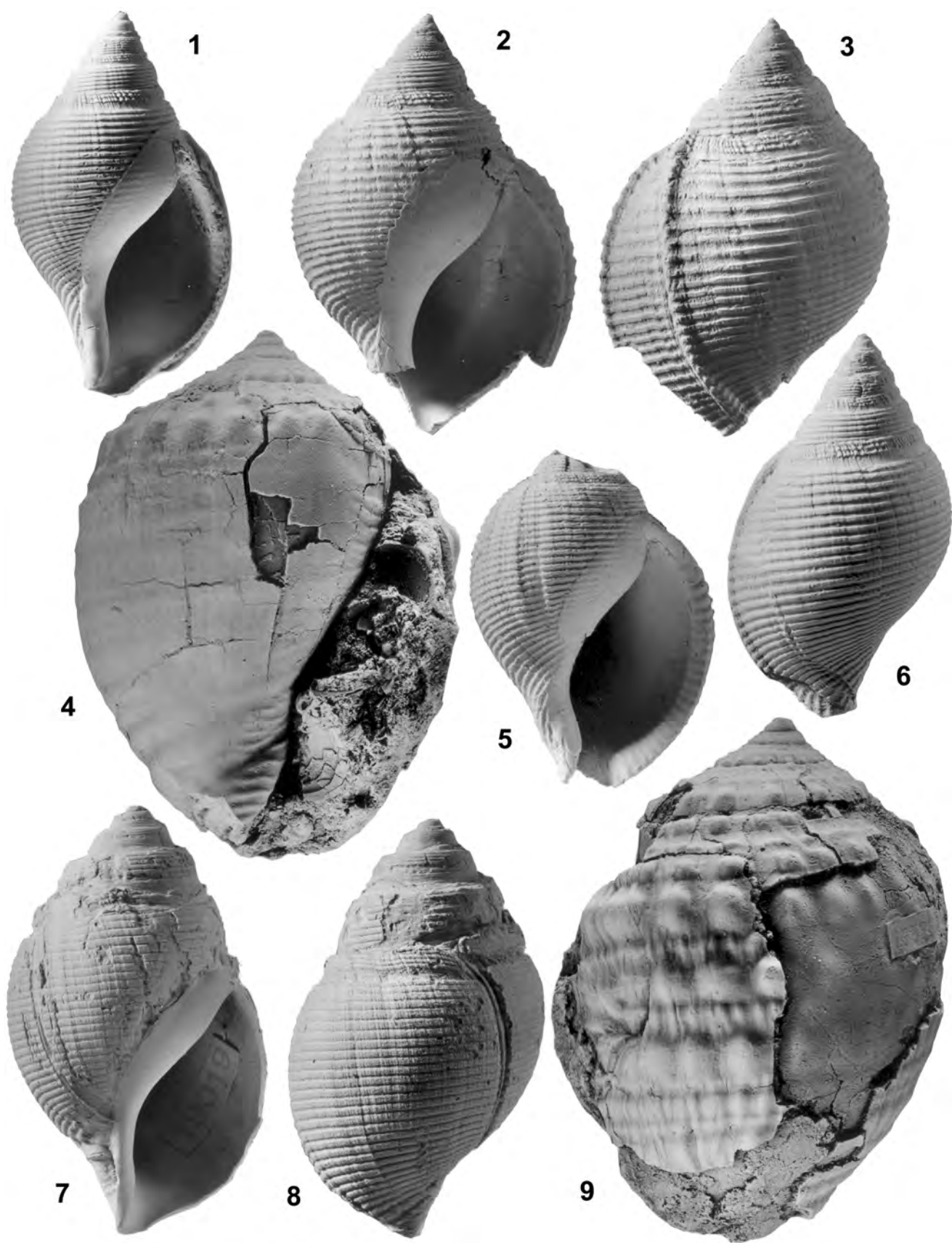
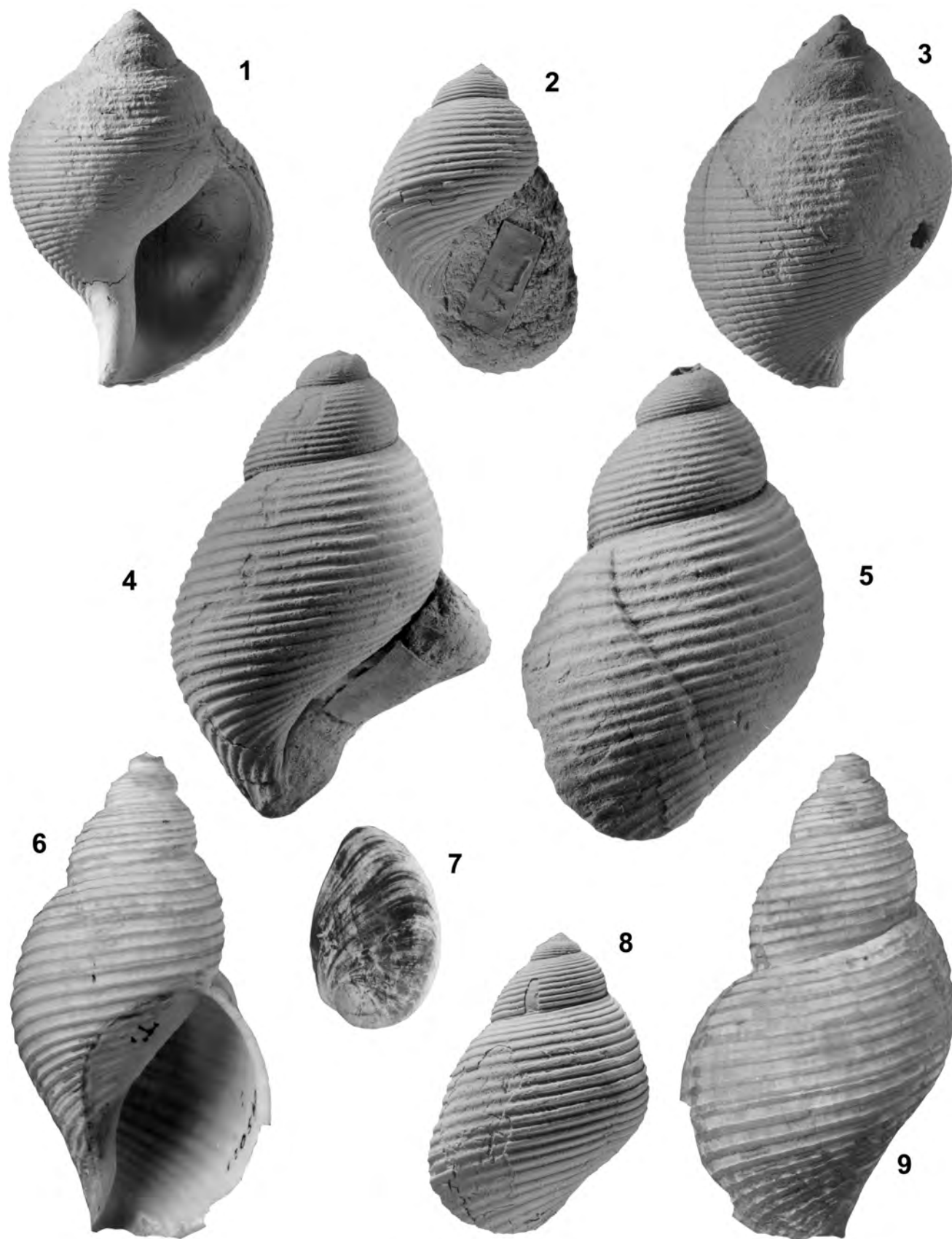


PLATE 64

Figure		Page
1-3, 5-6.	<i>Dalium dalli</i> Böse, 1906	239
	1, 6. NMB H 18007, deep-water facies of Gurabo Fm (Early Pliocene), loc. TU 1250 (= NMB 18558), Río Verde, 10 km N of La Vega, Dominican Republic; H 34.8 mm.	
	2-3, 5. NMB H 18008-9, 2 specimens, deep-water facies of Gurabo Fm (Early Pliocene), loc. TU 1357 (= NMB 19017), Río Yaque del Norte, bluff on W side above water plant at Bella Vista, 3 km S of bridge at Santiago de los Caballeros, Dominican Republic (Figs 2-3, H 38.2 mm; Fig. 5, H 30.6 mm).	
4, 9.	<i>Cypraecassis cantaurana</i> n. sp. NMB H 18052, incomplete specimen, upper shellbed, Cantaure Fm (late Early Miocene), loc. NMB 17520, near Casa Cantaure, Paraguaná Peninsula, Venezuela; H 65.1 mm.	225
7-8.	<i>Dalium ecuadorianum</i> Olsson, 1942. NMB H 17990, Onzole Fm (Early Pliocene), loc. TU 1398 (= NMB 19019), cutting on Esmeraldas-Camarones-Onzole road, immediately E of Quebrada Camarones, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town, Ecuador; H 38.4 mm.	240

PLATE 65

Figure		Page
1, 3.	<i>Oocorys cf. clericus</i> Quinn, 1980. NMB H 18006, Shark Hole Point Fm (Early Pliocene), loc. NMB 17857, <i>ca.</i> 1 km SW of Shark Hole Point, outer coast of Valiente Peninsula, Bocas del Toro Basin, Atlantic Panama; H 34.4 mm.	241
2, 4, 5, 8.	<i>Ipunina vladimiri</i> Nielsen & Frassinetti, 2008 (Litiopidae)	316
	2, 8. NMB H 17993, upper shellbed, Cantaure Fm (late Early Miocene), loc. NMB 17519, near Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; H 28.2 mm.	
	4-5. NMB H 17991, Cantaure Fm (late Early Miocene), loc. NMB 17241, near Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; H 45.3 mm.	
6-7, 9.	<i>Oocorys elevata</i> (Dall, 1908). USNM 110569, holotype, Recent, U. S. Fish Commission sta. 4649, 4,086 m, between the Galápagos Islands and Sechura Bay, Peru (teleoconch, H 58.5 mm; operculum, H 28 mm.	317



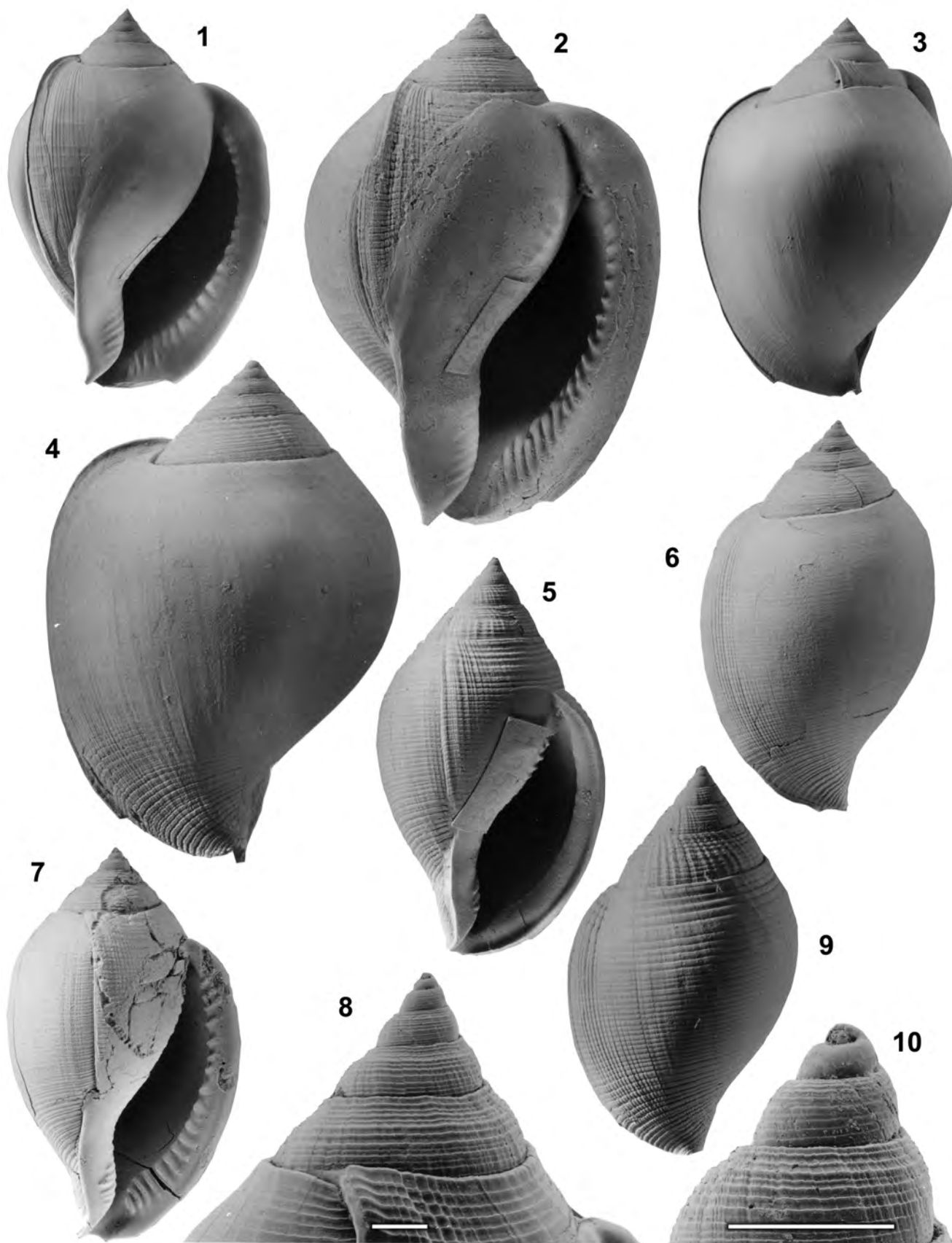


PLATE 66

Figure	Page
1-5, 8-10. <i>Sconsia laevigata</i> (G. B. Sowerby I, 1850)	236
1, 3. NMB H 18012, Gurabo Fm (Early Pliocene), loc. NMB 17267, near La Barranca, left bank Río Yaque del Norte, Dominican Republic; H 47.1 mm.	
2, 4. NMB H 18011, large adult, Gurabo Fm (Early Pliocene), loc. NMB 17270, Arroyo Zalaya, Santiago-Janico road, 9 km S of Santiago, Dominican Republic; H 68.9 mm.	
5, 9. NMB H 18013, juvenile specimen, Gurabo Fm (Early Pliocene), loc. TU 1227a (= NMB 18582), turbidity flow lens in Arroyo Zalaya, Santiago-Janico road, 9 km S of Santiago, Dominican Republic; H 35.5 mm.	
8, 10. NMB H 18039, Gurabo Fm (Early Pliocene), loc. NMB 15867, mouth of side stream at minor bend, Río Gurabo, Dominican Republic; SEM micrographs of spire and posterior part of last whorl of small juvenile (Fig. 8) and spire apex and protoconch (Fig. 10, protoconch incomplete; distinction from teleoconch obscure) (H 31.1 mm; scale bar = 1 mm).	
6-7. <i>Sconsia grayi</i> A. Adams, 1855. NMB H 18014, Cayo Agua Fm (Pliocene), loc. NMB 17808, ca. 1.5 km SE of Punta Norte, E coast of Cayo Agua, Bocas del Toro Basin, Atlantic Panama; H 47.3 mm (see also Pl. 67, Fig. 5).	232

PLATE 67

Figure	Page
1, 3, 5. <i>Sconsia grayi</i> A. Adams, 1855	232
1, 3. NMB H 18010, Escudo de Veraguas Fm (Pliocene), loc. NMB 18681, E end of Escudo de Veraguas Island, Bocas del Toro Basin, Atlantic Panama; H 54.3 mm.	
5. NMB H 18015, second small, inflated specimen in same lot as Pl. 66, Figs 6-7; H 49.1 mm.	
2. <i>Sconsia</i> cf. <i>laevigata</i> (G. B. Sowerby I, 1850). NMB H 1863, specimen figured by Rutsch (1934: 53, pl. 11, fig. 11) as <i>S. cf. striata</i> , Punta Gavilán Fm (Early Pliocene), Punta Gavilán, Venezuela; H 66.5 mm.	236
4, 6. <i>Neosconsia ecuadoriana</i> Olsson, 1964 (Buccinidae). NMB H 18017, Onzole Fm (Early Pliocene), loc. TU 1397 (= NMB 19018), 200 m up Quebrada Camarones, S of Esmeraldas-Camarones road, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town, Ecuador; H 44.5 mm.	318



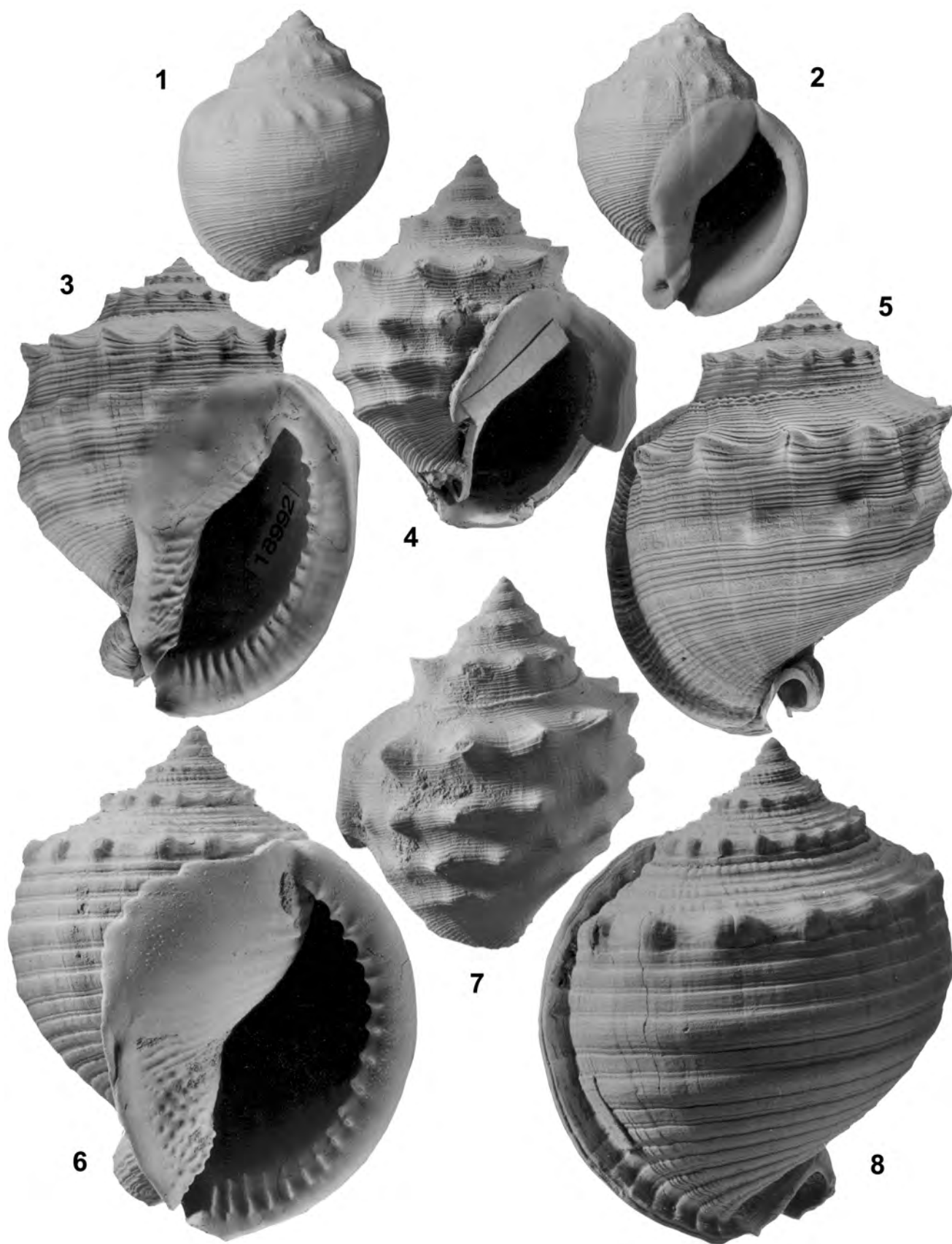
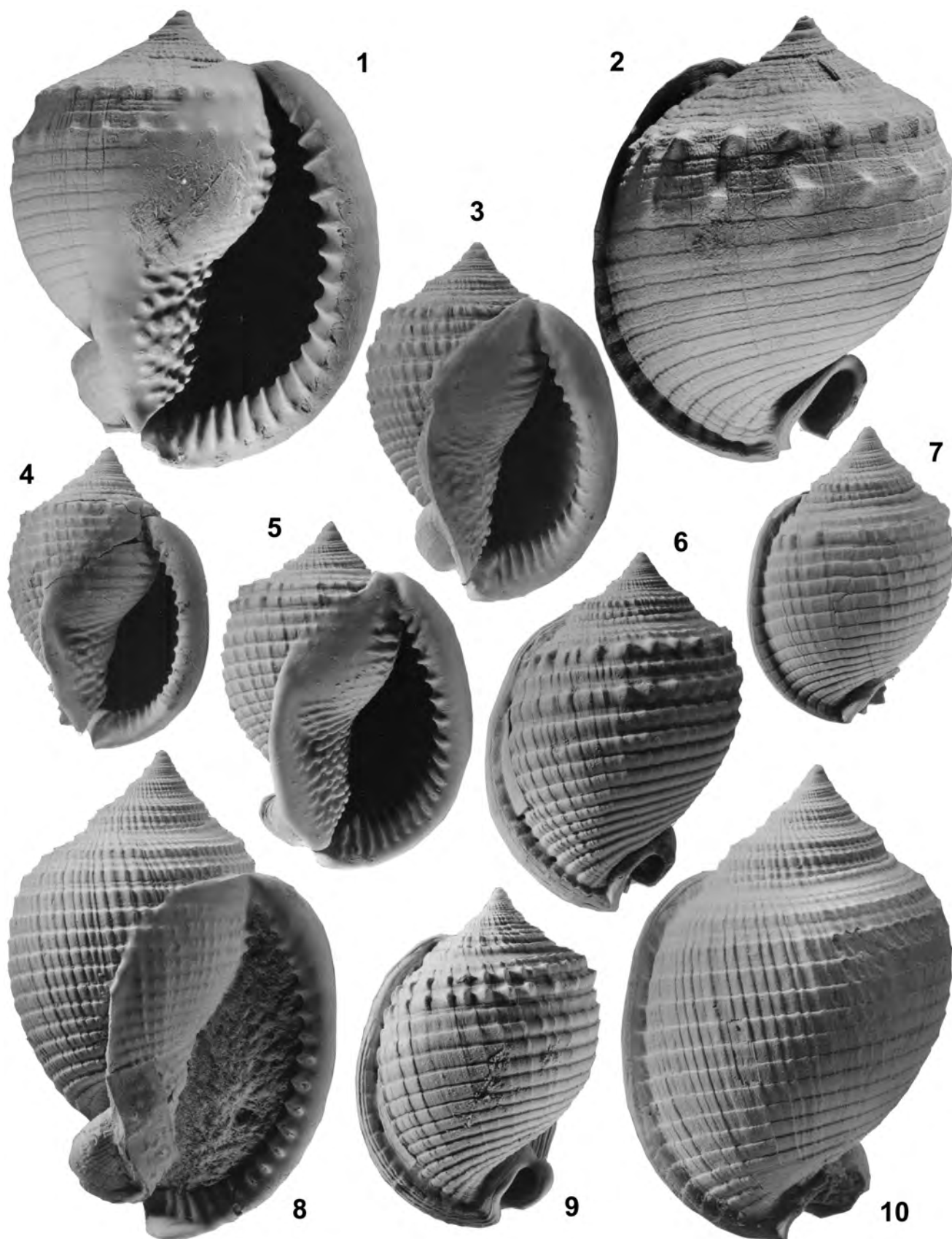


PLATE 68

Figure		Page
1-2.	<i>Echinophoria woodringi</i> Olsson, 1964	244
	1. NMB H 18304, Onzole Fm (Early Pliocene), loc. NMB 19136, lower course of Quebrada Camarones, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town, Ecuador; H 40.5 mm.	
	2. NMB H 18305, Onzole Fm (Early Pliocene), loc. NMB 19141, large road cut immediately W of Camarones, 20 km by road E of bridge over Río Esmeraldas and 11 km (straight line) E of Esmeraldas town, Ecuador; H 44.0 mm.	
3, 5.	<i>Echinophoria hadra</i> (Woodring & Olsson, 1957). NMB H 18018, Chagres Fm, Río Indio facies (latest Miocene), loc. NMB 18992, Punta Gavilán, 5.3 km (straight line) WSW of Río Indio, Colon, Atlantic Panama; H 55.0 mm.	243
4, 7.	<i>Galeodea</i> cf. <i>echinophora</i> (Linnaeus, 1758). NMB H 18005, Middle Miocene, Arroyo Najoyo, San Cristobal, Sec. Ingenio Nuevo, S Dominican Republic; H 33.7 mm.	231
6, 8.	<i>Semicassis aldrichi</i> (Dall, 1890). NMB H 18019, Cantaure Fm (late Early Miocene), loc. NMB 12842, near Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; H 47.1 mm.	246

PLATE 69

Figure		Page
1-2.	<i>Semicassis centiquadrata</i> (Valenciennes, 1832). NMB H 18067, Armuelles Fm (Pleistocene), loc. NMB 17441, float, Río Rabo de Puerco, W of Puerto Armuelles, Burica Peninsula, Pacific Panama; H 38.6 mm.	247
3-10.	<i>Semicassis reclusa</i> (Guppy, 1873)	251
	3-7, 9. NMB H 18021-18023, 3 small specimens from a sample of 11, Cercado Fm (Late Miocene), loc. NMB 15905, upper Río Gurabo, Dominican Republic (Figs 3, 6, H 32.6 mm; Figs 4, 7, H 31.3 mm; Figs 5, 9, H 26.9 mm).	
	8, 10. NMB H 18024, Baitoa Fm (late Early Miocene), loc. TU 1363 (= NMB 18559), above waterfall in Arroyo Hondo, Boca de los Ríos, Río Yaque del Norte, Dominican Republic; H 44.7 mm.	



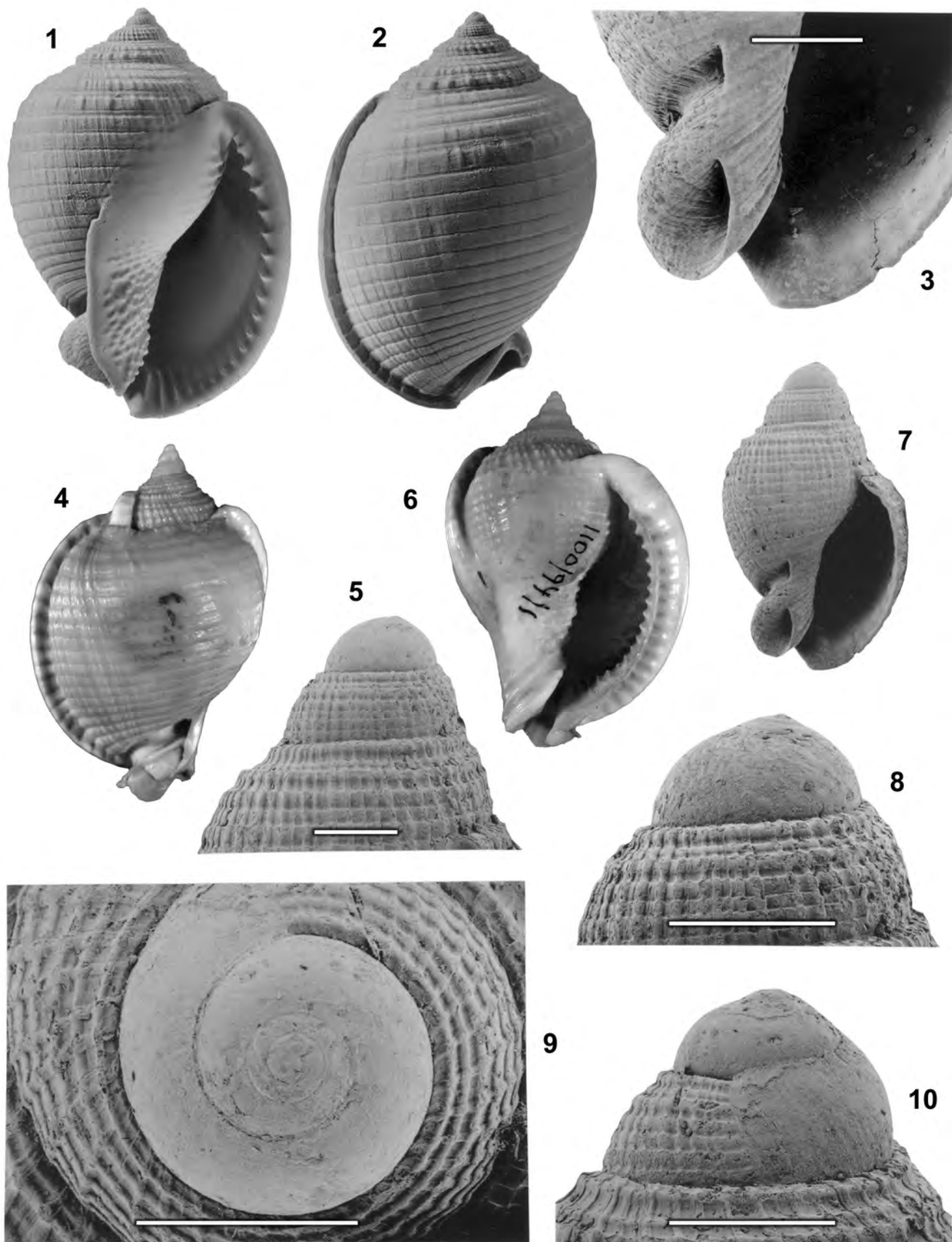
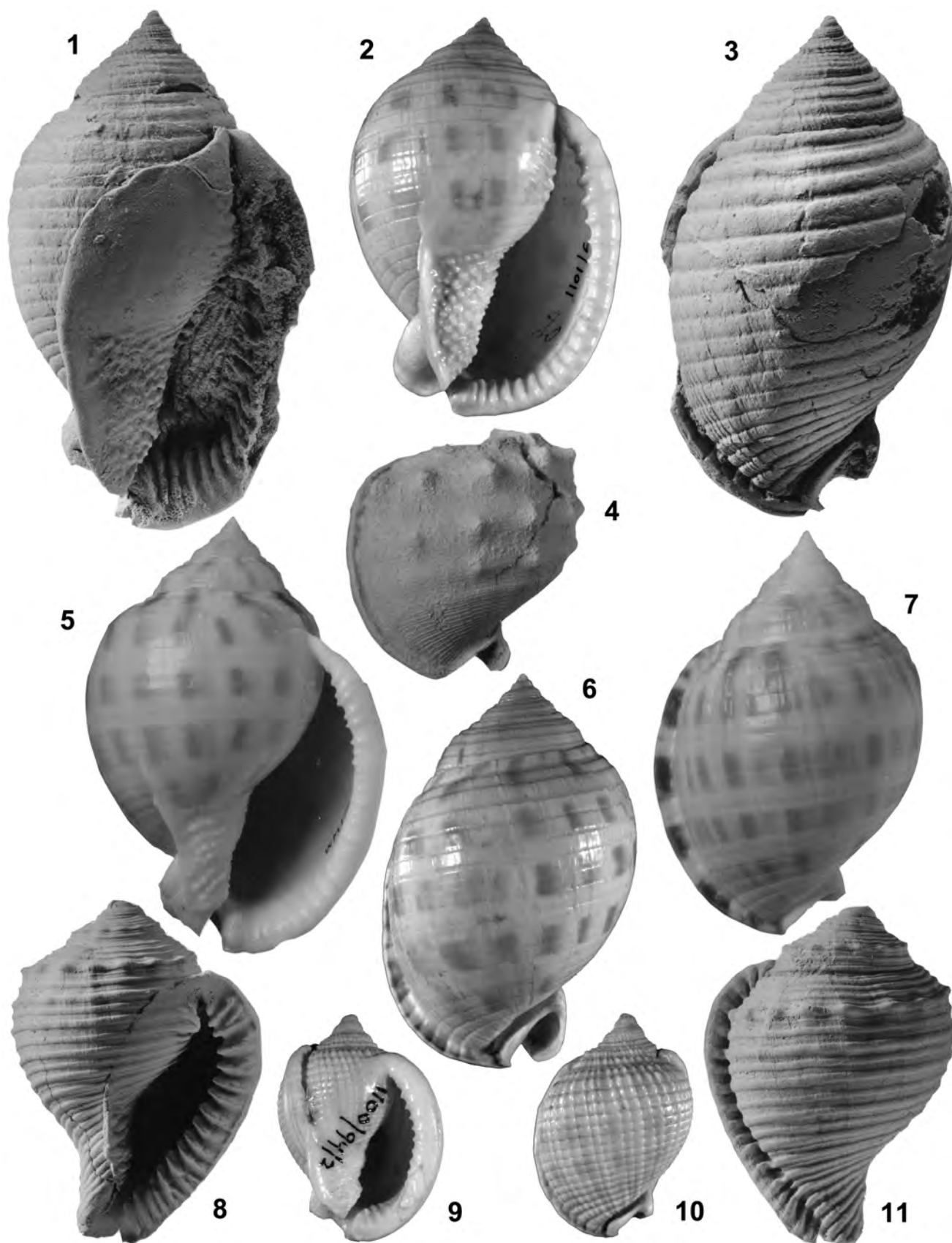


PLATE 70

Figure		Page
1-3, 5, 7-10.	<i>Semicassis reclusa</i> (Guppy, 1873)	251
	1-2. NMB H 18020, weakly sculptured specimen, Cercado Fm (Late Miocene), loc. NMB 16913, Bluff 3 of Maury, <i>ca.</i> 400 m upstream from crossing on Cercado-Bulla road, upper Río Mao, Dominican Republic; H 36.4 mm.	
	3, 5, 7-10. NMB H 18040-18041, 2 juvenile specimens, Cercado Fm (Late Miocene), loc. NMB 15907, upper Río Gurabo, Dominican Republic; SEM micrographs of entire specimen (Fig. 7, H 7.03 mm), anterior end and siphonal canal (Fig. 3), and protoconch and early teleoconch whorls (Figs 5, 8-10, all scale bars = 1 mm).	
4, 6.	<i>Semicassis granulata</i> (Born, 1778). MHNG 1100/94/1, lectotype of <i>Cassis abbreviata</i> Lamarck, 1822, Recent, western Atlantic [type locality here designated as Barbados]; H 44.5 mm (from a color transparency).	248

PLATE 71

Figure	Page
1, 3. <i>Semicassis senni</i> (Rutsch, 1934). NMB H 1866, holotype, Punta Gavilán Fm (Early Pliocene), Punta Gavilán, Venezuela; H 62 mm.	252
2, 5-7, 9-10. <i>Semicassis granulata</i> (Born, 1778)	248
2, 6. MHNG 1101/6, lectotype (designated here) of <i>Cassidea granulosa</i> Bruguière, 1792, and neotype of <i>Buccinum granulatum</i> Born, 1778, of <i>B. gibbum</i> and <i>B. recurvirostrum</i> of Gmelin, 1791, of <i>Cassis cepa</i> , <i>C. malum</i> , and <i>C. globulus</i> of Röding, 1798, of <i>B. inflatum</i> Shaw, 1811, of <i>C. corrugata</i> Swainson, 1822, of <i>C. minuta</i> Menke, 1828, and of <i>C. laevigata</i> Menke, 1829; Recent, "Barbados," West Indies; H 67 mm (from a color transparency).	
5, 7. GNS WM17118, 2 specimens, Recent, fishermen's traps, 250 m, Racket Bank, off of Barthelémy Island, West Indies, pres. D. Lamy (Fig. 5, H 78.5 mm; Fig. 7, H 72.5 mm).	
9-10. MHNG 1100/94/2, paralectotype of <i>Cassis abbreviata</i> , all data same as for lectotype (Pl. 70, Figs 4, 6); H 28.3 mm (from a color transparency).	
4. <i>Echinophoria hadra</i> (Woodring & Olsson, 1957). Incomplete specimen in collection of Bernard Landau, Cantaure Fm (late Early Miocene), near Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; H 30.5 mm.	243
8, 11. <i>Eudolium subfasciatum</i> Sacco, 1890. NMB H 18025, lower shellbed, Cantaure Fm (late Early Miocene), loc. NMB 17516, near Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; H 30.8 mm.	253



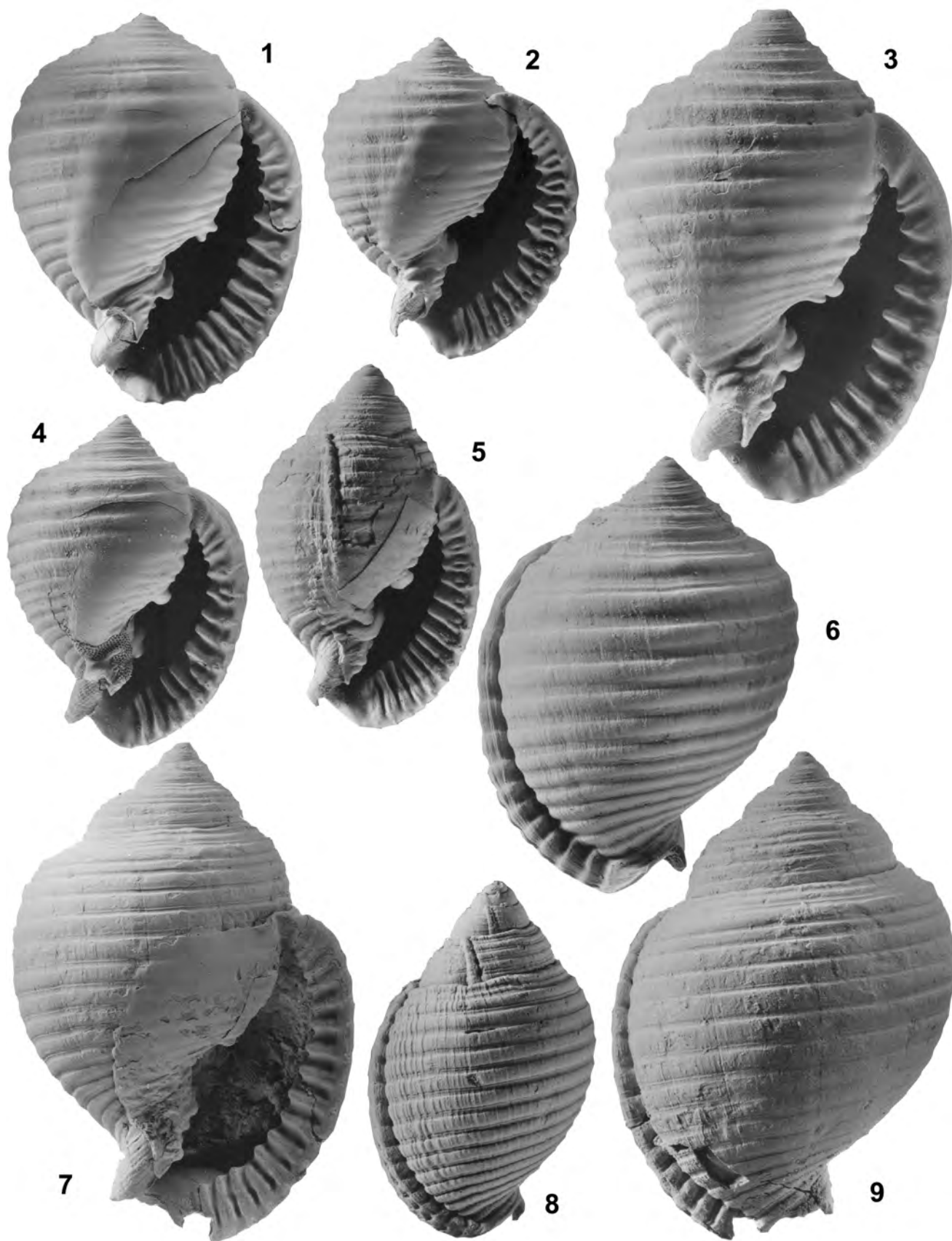
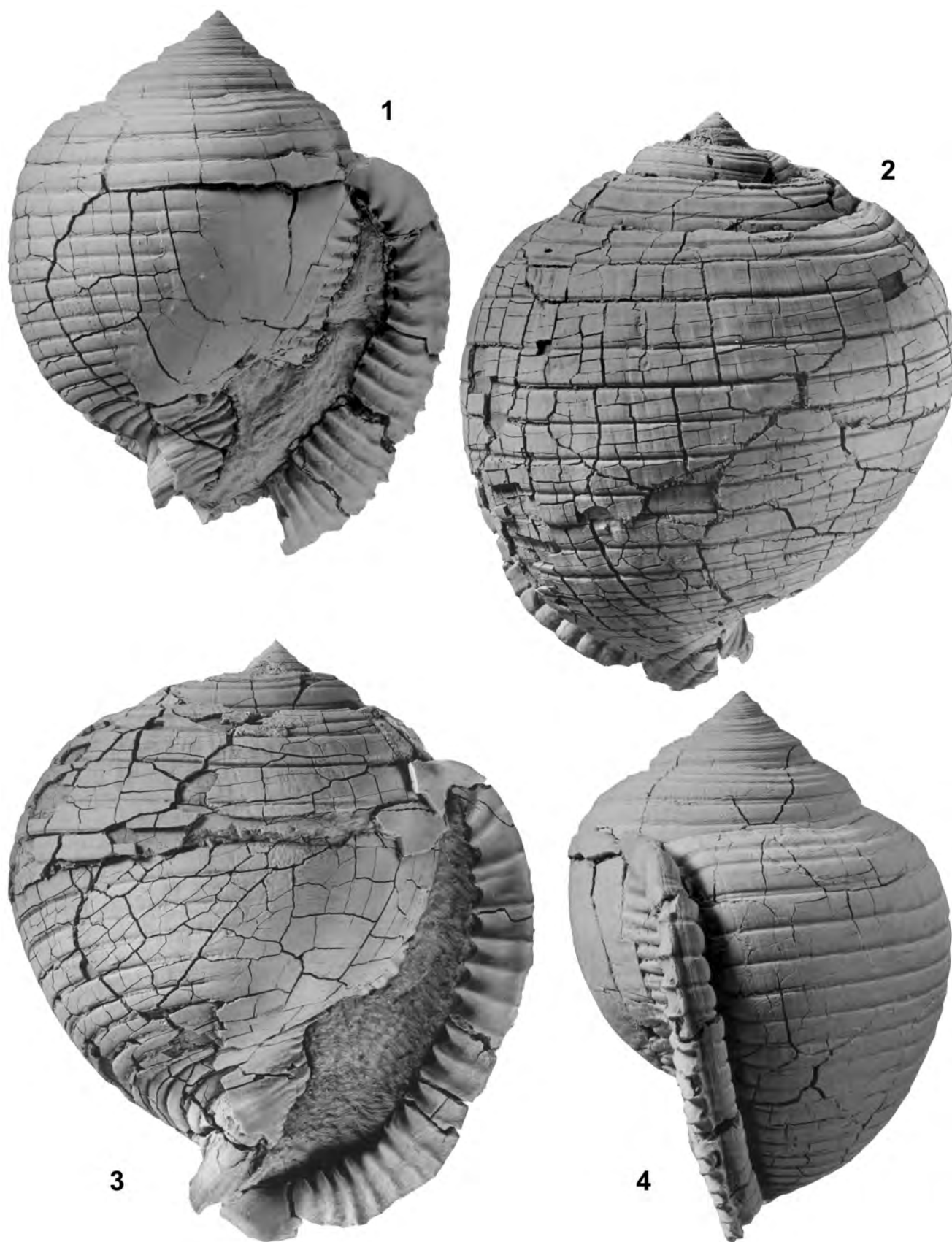


PLATE 72

Figure		Page
1-4, 6.	<i>Malea camura</i> Guppy, 1866	255
	1. NMB H 18026, "typical" specimen, Gurabo Fm (Late Miocene), loc. NMB 16919, mouth of Arroyo Bajón, upper Río Mao, Dominican Republic; H 71.2 mm.	
	2-4, 6. NMB H 18027-18029, 3 small specimens in one sample, Gurabo Fm (Late Miocene), loc. NMB 16913, Bluff 3 of Maury, <i>ca.</i> 400 m upstream from crossing on Cercado-Bulla road, upper Río Mao, Dominican Republic (Fig. 2, H 38.8 mm; Figs 3, 8, H 44.9 mm; Fig. 4, H 40.2 mm).	
5, 7-9.	<i>Malea elliptica</i> Pilsbry & Johnson, 1917	257
	5, 8. NMB H 18031, Cercado Fm (Late Miocene), loc. NMB 16842, Río Cana, just upstream from neck of major horseshoe bend at center of map in Saunders <i>et al.</i> (1986: text-fig. 15), Dominican Republic; H 32.7 mm.	
	7, 9. NMB H 18032, Baitoa Fm (late Early Miocene), loc. NMB 17283, bluff upstream from mouth of Arroyo Hondo, Río Yaque del Norte, Dominican Republic; H 76.4 mm.	

PLATE 73

Figure		Page
1-4.	<i>Malea goliath</i> Pilsbry & Johnson, 1917. NMB H 18034-18035, 2 specimens, Cayo Agua Fm (Pliocene), loc. NMB 18374, E side Punta Norte, Cayo Agua, Bocas del Toro Basin, Atlantic Panama (Figs 1, 4, H 102.6 mm; Figs 2-3, H 171 mm).	258



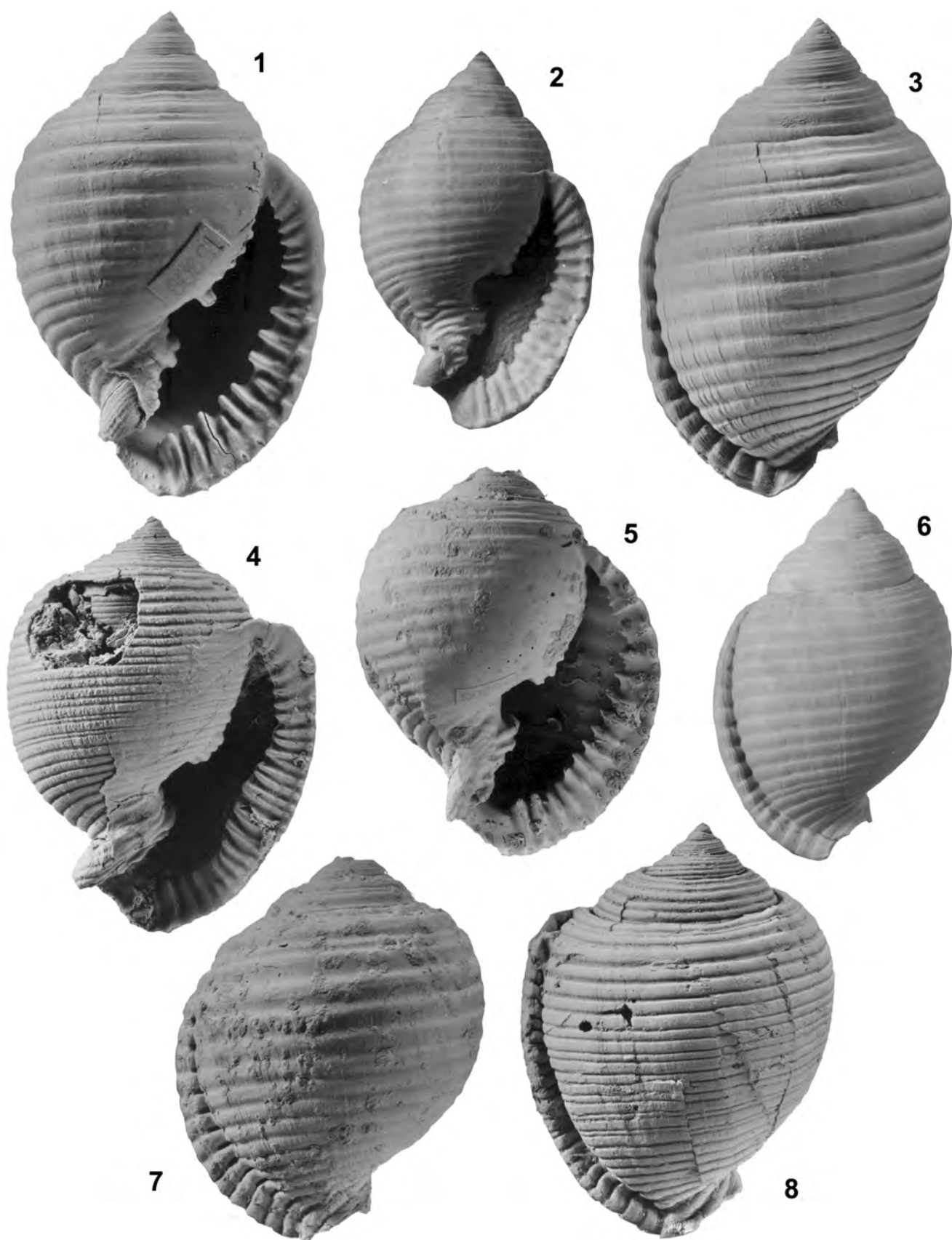
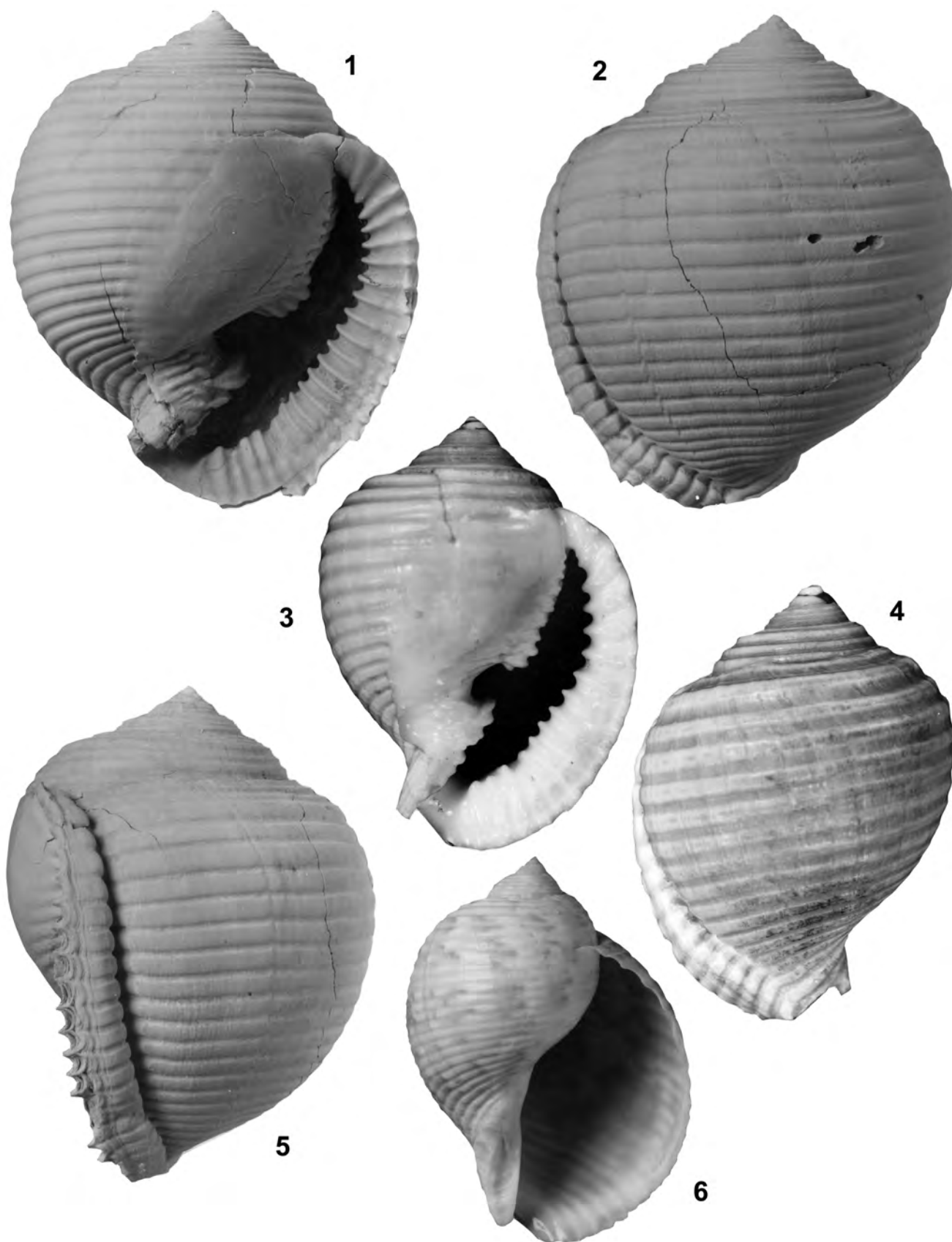


PLATE 74

Figure		Page
1-3, 6.	<i>Malea elliptica</i> Pilsbry & Johnson, 1917	257
	1, 3. NMB H 18030, Cercado Fm (Late Miocene), loc. NMB 15909, upper Río Gurabo, Dominican Republic; H 43.9 mm.	
	2, 6. ANSPIP 2590, holotype, Miocene-Early Pliocene, Dominican Republic, ex W. M. Gabb collection; H 53.5 mm.	
4, 8.	<i>Malea densecostata</i> (Rutsch, 1934). NMB H 1873, holotype, Punta Gavilán Fm (Early Pliocene), Punta Gavilán, Venezuela; H 76.3 mm.	257
5, 7.	<i>Malea ringens</i> (Swainson, 1822). NMB H 18036, Armuelles Fm (Pleistocene), loc. NMB 18306, S of Quebrada Corotú, 3.3 km N of Puerto Limones, Burica Peninsula, Pacific Panama; H 70.1 mm.	260

PLATE 75

Figure	Page
1-2, 5. <i>Malea goliath</i> Pilsbry & Johnson, 1917. Specimen in collection of Bernard Landau, Gurabo Fm (Early Pliocene), loc. TU 1215, Maury's zone D, bluffs for 1 km upstream from bridge on Los Quemados-Sabaneta road, Río Gurabo, Dominican Republic; H 60.1 mm. . . .	258
3-4. <i>Malea ringens</i> (Swainson, 1822). BMNH 1837.12.1.2718, lectotype, Recent, without locality [eastern Pacific; type locality here designated as Acapulco], ex Broderip and Bligh collections; H 52.2 mm.	260
6. <i>Tonna pennata</i> (Mörch, 1853). GNS WM14412, Recent, in turtlegrass on sand flats, South Bimini Island, Bahamas; H 103.7 mm.	266



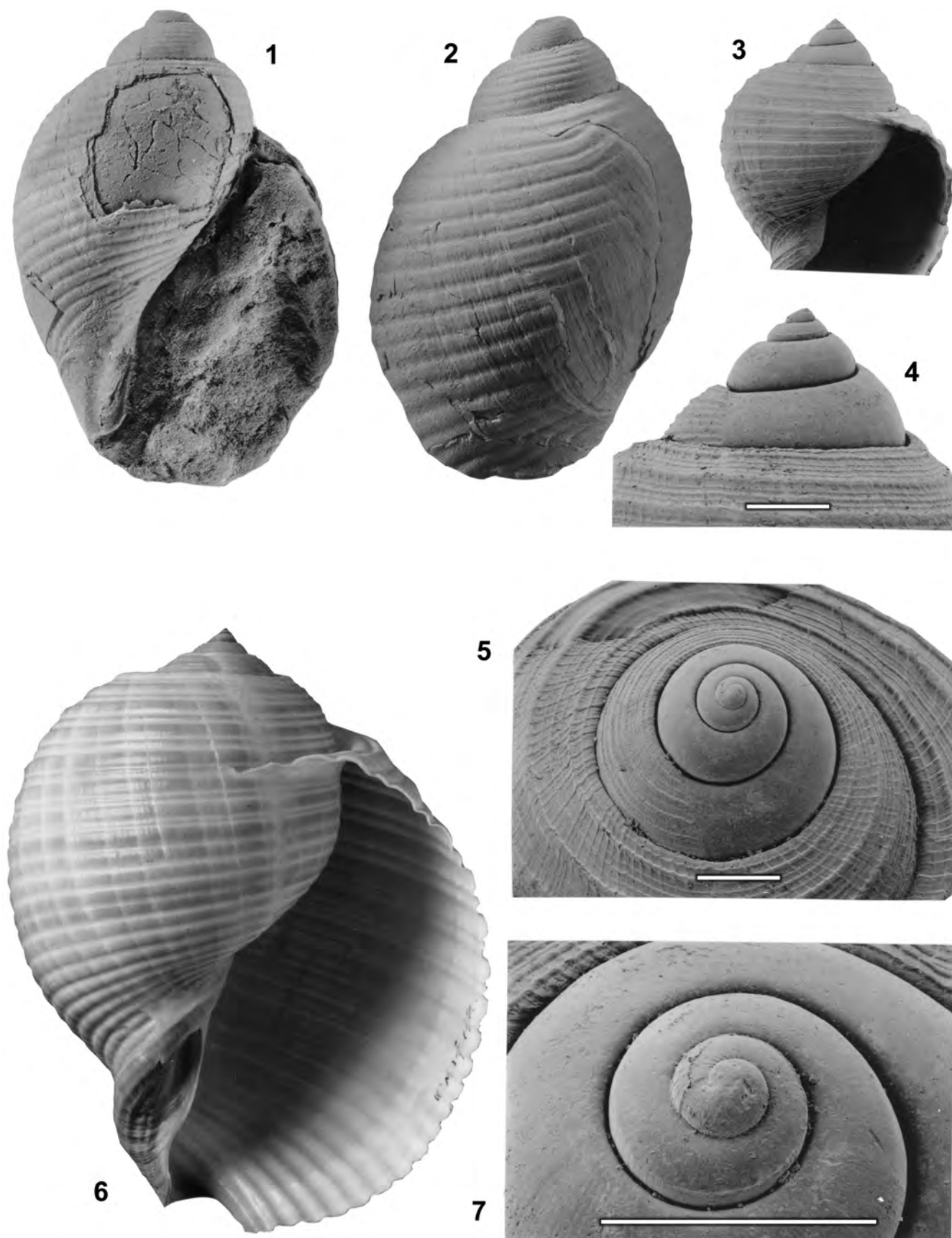
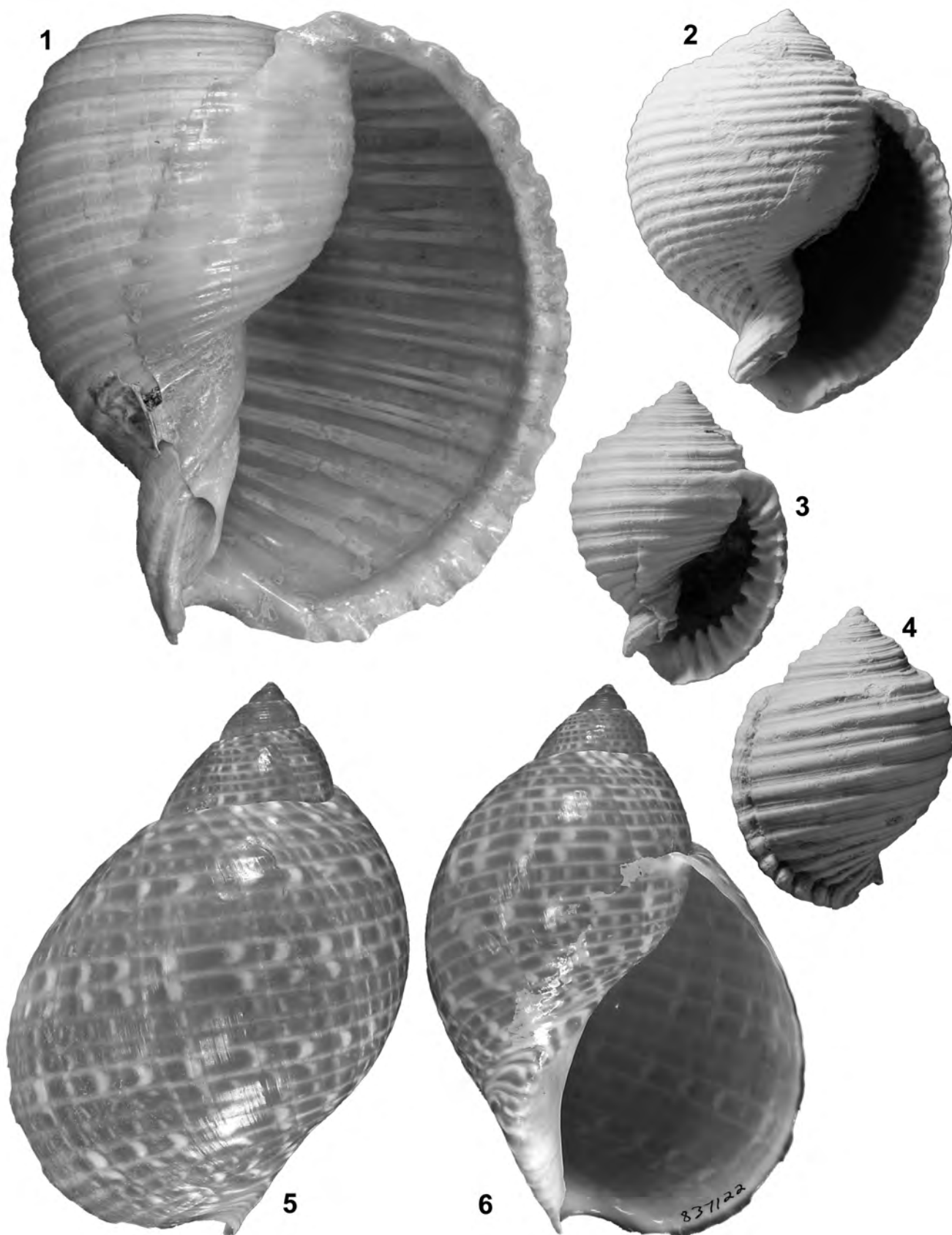


PLATE 76

Figure		Page
1-2.	<i>Tonna pennata</i> (Mörch, 1853). NMB H 18038, incomplete specimen, Gurabo Fm (Late Miocene/Early Pliocene), loc. TU 1246 (= NMB 19009), 1-2 km upstream from ford on Los Quemados-Sabaneta road, Río Gurabo, Dominican Republic; H 43.4 mm.	266
3-7.	<i>Tonna galea</i> (Linnaeus, 1758) 264 3-5, 7. NMB H 18037, Gurabo Fm (Late Miocene), loc. NMB 16928, mouth of Arroyo Bajón, upper Río Mao, Dominican Republic; SEM micrographs of juvenile specimen, showing most of specimen (Fig. 3, D 10.3 mm), protoconch and early teleoconch whorls (Figs 4-5) showing fine, regular axial ridges, and oblique view of protoconch apex (Fig. 7) showing low ridge demarcating protoconchs I and II; all scale bars = 1 mm. 6. GNS WM17122, Recent, dredged, 60 m, off coast of French Guyana, pres. D. Lamy; H 132.3 mm.	

PLATE 77		
Figure		Page
1.	<i>Tonna galea</i> (Linnaeus, 1758). USNM 125482, neotype (designated here) of <i>Dolium antillarum</i> var. <i>brasilianum</i> Mörch, 1877, Recent, off of Rio Grande do Sul, S Brazil; H 116 mm. . . .	264
2.	<i>Malea</i> n. sp. B. Specimen in collection of Bernard Landau, Cubagua Fm (Early Pliocene), Cañon de las Calderas, Cubagua Island, Venezuela; H 48.9 mm.	263
3-4.	<i>Malea</i> n. sp. A. Specimen in collection of Bernard Landau, Cantaure Fm (late Early Miocene), near Casa Cantaure, Paraguana Peninsula, Falcón, Venezuela; H 36.8 mm.	262
5-6.	<i>Tonna perdix</i> (Linnaeus, 1758). USNM 837122, neotype (designated here) of <i>Dolium plum-atum</i> Green, 1830, Recent, Bobi Island, Tobelo district, Halmahera Island, Indonesia; H 99.9 mm.	267



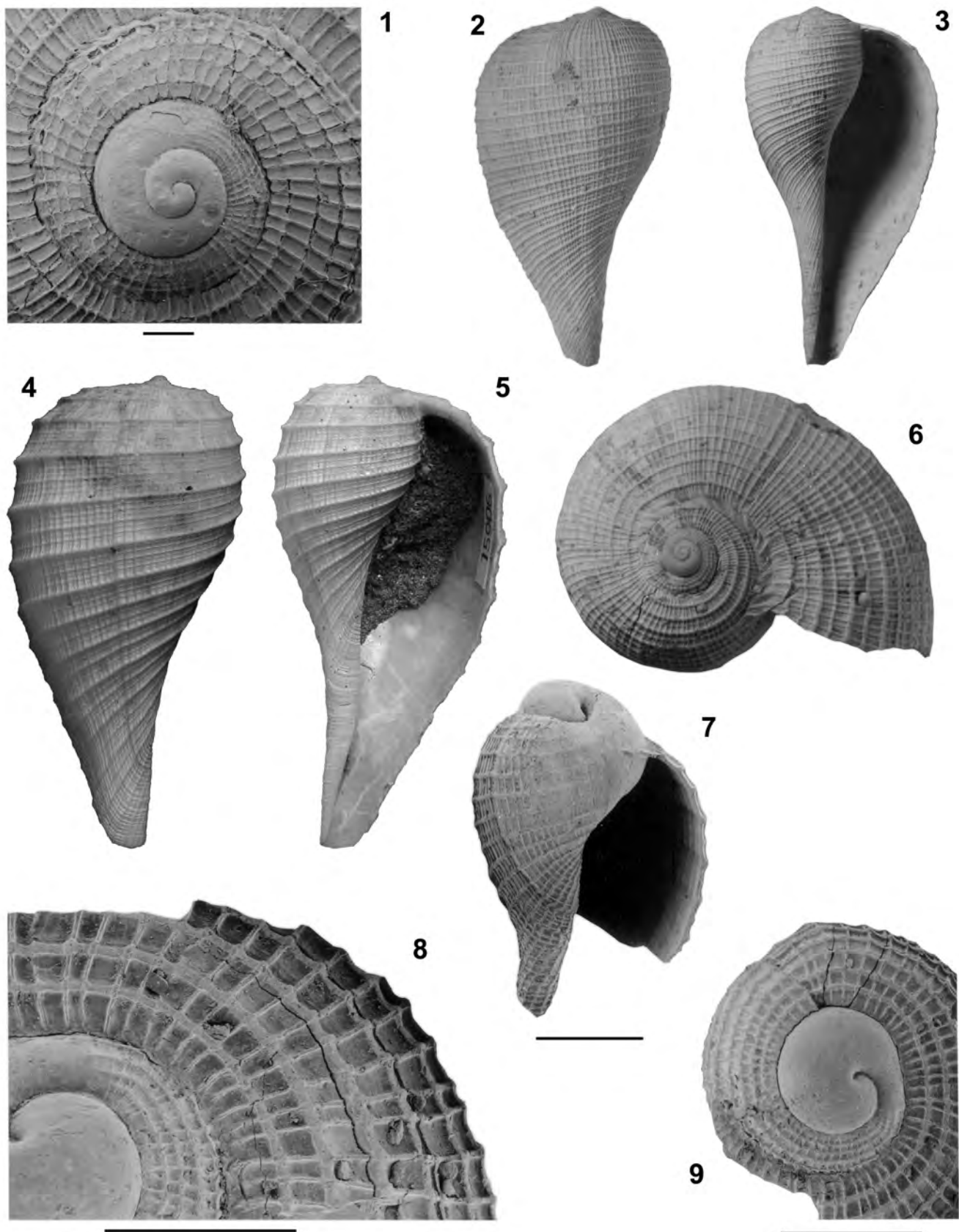
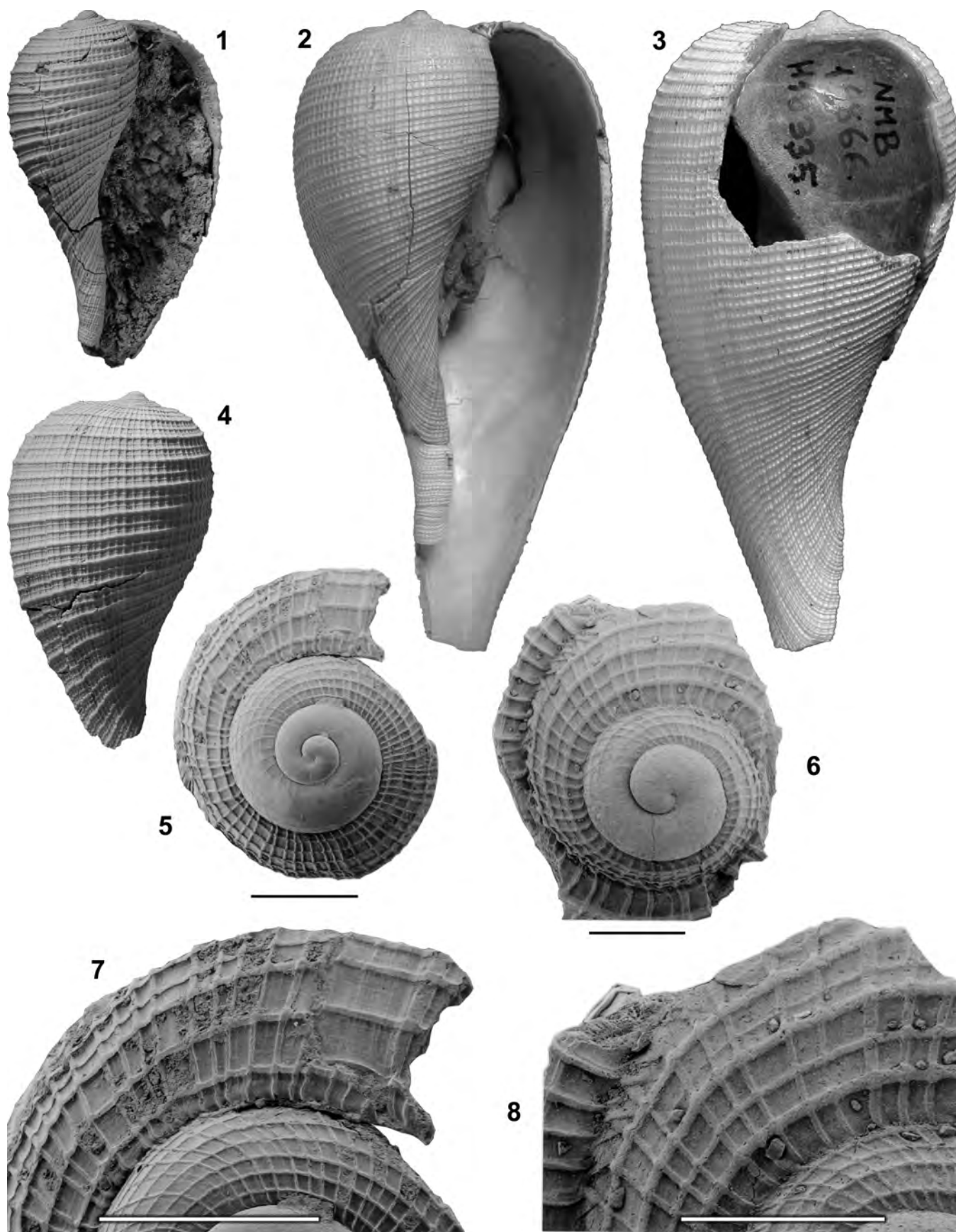


PLATE 78

Figure		Page
1-3, 6.	<i>Ficus pilsbryi</i> B. Smith, 1907	315
	1. USNM unreg., Bowden Shellbed (Late Pliocene), loc. USGS 2589, Bowden, Jamaica; SEM micrograph of protoconch of fragment; all scale bars = 1 mm.	
	2-3, 6. ANSP.IP 11144, lectotype (designated here), B. Smith's figured syntype, locality same as above; ventral and dorsal views (Figs 2-3, H 42.6 mm, D 23.5 mm) and apical view (Fig. 6, D 23.5 mm).	
4-5, 7-9.	<i>Ficus gibsonsmithi</i> n. sp.	313
	4-5. NMB H18340, holotype, Cercado Fm (Late Miocene), loc. NMB 15906, upper part of side stream entering at upper end of gorge, W bank, Río Gurabo, Dominican Republic; H 41.9 mm.	
	7-9. NMB H 18338, 2 juvenile paratypes, from type locality; apertural view (Fig. 7) and api- cal view (Figs 8-9, all scale bars = 1 mm) of specimen showing protoconch-teleoconch junc- tion clearly, and part of protoconch and sculpture of early teleoconch of second specimen.	

PLATE 79

Figure	Page
1, 4-5, 7. <i>Ficus bernardi</i> n. sp.	312
1, 4. BMNH Palaeontology Department, GG22903, holotype, Baitoa Fm (late Early Miocene), Arroyo Hondo, tributary of Río Yaque del Norte, Dominican Republic, coll. Bernard Landau; H 44.7 mm.	
5, 7. NMB H 18341, juvenile paratype, basal Mao Fm (Early Pliocene), loc. NMB 15833, E bank Río Gurabo, second bluff upstream from downstream end of exposure, near top of map of Saunders <i>et al.</i> (1986: text-fig. 4), Dominican Republic; SEM micrographs of protoconch (Fig. 5) and of early teleoconch sculpture (Fig. 7); all scale bars = 1 mm.	
2-3, 6, 8. <i>Ficus lisselongata</i> n. sp.	315
2-3. NMB H 18335, holotype, Gurabo Fm (Early Pliocene), loc. NMB 16866, Río Cana, Dominican Republic; W bank, next bluff downstream from NMB 16865, at upper quarter of map of localities in the Río Cana of Saunders <i>et al.</i> (1986: text-fig. 15); H 59.9 mm.	
6, 8. NMB H 18342, paratype, Cercado Fm (Late Miocene), loc. NMB 16857, 100-250 m upstream from ford, E bank, Río Cana, Dominican Republic; SEM micrographs of protoconch (Fig. 6) and of early teleoconch sculpture (Fig. 8); all scale bars = 1 mm.	



INDEX OF SUBJECTS AND FOSSIL LOCALITIES

This index is aimed particularly at providing access to fossil locality lists, and to places where species are recorded in detail from individual localities. Age abbreviations: Hol = Holocene; Pleist = Pleistocene; Plio = Pliocene; Mio = Miocene; E, M, L = Early, Middle, Late.

- abbreviations, institutions/repositories 40
ages of tropical American assemblages 9-11
Agueguexquite Fm, etc. (Plio), Mexico, species records
 Bursa
 corrugata 47
 rugosa 61
 Distorsio
 clathrata 82
 mcgintyi 93
 Monoplex aquatilis 147
Ameranella verruculosa, fossil records 117
Arbacia, echinoid, prey of *Cassis tuberosa* 223
Argobuccinum pustulosum, fossil records 103
Atlantic arrivals, Pleist-Hol 31-32, 34-35
Atlantic
 Costa Rica, see Costa Rica, Atlantic
 Panama, see Panama, Atlantic
Atlantiphile and Paciphile taxa 25-26
Aspa marginata, fossil records 67
Baitoa Fm (L Early Mio), Dominican Republic, species records
 Charonia lampas (?) 123
 Cymatiella vokesorum 209
 Cypraeacassis testiculus 229
 Distorsio
 mcgintyi 93
 simillima 98
 Ficus bernardi 313
 Malea
 elliptica 258
 goliath 259
 Monoplex
 cercadicus 148
 gurabonicus 155
 krebsii 159
 longispira 161
 parthenopeus 168
 pilearis 172
 Sconsia laevigata 237
 Semicassis reclusa 252
 Septa landaui 189
 Turritriton domingensis 193
Barbados
 fossil locality lists
 Naturhistorisches Museum Basel (NMB) 332
 United States Geological Survey (USGS) 340
 species records (Pleist)
 Bursa
 granularis 50
 rhodostoma 59
 Cassis flammea 217
 Charonia variegata 128
 Cypraeacassis testiculus 230
 Gutturium muricinum 139
 Monoplex
 aquatilis 147
 mundus 163
 pilearis 172
 Tonna pennata 268
 biogeographical faunal elements 23-25
 biogeography 8-35
 Bocas del Toro Basin (Mio-Pleist), Atlantic Panama, species records
 Bursa
 grayana 51
 ranelloides 56
 rugosa 61
 scrobilator 64
 Cassis
 altipsira 213
 costulifera 215
 Charonia variegata 128
 Crossata ventricosa 70
 Cymatium prae-femorale 133
 Distorsio
 clathrata 83
 decussata 89
 mcgintyi 93
 simillima 98
 Echinophoria hadra 243
 Linatella caudata 142
 Malea
 goliath 259
 ringens 261
 Marsupina bufo 74
 Monoplex
 krebsii 159
 panamensis 166
 Oocorys cf. *clericus* 241
 Semicassis granulata 250
 Tonna pennata 269
 Bowden, Jamaica (L Plio), species records
 Cassis
 altipsira (?) 213
 costulifera (?) 213, 215
 Cymatium femorale 132
 Distorsio
 clathrata 83
 mcgintyi 93
 simillima 98
 Ficus pilsbryi 316
 Malea camura 256
 Marsupina bufo 74
 Monoplex
 comptus 151
 krebsii 159
 parthenopeus 168
 Sconsia grayi 235
 Semicassis reclusa 252
 Turritriton labiosus 196
 Buccinidae, non-tonnoidean taxa referred 318
 Bursa, fossil records
 amphitrites 43
 chipolana 45
 corrugata 47-48
 granularis 50
 grayana 51
 natalensis 54

- ranelloides* 56
rhodostoma 59
rugosa 61-62
scrobilator 64
Bursidae, possible Cretaceous record 65
Cabestana felipponei, fossil records 120
CAI, see Central American Isthmus
California, USA (Plio-Pleist), species records
Cassis subtuberosa (= *C. flammea*?) 216-217
Crossata ventricosa 70
Distorsio constricta 86
Fusitriton oregonensis 107
Malea ringens 261-262
Monoplex amictus 145
Reticutriton elsmereensis 186-187
Turritriton gibbosus 195
Caloplaca sublobulata, lichen 202
Cantaure Fm (L Early Mio), Venezuela, species records
Bursa
rhodostoma 59
rugosa 62
Cypraeacassis
cantaurana 226
testiculus 229
Distorsio
biangulata 80
jungi 91
mcgintyi 94
Echinophoria hadra 244
Eudolium subfasciatum 254
Ipunina vladimiri (Litiopidae) 317
Malea n. sp. A 263
Monoplex
cercadicus 149
jackwinorum 155-156
krebsii 159
ritteri 173
Reticutriton n. sp.? 189
Sconsia laevigata 237
Semicassis aldrichi 246
Turritriton domingensis 194
Carriacou Island (Grenadine Islands)
fossil locality list, Naturhistorisches Museum Basel (NMB) 332
species records (M Mio)
Bursa rugosa 61
Distorsio
cf. *clathrata* 83
mcgintyi 94
Sassia cf. *apenninica* 200
Echinophoria famulans 242-243
Cassidulus cariboeorum (echinoid), prey of *Cassis tuberosa* 223
Cassis, fossil records
altispina 212-213
costulifera 215
delta 216
flammea 217
floridensis 218
jameshoubrieki 219
ketteri 219
madagascariensis 220
sulcifera 222-223
tuberosa 224
Cassis tuberosa, echinoid prey species 223
catalogs of tonnoideans, earlier 4-5
Caujarao Fm (Mio), Venezuela, species records
Bursa rugosa 62
Cassis cf. *sulcifera* 223
Distorsio mcgintyi 94
Malea camura 257
Monoplex lignarius 160
Semicassis reclusa 252
Turritriton domingensis 193-194
Central American Isthmus (CAI)
uplift, timing 4, 32-35, 35-38
uplift and geographical ranges 32-34
Bursa rugosa 33
Cassis 34
Crossata ventricosa 33
Distorsio
clathrata 33
decussata 33
Linatella caudata 33, 142
Malea ringens 34
Monoplex
lignarius 33
panamensis 33
wiegmanni 34
Sconsia grayi 34
Cercado Fm (L Mio), Dominican Republic, species records
Bursa
amphitrites 43
grayana 51
Cassis sulcifera 222
Charonia variegata 128
Cymatium praeferomale 133
Cypraeacassis testiculus 229
Distorsio
mcgintyi 93
simillima 98
Ficus
gibsonsmithi 314
lisselongata 315
Malea
camura 256
elliptica 258
goliath 258
Marsupina bufo 74
Monoplex
cercadicus 148-149
gurabonicus 155
parthenopeus 168
pilearis 172
Sconsia laevigata 237
Semicassis reclusa 252
Tonna
galea 266
pennata 269
Turritriton domingensis 194
Charonia, fossil records
lampas 123-124
variegata 128
Chile
species records (L Oligo-E Mio, Navidad Fm)
Ameranella verruculosa 117
Crassycymatium crassicornatum 130
Dalium cf. *dalli* 239

- Distorsio ringens* 96-97
Ranella chilena 112
Sassia
 armata 206
 kampyla (?) 203
 species records (Plio-Pleist)
 Argobuccinum pustulosum 103
 Fusitriton magellanicus 106
 Priene scabrum 110
Sassia
 kampyla 203
 leucostomoides 208
 Chipola Fm (L Early Mio), Florida, USA, species records
 Bursa
 chipolana 45
 rhodostoma 59
 Cassid delta 216
 Cypraeacassis chipolana 227
 Distorsio
 floridana (?) 89
 jungi (?) 91
 Eudolium subfasciatum 254
 Monoplex
 krebsii (?) 159
 ritteri 173
 n. sp. A 180-181
 Sconsia paralaevigata 238
 Semicassis aldrichi 246
 chiton, *Plaxiphora aurata* 202
 circum-Southern Ocean taxa, distributions 202
 chiton, *Plaxiphora aurata* 202
 lichens
 Caloplaca subglobulata 202
 Rinodina peloleuca 202
 Verrucaria durietzii 202
 Sassia kampyla 202
 tonnoideans 202
Clypeaster rosaceus & *C. subdepressus* (echinoids), prey of *Cassid tuberosa* 223
 Colombia
 fossil locality list, United States Geological Survey (USGS) 338
 species records (Mio-Plio)
 Bursa
 rugosa 61
 scrobilator 64
 Distorsio
 clathrata 83
 simillima 98
 Echinophoria hadra 243
 Linatella caudata 142
 Marsupina bufo 74
 Monoplex
 krebsii 159
 tranquebaricus 174
 Turritriton gibbosus 195
 species records (Pleist)
 Charonia variegata 128
 Cymatium femorale 132
 Marsupina bufo 74
 Monoplex
 nicobaricus 165
 pilearis 172
 comparison, time ranges, two coasts of America 26
- Costa Rica
 Atlantic 26-29
 fossil locality lists
 Naturhistorisches Museum Basel (NMB) 321
 Tulane University (TU) 335
 United States Geological Survey (USGS) 337
 species records, see Limón
 Pacific
 fossil locality lists
 Naturhistorisches Museum Basel (NMB) 322
 United States Geological Survey (USGS) 338
 species records (Mio-Pleist)
 Bursa rugosa 61
 Distorsio
 constricta 86
 decussata 88
 cf. *floridana* 90
 jenniernestae 90
 minoruohnishii 94
 Linatella caudata 142
 Malea ringens 261
 Marsupina
 bufo 74
 freya 75
 judensis 76
 nana 78
 Monoplex
 vestitus 178
 wiegmanni 180
 Semicassis centiquadrata 247
 Turritriton gibbosus 195
 species records (Pleist)
 Bursa rugosa 61
 Distorsio
 decussata 88
 jenniernestae 90
 minoruohnishii 94
 Malea ringens 261
 Marsupina
 bufo 74
 nana 78
 Monoplex wiegmanni 180
 Semicassis centiquadrata 247
 Turritriton gibbosus 195
Crassicymatium crassicornatum, fossil records 130
 Cretaceous, possible record of Bursidae 65
Crossata ventricosa, fossil records 70-71
 Cuba
 fossil locality list, United States Geological Survey (USGS) 339
 species records (Pleist)
 Bursa granularis 50
 Charonia variegata 128
 Cypraeacassis testiculus 230
 Gutturnium muricinum 139
 Monoplex
 aquatilis 147
 mundus 163
 pilearis 172
 Cubagua, Cumana & Punta Gavilán Fms (Plio), Venezuela, species records
 Bursa
 rhodostoma 59
 rugosa 62
 Cassid cf. flammea (?) 217

- Distorsio*
clathrata 83
mcgintyi 94
simillima 98
Echinophoria hadra 243-244
Linatella caudata 142
Malea
densecostata (Pta Gavilan) 257
n. sp. B (Cubagua) 263
Marsupina bufo 74
Monoplex
cercadicus 149
jackwinorum 156
krebsii 159
parthenopeus 169
tranquebaricus 174
Sconsia cf. *laevigata* 234
Semicassis senni 252
Turritriton domingensis 194
Cymatiella vokesorum, fossil records 209
Cymatium, fossil records
femorale 132
prae-femorale 133
tigrinum 136
Cypraeacassis, fossil records
cantaurana 226
chipolana 227
coarctata 227
tenuis 228
testiculus 229
wilmae 230
Dalium, fossil records
dalli 240
ecuadorianum 240
Darien (S Pacific Panama), see Panama, Darien
Diadema antillarum (echinoid), prey of *Cassia tuberosa* 233
Distorsio, fossil records 80
biangulata 80
clathrata 82-83
constricta 86
decussata 88-89
floridana 89-90
jenniernestae 90
jungi 91
mcgintyi 93-94
minoruohmishii (Pleist, Pacific Costa Rica) 94
ringens 96
simillima 98
distributions, circum-Southern Ocean taxa 202
chiton, *Plaxiphora aurata* 202
lichens
Caloplaca sublobulata 202
Rinodina peloleuca 202
Verrucaria durietzii 202
Sassia kampyla 202
tonnoideans 202
Dominican Republic
fossil locality lists
Naturhistorisches Museum Basel (NMB) 328
Tulane University (TU) 335
United States Geological Survey (USGS) 339
species records, see Baitoa, Cercado, Gurabo, Mao and unnamed formations
species records (Pleist)
Bursa granularis 50
Gutturium muricinum 139
Monoplex
aquatilis 147
nicobaricus 164
pilearis 172
Project 4, 7-8
early-named species, type material 38-40
Echinometra lucunter (echinoid), prey of *Cassia tuberosa* 223
echinoid prey species, *Cassia tuberosa* 223
Arbacia, *Cassidulus cariboeorum*, *Clypeaster rosaceus*, *C. subdepressus*,
Diadema antillarum, *Echinometra lucunter*, *Echinonius*, *Leodia*
sexiesperforata, *Lytechinus variegatus*, *Mellita quinquiesperforata*,
Meoma ventricosa, *Moiria*, *Plagiobrissus grandis*, *Tripneustes esculentus*, *T.*
subdepressus
Echinonius (echinoid), prey of *Cassia tuberosa* 223
Echinophoria, fossil records
famulans 243
hadra 243-244
woodringi 244
Ecuador
fossil locality lists
Naturhistorisches Museum Basel (NMB) 333
Tulane University (TU) 337
United States Geological Survey (USGS) 341
species records (Mio-Plio)
Bursa rugosa 62
Cassia cf. *altispira* 213
Crossata ventricosa 70
Dalium ecuadorianum 240
Distorsio
clathrata 83
decussata 89
sp. aff. *D. decussata* 88
Echinophoria woodringi 244
Malea ringens 261
Marsupina
freya 75
nana 78
Monoplex
amictus 145
aquatilis 147
panamensis 166
vestitus 178
wiegmanni 180
Neosconsia ecuadoriana (Buccinidae) 318
Semicassis centiquadrata 247
species records (Pleist)
Bursa corrugata 48
Cypraeacassis wilmae 230
Malea ringens 261
Semicassis centiquadrata 247
Turritriton labiosus 196
Eudolium subfasciatum, fossil records 254
extinction, geologically recent 30
faunal elements, biogeographical 23-25
Ficidae, non-tonnoidean taxa 311
Ficus, fossil records
bernardi 313
gibsonsmithi 314
lisselongata 315
pilsbryi 316

Florida, USA

fossil locality lists

- Naturhistorisches Museum Basel (NMB) 321
 Tulane University (TU) 334
 United States Geological Survey (USGS) 337

species records, see also Chipola and Shoal River Formations

species records (Plio-Hol)

Cassis

- floridensis* 218
jameshoubrieki 219
ketteri 219

Charonia lampas

- Distorsio clathrata* 82

- Eudolium marylandicum* (?) 254

- Linatella caudata* 142

Malea

- mareana* 259
springi 262

Monoplex

- krebsii* 159
nicobaricus 165
parthenopeus 168

Sconsia

- hodgii* 236
prolongata 238

- Semicassis granulata* 250

- Tonna galea* 266

fossil locality lists commence

Atlantic

- Costa Rica, see Costa Rica, Atlantic
 Panama, see Panama, Atlantic

Barbados

- Naturhistorisches Museum Basel (NMB) 332
 United States Geological Survey (USGS) 340

Carriacou Island, Grenadine Islands

- Naturhistorisches Museum Basel (NMB) 332

- Colombia, United States Geological Survey (USGS) 338

Costa Rica

Atlantic

- Naturhistorisches Museum Basel (NMB) 321
 Tulane University (TU) 335
 United States Geological Survey (USGS) 337

Pacific

- Naturhistorisches Museum Basel (NMB) 322
 United States Geological Survey (USGS) 338

- Cuba, United States Geological Survey (USGS) 339

Darien (S Pacific Panama), see Panama, Darien

Dominican Republic

- Naturhistorisches Museum Basel (NMB) 328
 Tulane University (TU) 335
 United States Geological Survey (USGS) 339

Ecuador

- Naturhistorisches Museum Basel (NMB) 333
 Tulane University (TU) 337
 United States Geological Survey (USGS) 341

Florida, USA

- Naturhistorisches Museum Basel (NMB) 321
 Tulane University (TU) 334
 United States Geological Survey (USGS) 337

- Guadeloupe, Naturhistorisches Museum Basel (NMB) 332

- Haiti, United States Geological Survey (USGS) 339

Jamaica

- Naturhistorisches Museum Basel (NMB) 328

- United States Geological Survey (USGS) 338

- Louisiana, USA, United States Geological Survey (USGS) 337

Mexico

- Naturhistorisches Museum Basel (NMB) 321

- Tulane University (TU) 335

- United States Geological Survey (USGS) 337

Pacific

- Costa Rica, see Costa Rica, Pacific

- Panama, see Panama, Pacific

Panama

Atlantic

- Naturhistorisches Museum Basel (NMB) 323

- Tulane University (TU) 335

- United States Geological Survey (USGS) 338

Darien

- Naturhistorisches Museum Basel (NMB) 327

- United States Geological Survey (USGS) 338

- Pacific, Naturhistorisches Museum Basel (NMB) 327

Trinidad

- Naturhistorisches Museum Basel (NMB) 332

- United States Geological Survey (USGS) 340

Venezuela

- Naturhistorisches Museum Basel (NMB) 332

- United States Geological Survey (USGS) 340

- Fusitriton oregonensis*, fossil records 107

- Galeodea* cf. *echinophora*, fossil records 232

Galapagos Islands (Plio-Pleist), species records

- Argobuccinum pustulosum* (?) 103

- Bursa corrugata* 47

- Cymatium tigrinum* 136

- Malea ringens* 261

- Monoplex keenae* 157

- Reticutriton lineatus* 187

Gatun Fm (M Mio-E Plio), Atlantic Panama, species records

- Bursa rugosa* 61

Distorsio

- clathrata* 83

- decussata* 88-89

- mcgintyi* 93

Malea

- ringens* 261

- n. sp. aff. *M. elliptica* 258

Monoplex

- aquaticus* 147

- cercadicus* 148

- gatunicus* 154

- krebsii* 158-159

- panamensis* 166

- parthenopeus* 168

- Sconsia grayi* 235

- Semicassis granulata* (?) 250

Turritriton

- domingensis* 193

- gibbosus* 195

- genera, geographically restricted 31

- geologically recent extinction 30

- geographically restricted genera 31

- geographical ranges and CAI uplift 32-34

- Bursa rugosa* 33

- Cassis* 34

- Crossata ventricosa* 33

Distorsio

- clathrata* 33

- decussata* 33
Linatella caudata 33, 142
Malea ringens 34
Monoplex
lignarius 33
panamensis 33
wiegmanni 34
Sconsia grayi 34
Guadeloupe
fossil locality list, Naturhistorisches Museum Basel (NMB) . . . 332
species records (Mio), *Charonia variegata* 128
Gurabo Fm (L Mio-E Plio), Dominican Republic, species records
Bursa
amphitrites 43
grayana 51
Cassis
altispira 213
sulcifera 222-223
Charonia
lampas 123
variegata 128
Cymatium praefermale 133
Cypraeacassis testiculus 229
Dalium dalli 240
Distorsio
clathrata 83
mcgintyi 93
simillima 98
Echinophoria hadra 243-244
Ficus lisselongata 315
Galeodea cf. *echinophora* 232
Malea
camura 256-257
elliptica 258
goliath 259
Marsupina bufo 74
Monoplex
cercadicus 148-149
gurabonicus 155
krebsii 159
longispira 161
parthenopeus 168
pilearis 172
Sassia warreni 200
Sconsia laevigata 237
Semicassis reclusa 252
Septa landaui 189
Tonna
galea 266
pennata 269
Turritriton domingensis 194
Gutturium muricinum, fossil records 139
Haiti
fossil locality list, United States Geological Survey (USGS) . . . 339
species records (Mio)
Charonia variegata 128
Dalium dalli 240
Distorsio simillima 98
Malea elliptica 256
Monoplex krebssii 158
Halgyrineum louisae, fossil records 108
Holocene-Pleistocene Atlantic arrivals 31-32, 34-35
Indian to Atlantic Oceans, larval transport 31-32
institutional abbreviations 40
Ipunina vladimiri (Litiopidae), fossil records 317
Jamaica
fossil locality lists
Naturhistorisches Museum Basel (NMB) 328
United States Geological Survey (USGS) 338
species records, see Bowden
larval transport, Indian to Atlantic Oceans 31-32
Leodia sexiesperforata (echinoid), prey of *Cassis tuberosa* 223
lichens
Caloplaca sublobulata 202
Rinodina peloleuca 202
Verrucaria durietzii 202
Limón, Atlantic Costa Rica (Plio-Pleist) (Moín & Banano Fms), species records
Aspa marginata 67
Bursa
natalensis 54
rhodostoma 59
scrobilator 64
Cassis altispira (?) 212-213
Charonia variegata 128
Cymatium femorale 132
Distorsio
clathrata 83
mcgintyi 93
simillima 98
Halgyrineum louisae 108-109
Malea ringens (?) 262
Marsupina bufo 74
Monoplex
comptus 151
krebsii 159
pilearis 172
Sconsia grayi 235
Semicassis granulata 250
Septa occidentalis 191
Tonna galea 266
Turritriton labiosus 196
Linatella caudata, fossil records 142
Litiopidae, non-tonnoidean taxa referred 316
locality maps
Bocas del Toro, Panama 11, Text-fig. 4
Dominican Republic 9-10, Text-figs 2-3
tropical America 8, Text-fig. 1
Louisiana, USA, fossil locality list, United States Geological Survey (USGS) 337
Lytechinus variegatus (echinoid), prey of *Cassis tuberosa* 223
Malea, fossil records
camura 256-257
densecostata 257
elliptica 258
goliath 259
mareana 260
ringens 261
springi 262
n. sp. A (Cantaure) 263
n. sp. B (Cubagua) 263
Mao Fm (E Plio), Dominican Republic, species records
Bursa
amphitrites 43
grayana 51
Cymatium praefermale 133

<i>Ficus bernardi</i>	313	<i>longispira</i>	161
<i>Marsupina bufo</i>	74	<i>mundus</i>	163
<i>Malea camura</i>	257	<i>nicobaricus</i>	164-165
<i>Monoplex parthenopeus</i>	168	<i>panamensis</i>	165-166
<i>Sassia warreni</i>	200	<i>parthenopeus</i>	168-169
<i>Sconsia laevigata</i>	237	<i>pilearis</i>	172
maps, localities		<i>ritteri</i>	173
Bocas del Toro, Panama	11, Text-fig. 4	<i>tranquebaricus</i>	174-175
Dominican Republic	9-10, Text-figs 2-3	<i>vestitus</i>	178
tropical America	8, Text-fig. 1	<i>wiegmanni</i>	180
Mare Fm (L Plio), Venezuela, species records		n. sp. A (Chipola)	180
<i>Cassis</i>		n. sp. B (Gatun)	181
<i>altispira</i>	213	Muricidae, non-tonnoidean taxa referred	318
<i>flammea</i>	217	museums visited	6-7
<i>madagascariensis</i>	220	Naturhistorisches Museum Basel (NMB) fossil locality lists	
<i>tuberosa</i>	224	Atlantic	
<i>Charonia lampas</i>	124	Costa Rica, see Costa Rica, Atlantic	
<i>Cymatium femorale</i>	132	Panama, see Panama, Atlantic	
<i>Distorsio clathrata</i>	83	Barbados	332
<i>Malea mareana</i>	259	Carriacou Island, Grenadine Islands	332
<i>Monoplex</i>		Costa Rica	
<i>krebsii</i>	159	Atlantic	321
<i>parthenopeus</i>	169	Pacific	322
<i>Semicassis granulata</i>	250	Darien (S Pacific Panama), see Panama, Darien	
<i>Tonna</i>		Dominican Republic	328
<i>galea</i>	266	Ecuador	333
<i>pennata</i>	269	Florida, USA	321
<i>Marsupina</i> , fossil records		Guadeloupe	332
<i>bufo</i>	74-75	Jamaica	328
<i>freya</i>	75	Mexico	321
<i>judensis</i>	76	Panama	
<i>nana</i>	78	Atlantic	323
<i>strongi</i>	79	Darien	327
<i>Mellita quinquesperforata</i> (echinoid), prey of <i>Cassis tuberosa</i>	223	Pacific	327
<i>Meoma ventricosa</i> (echinoid), prey of <i>Cassis tuberosa</i>	223	Trinidad	332
Mexico		Venezuela	332
fossil locality lists		<i>Neosconsia ecuadoriana</i> (Buccinidae), fossil records	318
Naturhistorisches Museum Basel (NMB)	321	non-tonnoidean families, taxa referred	
Tulane University (TU)	335	Buccinidae	318
United States Geological Survey (USGS)	337	Ficidae	311
Pacific (Pleist), species records		Litiopidae	316
<i>Crossata ventricosa</i>	70	Muricidae	318
<i>Cypraecassis</i>		<i>Oocorys</i> cf. <i>clericus</i> , fossil records	241
<i>coarctata</i>	227	operculum, <i>Tonna</i> , post-metamorphic	253
<i>wilmae</i>	230	Pacific	
<i>Fusitriton oregonensis</i>	107	Costa Rica, see Costa Rica, Pacific	
<i>Malea ringens</i>	261	Panama, see Panama, Pacific	
<i>Marsupina strongi</i>	79	Paciphile and Atlantiphile taxa	25-26
<i>Reticutriton lineatus</i>	187	Panama	
<i>Semicassis centiquadrata</i>	247	Atlantic	
species records, see Agueguexquite Fm		fossil locality lists	
<i>Moiria</i> (echinoid), prey of <i>Cassis tuberosa</i>	223	Naturhistorisches Museum Basel (NMB)	323
<i>Monoplex</i> , fossil records		Tulane University (TU)	335
<i>amictus</i>	145	United States Geological Survey (USGS)	338
<i>aquatilis</i>	147	species records, see Bocas del Toro Basin & Gatun Fm	
<i>cercadicus</i>	148-149	species records (Pleist)	
<i>comptus</i>	151	<i>Bursa</i>	
<i>gatunicus</i>	154	<i>granularis</i>	50
<i>gurabonicus</i>	155	<i>scrobilator</i>	64
<i>jackwinorum</i>	155-156	<i>Charonia variegata</i>	128
<i>keanae</i>	157	<i>Distorsio mcgintyi</i>	93
<i>krebsii</i>	159	<i>Monoplex</i>	
<i>lignarius</i>	160	<i>comptus</i>	151

- krebsii* 159
nicobaricus 164-165
pilearis 172
Sconsia grayi 235
 species records, see Bocas del Toro Basin and Gatun Fm
- Darien
- fossil locality lists
 Naturhistorisches Museum Basel (NMB) 327
 United States Geological Survey (USGS) 338
 species records (M-L Mio)
 Bursa rugosa 61
 Cassis cf. *altispira* 213
 Distorsio decussata 89
 Malea ringens 261
 Marsupina nana 78
 Monoplex
 panamensis 165-166
 wiegmanni 180
 Sconsia grayi 235
 Semicassis centiquadrata 247
- Pacific
- fossil locality list, Naturhistorisches Museum Basel (NMB) . . 327
 species records (Plio-Pleist)
 Bursa rugosa 61
 Cypraeacassis wilmae 230
 Distorsio
 constricta 86
 decussata 89
 Linatella caudata 142
 Malea ringens 261
 Marsupina nana 78
 Monoplex
 keenae 157
 vestitus 178
 wiegmanni 180
 Semicassis centiquadrata 247
- Paleontology Project (PPP) 4, 7-8
- Peru (Mio-Pleist), species records
- Crossata ventricosa* 70
Distorsio ringens 97
Marsupina freya 75
Priene scabrum 110-111
- phylogeny, Tonnoidea 4
- Plagiobrissus grandis* (echinoid), prey of *Cassis tuberosa* 223
- planktotrophy 4-6, 31-32, 202
- Plaxiphora aurata*, chiton 202
- Pleistocene-Holocene Atlantic arrivals 31-32, 34-35
- possible record of Bursidae, Cretaceous 65
- post-metamorphic operculum, *Tonna* 253
- prey species (echinoids), *Cassis tuberosa* 223
- Priene scabrum*, fossil records 110
- Ranella chilena*, fossil records 112
- Ranularia cynocephalum*, fossil records 183
- Recent tonnoideans listed
- eastern Atlantic/Mediterranean 22
 eastern Pacific 21
 Indo-West Pacific 22
 western Atlantic 21
- record of Bursidae, Cretaceous, possible 65
- referrals of taxa to non-tonnoidean families
- Buccinidae 318
 Ficidae 311
 Litiopidae 316
- Muricidae 318
 restricted genera, geographically 31
 repositories, abbreviations 40
Reticutriton, fossil records
 carlottae 186
 elsmerensis 186-187
 lineatus 187
 n. sp. (Cantaure) 189
 revisions of tonnoideans, earlier 4-5
Rinodina peloleuca, lichen 202
Sassia, fossil records
 cf. *apenninica* 200
 armata (= *bicegoi*) 206
 kampyla 203
 leucostomoides 208
 morgani 207
 warreni 200
Sconsia, fossil records
 grayi 235
 hodgii 236
 laevigata 237
 paralaevigata 238
 prolongata 238
Semicassis, fossil records
 aldrichi 246
 centiquadrata 247
 granulata 250
 reclusa 252
 senni 252
Septa, fossil records
 landaui 190
 occidentalis 191
 Shoal River Fm (M Mio), Florida, USA, species records
 Distorsio floridana 90
 Marsupina bufo 74
 Semicassis murrayi 246
 similarity indices 18-21, Tables 4-5
 Southern Ocean taxa, distributions 202
 chiton, *Plaxiphora aurata* 202
 lichens
 Caloplaca subglobulata 202
 Rinodina peloleuca 202
 Verrucaria durietzii 202
 Sassia kampyla 202
 tonnoideans 202
 speciation and width of ranges 29-30
 taxa referred to non-tonnoidean families
 Buccinidae 318
 Ficidae 311
 Litiopidae 316
 Muricidae 318
 teleplanic Tonnoidea 4-6, 31-32, 202
 time ranges, comparison, two coasts of America 26-29
 timing, uplift of CAI (Central American Isthmus) 4, 32-35, 35-38
Tonna
 fossil records
 galea 266
 pennata 269
 post-metamorphic operculum 253
 Tonnoidea
 circum-Southern Ocean 202
 composition of tropical American assemblages 11
 Dominican Republic 12-16, Table 1

other faunas	18, Table 3	<i>Malea camura</i>	256
Panama, Atlantic	16-18, Table 2	<i>Monoplex gurabonicus</i>	155
similarity indices	18-21, Tables 4-5	<i>Sconsia laevigata</i>	237
planktotrophic	4-6, 31-32, 202	<i>Tonna</i>	
tonnoideans, Recent faunas listed		<i>galea</i>	266
eastern Atlantic/Mediterranean	22	<i>pennata</i>	269
eastern Pacific	21	United States Geological Survey (USGS) fossil locality lists	
Indo-West Pacific	22	Atlantic	
western Atlantic	21	Costa Rica, see Costa Rica, Atlantic	
transport, larval, Indian to Atlantic Oceans	31-32	Panama, see Panama, Atlantic	
Trinidad		Barbados	340
fossil locality lists		Colombia	338
Naturhistorisches Museum Basel (NMB)	332	Costa Rica	
United States Geological Survey (USGS)	340	Atlantic	337
species records (Mio-Plio)		Pacific	338
<i>Bursa</i>		Cuba	339
<i>ranelloides</i>	56	Darien (S Pacific Panama), see Panama, Darien	
<i>rhodostoma</i>	59	Dominican Republic	339
<i>Charonia variegata</i>	128	Ecuador	341
<i>Cymatiella vokesorum</i>	209	Florida, USA	337
<i>Distorsio</i>		Haiti	339
<i>mcgintyi</i>	94	Jamaica	338
<i>simillima</i>	98	Louisiana, USA	337
<i>Linatella caudata</i>	142	Mexico	337
<i>Malea</i> cf. <i>camura</i> (?)	258	Panama	
<i>Monoplex lignarius</i>	160	Atlantic	338
<i>Semicassis maleaformis</i>	251	Darien	338
species records (Pleist-Hol)		Trinidad	340
<i>Marsupina bufo</i>	74	Venezuela	340
<i>Monoplex</i>		uplift, timing of CAI (Central American Isthmus)	4, 32-35, 35-38
<i>krebsii</i>	159	Venezuela	
<i>pilearis</i>	172	fossil locality lists	
<i>Tripneustes esculentus</i> , <i>T. subdepressus</i> (echinoids), prey of <i>Cassia tuberosa</i>	223	Naturhistorisches Museum Basel (NMB)	332
tropical American assemblages		United States Geological Survey (USGS)	340
ages	9-11	species records (Pleist-Hol)	
composition, Tonnoidea	11	<i>Bursa corrugata</i>	47
Dominican Republic	12-16, Table 1	<i>Charonia variegata</i>	128
other faunas	18, Table 3	<i>Cassia</i>	
Panama, Atlantic	16-18, Table 2	<i>flammea</i>	217
similarity indices	18-21, Tables 4-5	<i>tuberosa</i>	224
Tulane University (TU) locality lists		<i>Cypraeacassis testiculus</i>	229
Costa Rica, Atlantic	335	<i>Distorsio clathrata</i>	83
Dominican Republic	335	<i>Gutturnium muricinum</i>	139
Ecuador	337	<i>Linatella caudata</i>	142
Florida, USA	334	<i>Marsupina bufo</i>	74
Mexico	335	<i>Monoplex</i>	
Panama, Atlantic	335	<i>krebsii</i>	159
<i>Turritriton</i> , fossil records		<i>nicobaricus</i>	165
<i>domingensis</i>	193-194	<i>parthenopeus</i>	169
<i>gibbosus</i>	195	<i>pilearis</i>	172
<i>labiosus</i>	196	<i>tranquebaricus</i>	174
two coasts of America, time ranges, comparison	26-29	<i>Ranularia cynocephalum</i>	183
type material, early-named species	38-40	<i>Semicassis granulata</i>	250
unnamed formation (L Mio-E Plio), Dominican Republic, species records		<i>Tonna pennata</i>	269
<i>Cassia sulcifera</i>	222	species records, see Cantaure, Caujarao, Cubagua (etc.) and Mare Fms	
<i>Cypraeacassis testiculus</i>	229	<i>Verrucaria durietzii</i> , lichen	202
<i>Ficus bernardi</i>	313	width of ranges and speciation	29-30

INDEX OF TAXONOMIC NAMES

Bold page numbers refer to the main entries, at which genera and species are described. New names in this work also are in bold type. Many of the minor varieties proposed by (*e.g.*) de Gregorio, Sacco, and Settepasi are not indexed.

- abbotti*
Cassis 23, 211
Sassia 205
Tonna galea 265, 266
- abbreviata*
Cassis 247-250, 481-482; Pl. 70, Figs 4, 5; Pl. 71, Figs 9-10
Semicassis gibba 245
var. *centiquadrata*, *Phalium granulatum* 247
abbreviatum, *Phalium* (*Bezoardica*) *sulcosum* var. 247
abbreviatus, *Triton* 166
abyssorum, *Benthodolium* 240
acclivis, *Triton* (*Simpulum*) 166, 168
acuta occidentalis, *Distorsio* 81
adairense, *Cymatium* 194, 438; Pl. 49, Fig. 10
adansonii, *Tritonium* 173
adcocki, *Antephalium* 245, 306
aegrotum, *Cymatium* (*Ranularia*) 183
aegrotus, *Triton* 183-184, 433; Pl. 46, Figs 4, 8
affine var. *cubaniana*, *Gyrineum* 48
- affinis*
Bursa 48
granularis 48
Ranella 48
(*Bursa*) 48
afine var. *cubaniatum*, *Gyrineum* 48
africana, *Cabestana* 118
Afrocanidea gemma 138-139
- Akibumia*
flexibilis 23
n. sp. 22-23
orientalis 22
- alanbeui*, *Tonna* 23
alba, *Cassis* 216
albifasciata, *Ranella* 77
albocingulatus, *Triton* 138
- albofasciata*
boussingaulti, *Bursa* (*Marsupina*) 43, 59-62, 350, 353; Pl. 5, Fig. 14
Bursa 60
(*Colubrellina*) *nana* 77
Ranella 60, 77-78, 361, 362; Pl. 11, Fig. 1-2
- album*, *Dolium* 266, 268
alcocki, *Galeodea* 23
- aldrichi*
Cassis (*Phalium*) 246
Phalium (*Tylocassis*) 246
Semicassis 20, 24, 27, 173, **246**-247, 477; Pl. 68, Figs 6, 8
(*Tylocassis*) 246
- alexarthuri*, *Sconsia* 22, 32, 212, 235
- alfredensis*
Bursa 48, 50
Charonia 121
(*Negyrina*) 121
Nyctilochus 121, 123
- algoensis*, *Fusitriton* 105
- allani*
Galeodea (*Taieria*) 231
Taieria 231
- alligator*, *Phalium* 248, 250
allium, *Tonna* 23, 260
- altispira***, *Cassis* 13, 15-18, 20, 24, 27, 34, **212**-216, 219, 221-222, 450, 453; Pl. 55, Figs 1-3; Pl. 56, Figs 1, 3, 7
americanum, *Triton* 166, 168, 422; Pl. 41, Fig. 4
americanus, *Tritonium* 166
- Ameranella* **116**
keui 117
terrysmithae 117
verruculosa 113, **117**, 206, 390, 394, 397; Pl. 25, Figs 1, 4, 10, 12; Pl. 27, Figs 2, 4, 6; Pl. 28, Figs 2, 4, 6
- amictioideum*
Cymatium 143-144
Cymatium (*Gutturnium*) 143-144
- amictum*
Cymatium 143
Cymatium corrugatum 143
Cymatium (*Gutturnium*) 143
Cymatium (*Monoplex*) 143
Cymatium (*Monoplex*) *corrugatum* 143, 158
Cymatium (*Septa*) 143
tremperi, *Cymatium* (*Septa*) 143
Triton 143-144
- amictus*
Monoplex 19, 21, 25, 28-29, 44, 107, **144**-145, 158, 405, 410; Pl. 32, Figs 4-5; Pl. 35, Figs 1-5, 7
Triton (*Gutturnium*) 143
- amphiatlanticum*, *Cymatium comptum* 149, 151
- amphitrites*, *Bursa* 12-13, 24, 27, **42**-43, 59-60, 62, 72, 74-75, 77, 342; Pl. 1, Figs 1-4, 8
(*Colubrellina*) *caelata* 42-43, 59, 76-77
(*Lampasopsis*) 42, 60
(*Ranella*) 59
- Amphychthys cryptocentrus* . 94, 152, 173, 183, 192, 197, 225, 230, 270
- amphytridis*, *Tritocurrus* 39, 130, 135-**136**
- amplectens*, *Morionassa* 232
- ampullacea*
Ranella 101-103
Tonna 23
- anceps*
Cassis 210
Cassis (*Galeodocassis*) 210
- andamanensis*, *Ranularia* 23
- andersoni*
Echinophoria 242-244
Phalium (*Echinophoria*) 243
- andoi*, *Cymatium* 140, 170-171
- angasi*, *Semicassis* 23
- angelensis*
Priene oregonensis var. 106-107
Ranella (*Priene*) *oregonensis* var. 106
- Annaperenna verrucosa* 42
- Antephalium* 245
adcocki 245
semigranosum 245
sinuosum 245
sufflatum 245
- antillarum*

- Diadema* 223
Dolium 264-266
Simpulum 148
Triton 138-140
Triton (Gutturium) 138
 var. *brasiliensis*, *Dolium* 264-266, 494; Pl. 77, Fig. 1
 var. *cercadicum*, *Simpulum* 148-149
antiquum
Eudolium 253
Tuberculodolium 253
anus
Distorsio 23, 79-80
Distorta 79
Distortrix 79
Murex 79
Persona 79
apenes, *Semicassis (Echinophoria)* 228
apenninica
Charonia (Sassia) 199
Sassia 6, 15, 20,
 22, 27, 198-199, 200-202, 208, 242, 317, 441; Pl. 50, Fig. 1
apenninicum, *Triton* 198-199
aperturale, *Eutritonium (Sassia)* 121
Apollon
giganteus 114
marginatus 66
quercina 62, 64
 (Apollon)
Bursa
prodit 101
proditor 101
Ranella
argus 101
caelata 45
gigantea 114
nodosa 62
proditor 101-103
vexillum 101
aquatile
Cymatium 134, 145, 164, 170
 (Monoplex) 145
 (Septa) 145
occidentale, *Triton (Simpulum)* 145, 147
Tritonium 145
aquaticus
Cymatium (Lampusia) 145
Monoplex . 17, 19, 21-25, 27-28, **145**-149, 155, 158, 161-162, 169-
 172, 178, 191, 410, 413; Pl. 35, Figs 6, 8-16; Pl. 36, Figs 1-2
Triton 145, 147
 (Lampusia) 145
 (Simpulum) *pilearis* var. 145
Aquillus 118
cutaceus 118
pilearis 170
archipatagonica, *Urosalpinx* 320
Arbacia (echinoid) 223
Arcobelia limonensis 265
areola, *Phalium* 23
Argentina emilyae 319
Argobuccinum **100**
argus 101, 103
argus 101
ranelliforme 101
tumidum 101
casus 119
gemmiferum 113
giganteum 114-115
mediocre 100-101, 107
proditor 101-102, 116
proditor 101
tristanense 101, 103
pustulosum 4, 6, 21, **101**-103, 110,
 114, 202, 386, 389; Pl. 23, Figs 1, 3, 5, 7-9; Pl. 24, Figs 1-3
pustulosum 102
ranelliforme 102
tumidum 102
ranelliforme 101-102
proditor 101-102, 113-114
ranelliforme 101
tumidum 101
ranelliformis
ranelliformis 101
tumidum 101
retiolium 105
rude 109
scabrum 109
succinctum 137
sylviaense 106
tristanense 101-102
tumidum 101-102
vexillum 101
Argobuccinum
 (Eugyria) *gemmifera* 113
 (Fusitriton)
cancellatum cancellatum 105
cancellatum oregonense 106
cancellatum retiolium 105
coosense 106-107
laudandum 105
magellanicum 105
murrayi 105
oregonensis 106
 (Mayena) *australasium gemmiferum* 113
 (Priene)
pacifica 106-107
rude 109-110
scaber 109
scabrum 109
 (Ranella) *olearium* 114
 (Argobuccinum)
Ranella gigantea 114
Triton dautzenbergi 319-320
Tritonium
rude 109
scaber 109
argo-buccinum, *Tritonium* 101-102, 386
argus
Argobuccinum 101, 103
Murex 100-102, 179, 386
Ranella 101-102
 (Apollon) 101
 (Argobuccinum) 101
armata
Lotoria 23
Sassia 112, 117,
205-207, 445-446; Pl. 52, Figs 1-6, 12; Pl. 53, Figs. 3, 5-6

- armatus*, Triton 206, 446
armatum, Triton 205
arthritica
 Charonia (*Charoniella*) 198
 Proxicharonia 198
 Sassia 198
arthuri, *Ranularia* 23
Aspa 65
 depressa 66
 laevigata 66-67
 marginata 6, 19, 22, 24-25, 27, 41, 63, 66-68,
 354, 362, 442; Pl. 7, Fig. 2; Pl. 11, Fig. 3; Pl. 51, Figs 1-3
 subgranulata 66
 (*Aspa*)
 Bursa marginata 66
 Gyrineum marginatum 66
 Ranella marginata 66
asperrima, *Bursa* 21-22, 24, 28, 43-44, 342; Pl. 1, Fig. 9
atlantica
 Casmaria 22, 26
 Ranella gigantea var. 114
 Triton 126-127
aurata, *Plaxiphora* 202
australasia
 Biplex 111
 gemmifera
 Argobuccinum 113
 Ranella 113
 Mayena 111
 Ranella 4, 22, 111-113
 australasiana, *Charonia* 113
 australasium gemmiferum, *Argobuccinum* (*Mayena*) 113
 australasiae, *Monoplex* 142, 166, 168
australe
 Triton 121, 123
 Tritonium 121
australis, *Triton* 121
austriaca, *Bursa* (*Lampas*) 55
Austrofusus
 cancellatus 105
 glans 205
Austrosassia parkinsonia 198
Austrotriton radialis 198
awatii, *Bursa* 22
balteatus, *Triton* 173
bandatum, *Phalium*
 bandatum 23
 exaratum 23
bantamensis, *Purpura* (*Polytropha*) 140
barboui, *Eucorys* 22
barbudensis, *Sconsia* 233-235
barcellosi
 Bursa 114-116, 397; Pl. 28, Figs. 3, 7
 Ranella olearium 114
bardeyi, *Tutufa* (*Tutufa*) 22
bartschi
 clericus, *Oocorys* 241
 Eucorys 22
 Oocorys 241, 317
barthelemyi, *Triton* 119, 179
Bathgalea
 coronadoi 242
 (*Miogalea*)
- dalli* 243
 famulans 242
 hadra 242-243
bayeri, *Cymatium* 144, 177, 187, 188
 (*Gutturium*) 187
 (*Lampusia*) 177
beccarii, *Tritonium* 171
 (*Simpulum*) 170-171
Bechtelia strongi 71, 78
 (*Bechtelia*), *Gyrineum strongi* 78-79
Benthodolium abyssorum 240
benvegnuae, *Bursa*
 (*Bufonariella*) *ranelloides* 54-55
 (*Colubrillina*) 54-56, 349
 ranelloides 54
 ranelloides 54
bergeri
 Bursa 58
 Ranella 57-58
bernardi, *Ficus* 312-313, 315, 498; Pl. 79, Figs 1, 4-5, 7
berthae, *Tonna* 23
beui
 Cymatium (*Septa*) 191-192
 Personopsis 100
Bezoardica 244
 (*Bezoardica*), *Phalium sulcosum* var. *abbreviatum* 247
Bezoardicella 244
biangulata, *Distorsio*
 19, 24, 27, 80-81, 385; Pl. 22, Figs 4, 7; Pl. 51, Figs 4-5
bibbeyi, *Septa* 23, 191
bicarinata var. *decrensis*, *Cassis* (*Hypocassis*) 211
bicegoi
 Sassia 117, 205
 Tritonium 205-206, 445; Pl. 52, Figs 6, 12
 Tritonium (*Lotorium*) 117, 205
Biplex 31, 143
 aculeata 22, 77
 australasia 111
 bozzettii 22
 corrugata 45, 47-48
 perca 22
 pulchella 22
 pulchra 22, 77
 rubicola 48-50
bisulcata
 Cassis 244-245
 Semicassis 23, 244-245
bituberculare, *Gyrineum* 22
bituberculosa, *Echinophoria* 23
bituminata, *Galeodea* 23
blacketi, *Septa* 190-191, 437; Pl. 48, Fig. 9
bocasensis, *Sconsia* 233-235
boholic, *Tutufa* (*Tutufella*) 22
bondarevi, *Semicassis* 23
borisbeckeri, *Bursina* 22
borneana, *Cymatium* (*Lampusia*) *pileare* var. 177
boschi, *Ranularia* 23
boucheti, *Tonna* 23
boussingaulti, *Bursa* (*Marsupina*) *albofasciata*
 43, 59-62, 350; Pl. 5, Fig. 14
bowdenensis, *Bursa*
 crassa 72-73, 358; Pl. 9, Figs 7-8
 (*Marsupina*) *proavus* 72

- bozzettii*, *Biplex* 22
- brasiliiana*
- Dolium*
- antillarum* var. 264-266, 494; Pl. 77, Fig. 1
- perdix* var. 264, 266
- Tonna galea* 265, 494; Pl. 77, Fig. 1
- brasilianum*, *Triton* 166, 168
- brasiliensis*, *Fusitriton* 21, **104**-105
- breviaxis*, *Pisanianura* 23
- brocchii*, *Ranella* 66
- bronni*, *Ranella* 114
- bubo*, *Tutufa* 123, 132
- (*Tutufa*) 22
- Buccinatorium*
- marmoratum* 126
- nobile* 120
- variegatum* 120
- (*Buccinatorium*), *Triton nobilis* 126
- Buccinidae* 130, 239, 318, 474
- Buccinulum* 320
- Buccinum*
- caudatum* 137, 140-141
- cicatricosum* 248
- cornutum* 210
- gibbum* 248
- granulatum* 248-249, 482; Pl. 71, Figs 2, 6
- echinophorum* 230-232
- flammeum* 216
- fusoides* 122
- galea* 263-264
- inflatum* 244, 248
- intermedium* 242
- maculosum* 266-268
- marginatum* 65-67
- olearium* 264
- perdix* 263, 268
- pleurotoma* 66-67
- plicatum* 223-224
- pomum* 255
- pustulosum* 100-102, 113, 386; Pl. 23, Figs 5, 8
- recurvirostrum* 248
- ringens* 260-261
- rufum* 225
- striatum* 223
- tessellatum* 248
- testiculus* 228-229
- tuberosum* 221, 223-224
- undosum* 140
- undulatum* 248
- (*Buccinum*), *Triton cancellatum* 106
- Buffo bufo* 71
- Bufo bufo* 71
- bufo*
- Buffo* 71
- Bufo* 71
- Bufonaria* 72
- (*Marsupina*) 72
- Bursa* 72
- (*Colubrellina*) 72
- (*Marsupina*) 72
- Marsupina* . 12-13, 15-19, 21, 25, 27, 33, 35, 42, 60, 62, **72**-73, 75, 77, 123, 268, 358, 361; Pl. 9, Figs 1, 3-15; Pl. 10, Figs 1-3, 5
- Murex* 71-73
- Tutufa* (*Tutufa*) 22
- Bufonaria* 31, 65-66, 72, 75, 138, 241
- (*Aspa*) *marginata* 66
- bufo* 72
- cavitensis* 22
- cristinae* 22
- crumena* 22
- echinata* 22
- elegans* 22
- foliata* 22
- margaritula* 22, 66
- marginata* 66
- (*Marsupina*)
- bufo* 72
- nana* 77
- perelegans* 22
- pesleonis* 62, 64
- rana* 22
- scrobiculator* 62
- var. *minor* 62
- thersites* 22, 40
- (*Bufonaria*)
- Bursa*
- californica* 68
- spadicea* 72
- Bufonariella ranelloides* 54, 57
- (*Bufonariella*), *Bursa* 41
- chipolana* 44-45
- granularis* 49
- latitudo natalensis* 52
- nodosa* 63
- pelouatensis* 44
- ranelloides*
- benvegnuae* 54-55
- ranelloides* 54
- tenuisculpta* 54
- scrobiculata* 62
- scrobiculator* 62
- scrobilator* 63
- bufonia*, *Bursa* 22
- bufoniopsis*, *Bursa* 50-51
- bufonius*, *Murex* 41, 57
- Bulla ficus* 312
- bulla*, *Semicassis* 23
- burgessi*, *Distorsio* 23, 79
- Bursa* **41**
- affinis* 48
- albofasciata* 61
- alfredensis* 48, 50
- amphitrites* 12-13, 24, 27, **42**-43, 59-60, 62, 72, 74-75, 77, 342; Pl. 1, Figs 1-4, 8
- (*Apollon*)
- prodita* 101
- proditor* 101
- asperrima* 21-22, 24, 28, **43**-44, 342; Pl. 1, Fig. 9
- awatii* 22
- barcellosi* 114-116, 397; Pl. 28, Figs 3, 7
- bergeri* 57-58
- bufo* 72
- (*Bufonaria*)
- californica* 68
- spadicea* 72
- (*Bufonariella*)

- chipolana* 44-45
granularis 49
latitudo natalensis 52
nodosa 63
pelouatensis 44
ranelloides
 benvegnucae 54-55
 ranelloides 54
 tenuisculpta 54
scrobiculata 62
scrobiculator 62
scrobilator 63
bufonia 22
bufoniopsis 50-51
caelata 45, 47
 amphitrites 43, 59, 76-77
 louisa 45, 47
calcipicta 43, 59-60, 62, 68-70
californica 68
 sonorana 68-69
chipolana 19-20, 24-25, 27, 42-44, 45, 342; Pl. 1, Figs 5-7, 10
 (Colubrellina)
 benvegnucae 54, 56, 349
 bufo 72
 caelata 45
 amphitrites 42-43, 59, 75, 77
 candisata 41
 condita 41
 corrugata 45
 corrugata 45
 ponderosa 45
 pustulosa 45
 cubaniana 48
 finlayi 52
 granularia 49
 cubaniana 49
 granularis 48
 cubaniana 45, 48
 granularis 49
 latitudo natalensis 52
 nana albofasciata 77
 natalensis 52-53
 ranelloides
 benvegnucae 54
 ranelloides 54
 tenuisculpta 54
 tenuisculpta 54
 sp. A 59-60
 (Colubrinella) *canarica* 54-56
condita 22, 52
corrugata 19, 21-22, 24-25, 27-30, 34, 45-49, 52-53, 55,
 64-65, 176, 186, 342, 345; Pl. 1, Figs 11-13; Pl. 2, Figs 1-4, 6-7
 corrugata 45
 lineata 48, 50
 pustulosa 45
crassa 72
 bowdenensis 72-73, 358; Pl. 9, Figs 7-8
 caribbaea 72
 colombiana 72, 358; Pl. 9, Figs 3, 5
 proavus 72-73, 358; Pl. 9, Fig. 14
 (Crossata)
 californica 68
 ventricosa 68
cruentata 22, 43-44, 66-67
cubaniana 48
 intermedia 48, 50
cumingiana 48-49
dauidboschi 22
finlayi 52-54, 56
fosteri 22, 42
gibbosa 72-73, 361; Pl. 10, Figs 1-2
granularis 5, 21-22, 24-25, 27-
 28, 32, 42, 45-46, 48-50, 52, 54-55, 139, 346; Pl. 3, Figs 1, 3
 affinis 48
 cubaniana 48
grayana 12-
 13, 16-17, 21, 27, 45, 50-51, 57-58, 346; Pl. 3, Figs 2, 5-9
humilis 22
kowiensis 48-50
lamarckii 22
 (Lampadopsis)
 calcipicta 68, 70, 357; Pl. 8, Figs 3-4
 thomae 57
 (Lampas)
 austriaca 55
 cruentata 66
 ranelloides var. *tenuisculpta* 54, 56
 (Lampasopsis)
 amphitrites 42, 60
 rhodostoma 57
 thomae 57-58
latitudo 12, 22, 25, 42, 52-53
 natalensis 52
lessonae race *occidentalis* 55
lucaensis 22
luteostoma 22
mammata 57
marginata 66
 (Marsupina)
 albofasciata boussingaulti 43, 59-61, 350, 353; Pl. 5, Fig. 14
 bufo 72
 freya 75
 proavus 72
 bowdenensis 72
 spadicea 72
mexicana 45, 47, 342; Pl. 1, Fig. 12
monitata 41
nana 72, 75, 77
 jamanensis 76-77
natalensis 12,
 19, 21, 25, 37, 42-43, 52-54, 56, 63, 346; Pl. 3, Figs 10-13
nodosa 63
pelouatensis 43-45
pustulosa 29, 45, 47-48
 var. *jabik* 45, 47
pygmaea 54-56
quirihorai 22
 (Ranella)
 amphitrites 59
 rhodostoma 58
ranelloides 17-18, 22, 24, 27, 31-32, 34, 42,
 53-54, 55-57, 349; Pl. 4, Figs 1-9; Pl. 5, Figs 1-4, 6, 8
 benvegnucae 54-55
 ranelloides 54
 tenuisculpta 54
rhodostoma 18-19, 22, 24-

- 25, 27, 41, 49-52, **57-59**, 173, 350; Pl. 5, Figs 5, 7, 10-12, 15
rhodostoma 57
thomae 57-58
rosa 22
rugosa 2, 16-19, 21-22, 24, 26-28, 33, 42-45, **59-62**, 68-69,
160, 186, 242, 350, 353; Pl. 5, Figs 9, 13-14; Pl. 6, Figs 1-10
saundersi 41
scribiculator 62
scrobalator 6, 17,
19, 22, 24, 27, 41-42, 50, **62-64**, 354; Pl. 7, Figs 3-4, 6-7
scrubulator 63
sonorana 68, 70
spadicea 72
thomae 50, 57
(Tritonoranella) ranelloides 54
tuberosissima 22
tumida 100-103, 386; Pl. 23, Figs 1, 7
ventricosa 68
venustula 58
verrucosa 22
victrix 46, **65**, 345; Pl. 2, Fig. 5
zelebori 101
(Bursa), *Ranella*
affinis 48
thomae 57
Bursidae **41**
Bursina 31, 66, 72
borisbeckeri 22
fernandesi 22
fijiensis 22
gnorima 22
ignobilis 22
nobilis 22, 44
Cabestana **118**
africana 118-119
casus 118
cutacea 22, 119, 140, 175
dolarium 119
felipponei 21, **119-120**, 168, 397; Pl. 28, Figs 5, 8
gibbosa 194
labiosa 195
spengleri 119
tabulata 119
tetleyi 119
(Cabestana)
Cymatium
costatum 167
felipponei 119
labiosum 195
parthenopeus 167
tenuiliratum 197
tenuiliratus 197
Triton
labiosum 195
labiosus 195
Tritonium verbeeki 140-141
Cabestaninimorpha 142
euclia 152-153
exarata 152
tabulata 152
Cadium 263
galea 264
perdix 263
caduceus, *Dolarium* 118
Cadus 263-264
corturnix 268
galea 264
meleagris 268
perdix 263
(Cadus) *maculosa*, *Tonna* 267
mareana 267
caelata
amphitrites, *Bursa* 43
(Colubrellina) 42, 59, 75, 77
Bursa 43, 45-46
(Colubrellina) 45
louisia, *Bursa* 45, 47
Ranella 45, 47, 345; Pl. 2, Figs 1, 3
(Apollon) 45
caelatura
Cassis 242
Mariacassis 242
calata, *Ranella* 45
Calcarella spinosa 79, 82
calcipicta, *Bursa* 43, 59, 60, 62, 68-70
(Lampadopsis) 59, 68, 70, 357; Pl. 8, Figs 3-4
Caliagaleodea 231
(Caliagaleodea), *Galeodea californica* 231
californica
Bursa 68-69
(Bufonaria) 68
(Crossata) 68
californica, *Crossata* 68
Galeodea (Caliagaleodea) 231
Crossata 68-69, 71
Ranella 68-70, 357; Pl. 8, Fig. 7
(Lampas) 68
sonorana, *Crossata* 68
Caloplaca sublobulata (lichen) 202
Calydon 319
cameo, *Cassis* 219-220
camura
Dolium (Malea) 260
Malea
13, 16, 20, 24, 27, **255**, 256-261, 263, 485; Pl. 72, Figs 1-4, 6
var. *elliptica*, *Malea* 257
canaliculata
Semicassis 23
Tonna 23, 265, 267
canarica, *Bursa (Colubrinella)* 54-56
Cancellaria cossmanni 81-82
cancellatum
cancellatum, *Argobuccinum (Fusitriton)* 105
Fusitriton 105
oregonense, *Argobuccinum (Fusitriton)* 106
retiolium, *Argobuccinum (Fusitriton)* 105
Triton 104
(Buccinum) 106
(Lagena) 104
cancellatus
Austrofusus 105
Fusitriton 105
Fusus 104
murrayi, *Fusitriton* 105
Priene (Fusitriton) 104
Triton 104-106, 389; Pl. 23, Figs 2, 6; Pl. 24, Figs 5-6

- (Priene) 104
Tritonium (Priene) 106
cancellina, *Distorsio* 81, 99-100
candisata, *Ranella* 41
cantaurana, *Cypraecassis* 20, 27, 29,
 173, **225**, 226-229, 466, 469; Pl. 63, Figs 3-7; Pl. 64, Figs 4, 9
capax
Charonia 121, 123
lampas 121
euclioides, *Charonia* 121, 123
carbacea
Ficus 313-315
Pyrula 313
caribbaea, *Bursa crassa* 72-73
caribbaeum, *Cymatium* 182-183
 (Ranularia) 182, 195
moritinctum 182
cariboeum, *Cassidulus* (echinoid) 223
carlotae
Cymatium (Septra) 186
Simpulum 186
carlotae, *Reticutriton* 24-25, 27, **186**, 188-189
carnosa, *Echinophoria* 23
Casmaria 241
atlantica 22, 26
erinaceus 23
kalosmodix 23
nipponensis 23
perryi 23
ponderosa
ponderosa 23
unicolor 23
vibexmexicana 26
Cassida 210
Cassidae **210**
Cassidaria 230
cingulata 140-141
cingulifera 254
echinophora 230
laevigata 237
mutica 253
planotecta 231
 (Sconsia) *striata* 233
setosa 179
striata 232, 234
striatula 232
sublaevigata 233-235
washingtoniana 31
Cassidea 210
flammea 216
granulosa 248-251, 482; Pl. 71, Figs 2, 6
royana 244
sulcifera 221
testiculus 228
tuberosa 223
 (Cassidea), *Cassis*
tenuis 228
testiculus 228
Cassididae 210
Cassidulus cariboeum (echinoid) 223
Cassinac **210**
Cassinia 210
Cassis **210**
abbotti 23, 211
abbreviata 247-250, 481-482; Pl. 70, Figs 4, 6; Pl. 71, Figs 9-10
alba 216
altispira 13, 15-18, 20, 24, 27, 34, **212**-216,
 219, 221-222, 450, 453; Pl. 55, Figs 1-3; Pl. 56, Figs 1, 3, 7
anceps 210
bicarinata var. *decrensensis* 211
bisulcata 244-245
caelatura 242
cameo 219-220
 (Cassidea)
tenuis 228
testiculus 228
centiquadrata 247-248, 250
cepa 248-249, 482; Pl. 71, Figs 2, 6
coarctata 225-227
cornuta 23, 211, 220-221, 223-224
coronadoi 242
corrugata 248, 250, 482; Pl. 71, Figs 2, 6
costulifera 17,
 20, 24, 27, 213-**214**, 215, 217, 232, 453; Pl. 56, Figs 2, 4-6
 (Cypraecassis)
tenuis 228
testiculus 228
delta 20, 27, **215**-216, 222
doliata 247
fimbriata 23, 211
flammea 20, 22, 24, 27, 34,
 39, 212-215, **216**-217, 220-221, 224, 462; Pl. 61, Figs 1-2
flintensis **217**-218, 221
floridensis 24, 27, 214-215, **218**-219, 221-222, 454; Pl. 57, Figs 2-3
ketteri 219
 (Galeodocassis)
anceps 210
saccoi 210
globulus 248-249, 482; Pl. 71, Figs 2, 6
 (Goniogalea)
flammea 216
madagascariensis 210, 219
tuberosa 211
granulosa 248-250
hodgii 235-236
 (Hypocassis)
bicarinata var. *decrensensis* 211
fimbriata 211
inflata 248
monilifera 251
intermedia 251
jameshoubrieki 215, **218**-219
japonica 244
ketteri 24, 27, 213-215, **219**, 454; Pl. 57, Figs 1, 4
kreipli 23, 211
labiata 223-224
lactea 247-248
laevigata 248-249, 482; Pl. 71, Figs 2, 6
 (Levenia)
coarctata 225, 227, 230
coarctatus 227
madagascariensis 220
madagascariensis 20, 22, 24, 27, 210, 213-216,
 218-**219**, 220-224, 457-458; Pl. 58, Figs 1, 5; Pl. 59, Figs 1, 4
spinella 218, 220-221

- malum* 248-249, 482; Pl. 71, Figs 2, 6
mammillaris 211
(Mangalia) martini 211
marginata 66
marmorata 216
massenae 227-228, 457-458; Pl. 58, Fig. 4; Pl. 59, Fig. 3
minuta 248-249, 482; Pl. 71, Figs 2, 6
monilifer 251
monilifera 251-252
nana 23, 211
(Nannocassis) nana 211
norai 7, 22-25, 27, 213, 215-216, **221**, 450; Pl. 55, Figs 4-5
patamakanthini 23, 211
(Phalium)
 aldrichi 246
 dalli 242-243
 moniliferum 251
plicata 217, 223-224
pyrum 244
reclusa 248, 251-252
recurvirostrum 248
ringens 254-255, 260
rotundata 219-220
schnireli 218-219
(Semicassis)
 abbreviata 248
 centiquadrata 247
 gibba 248
 granulata 248
 granulatus 247
 inflata 248
 lactea 248
 tegalensis 140
 undulata 248
spinella 218
striata 233-234
striatula 232
subtuberosa 34, 216-217
sulcifera 13, 15, 20, 24, 27,
 213-217, **221**-223, 458, 461; Pl. 59, Fig. 2; Pl. 60, Figs 1-8
tegalensis 141
tenuis 227-228
tessellata 22, 214, 219, 248
testiculus 228-229
torva 23, 211
triangularis 223-224
tuberosa 15, 20, 22,
 24-25, 27, 212-217, 219-**223**, 224-225, 462; Pl. 61, Figs 4-5
 echinoid prey species listed 223
ventricosa 248
Cassidoma saccoi 210
casus
 Argobuccinum 119
 Cabestana 118-119
caudata
 Linatella 6, 17, 19, 21-28, 33-34, **140**-, 148,
 166, 179, 274, 409, 466; Pl. 34, Figs 6-9; Pl. 63, Figs 8, 11
 (*Linatella*) 140
 Ranella 175
 Ranularia 23, 140
 Tritonocauda 181
caudatum
 Buccinum 137, 140-141
 Cymatium 140
 (*Linatella*) 140
 (*Ranularia*) 140
caudatus
 Murex 140, 181
 Triton 175
cavitensis, Bufonaria 22
cecilianum, Cymatium 147-148
cecilianus, Monoplex **147**-148, 413; Pl. 36, Fig. 4
Celatoconus 318
centiquadrata
 Cassis 247-248, 250
 (*Semicassis*) 247
 Phalium granulatum abbreviata var. 247
 Semicassis 20, 22,
 25, 28-29, 33, 35, 186, **247**, 250-251, 478; Pl. 69, Figs 1-2
 granulata 247
centiquadratum, Phalium (Tylocassis) granulatum 245, 247
cepa, Cassis 248-249, 482; Pl. 71, Figs 2, 6
cercadicum, Simpulium antillarum var. 148
cercadicus, Monoplex . 13-14, 16-17, 19, 24-25, 28, 37, **148**-149, 155-
 156, 161, 173, 179-180, 413, 434; Pl. 36, Figs 6-9, 11; Pl. 47, Fig. 16
Charonia **120**
 alfredensis 121
 australasiana 113
 capax 121
 euclioides 121
 (*Charoniella*) *arthritica* 198
 crassa 120
 euclia 121
 instructa 121
 guichemerri 120
 gyrinoidea 121
 rubicunda 121
 var. *sauliae* 121
 lampas 4, 6, 13-14, 19, 22, 24, 32, 113, 115-
 116, **120**, 121-122, 124, 132, 153, 169, 202, 398; Pl. 29, Figs 1-6
 capax 121-122
 lampas 121-122
 macilenta 122
 pustulata 121-122
 rubicunda 121-122
 sauliae 121-122
 weisbordi 121-124, 398; Pl. 29, Figs 4, 6
mirabilis 121, 123
(Negyrina)
 alfredensis 121
 kampyla 202
 nobilis 127
 nodifera 121
 nodiferum mirabilis 121
 poecilostoma 113
 powelli 121, 123
 pumilio 208
 pustulata 121
 sauliae 121
 macilenta 121, 123
 seguenzae 22, 25, **124**-125, 127-128
 tritonis 21, 22, 24-25, 28, 31-32, 113, 120, 122, **125**-128
 nobilis 127
 tritonis 126
 variegata 125, 127
 var. *nobilis* 127

- variegata* 13-14, 16-17, 19,
 21-22, 24, 27, 59, 122, 124-**126**, 127-128, 401; Pl. 30, Figs 1-2
ventricosa 120
veterior 120
 (Charonia), Tritonium
 nodiferum 121
 mirabilis 121
Charoniella subdistorta 198
 (Charoniella), Charonia *arthritica* 198
chemnitzii, Triton 141, 173, 179
chilena, Ranella **111**-112, 393; Pl. 26, Figs 1-4, 6-8
chinensis, Tonna 23
chipolana
 Bursa 19-20, 24, 27, 42-**44**, 45, 342; Pl. 1, Figs 5-7, 10
 Cypraeacassis 20, 25, 27-
 28, 35, 173, **226**-227, 457, 465; Pl. 58, Figs 2-3; Pl. 62, Fig. 7
china, Marsupina 72, 75
chlorostoma
 Cymatium 164
 (*Lampusia*) 164
 Lampusia 164
 Triton 164
chlorostomum
 Cymatium 164
 Triton 163, 164
 (*Lampusia*) 164
 (*Simpulum*) 164
 var. *pumilio*, Triton (*Lampusia*) 164
chlorostomus, Triton 163
 (*Lampresia*) 164
 (*Simpulum*) 164
chlorostomoides
 Cymatium (*Septa*) 149
 Monoplex 24, **149**, 155, 180
 Simpulum 149
cicatricosa
 Cassis (*Semicassis*) 245, 248
 peristephes, *Semicassis* 245, 248, 250
 Semicassis 248
cicatricosum
 Buccinum 248-249
 Phalium 248-249
 (*Semicassis*) 248
 (*Tylocassis*) 245, 248
 granulatum forma 248
cinereus, *Fusus* 319
cingulata
 Cassidaria 140, 141
 Linatella 140, 141
cingulatum
 Cymatium 140
 (*Linatella*) 140
 peninsulum, *Cymatium* (*Linatella*) 140, 141
cingulifera, *Cassidaria* 254
clandestina, *Gelagna* 137
clandestinum
 Cymatium (*Linatella*) 137
 Triton 137
 (*Lagena*) 137
 Tritonium (*Gelagna*) 137
clandestinus
 Murex 137
 Ranularia (*Lagena*) 137
 Triton 137
 (*Linatella*) 137
clathrata
 Distorsio 13, 16-19, 21, 24, 26-
 28, 33, 80, **81**, 82-87, 89, 92, 95, 365; Pl. 12, Figs 1-10
 (*Rhysema*) 81, 99
 reticulatus var. 81
 forma *robinsoni*, *Distorsio* 81
 Persona 81
clathratum, Triton 81
clathratus
 Distorsio 81
 reticularis var. 81
 Distortrix reticulata var. 81, 92
 gatunensis, *Distorsio* 81, 83, 87
clatrata, *Distorsio* 81
clavator, *Murex* 181
clericus, *Oocorys* 17, 22, 27, **241**, 317, 470; Pl. 65, Figs 1, 3
 bartschi 241
closeli, *Septa* 23, 191
Clypeaster (echinoid)
 rosaceus 223
 subdepressus 223
coarctata
 Cassis 225, 227
 (*Levenia*) 227
 Cypraeacassis 21,
 28, 225-**227**, 230, 245, 465, 466; Pl. 62, Fig. 2; Pl. 63, Figs 1-2
 (*Levenia*) 227, 230
coarctatus, *Cassis* (*Levenia*) 227
cochlear
 Ostrea 100
 Pycnodonte 100
colombiana, *Bursa crassa* 72, 358; Pl. 9, Figs 3, 5
Colubrellina
 corrugata 48
 (*Dulcerana*) *granularis* 48
 granularis 48
 jabick 48
 semigranosa 48
 (Colubrellina), *Bursa*
 benvegnuae 54, 56, 351
 bufo 72
 caelata 45
 amphitrites 42, 59, 75, 77
 canarica 54, 56
 candisata 41
 condita 41
 corrugata 45
 corrugata 45
 ponderosa 45
 pustulosa 45
 cubaniana 48
 finlayi 52
 granularia 49
 cubaniana 49
 granularis 49
 cubaniana 45, 48
 granularis 49
 latitudo natalensis 52
 nana albofasciata 77
 natalensis 52-53
 ranelloides 54

- benvegnuae* 54
ranelloides 54
tenuisculpta 54
scrobilator
scrobilator 63
coriacea 63
tenuisculpta 54
 sp. A 59-60
Cominella maculosa 267
communis, Ficus 314-315
commutatum, Tritonium 59
commutatus, Triton 126
comptum
amphiatlanticum, Cymatium 149, 151
Cymatium 149, 177, 184
 (Monoplex) 149, 154
 (Septa) 149
 (Turrtriton) 149
comptus
 Monoplex 14, 19, 21-25,
 27, 32, **149**, 150-152, 154, 177, 188, 413; Pl. 36, Figs 10, 14
 Triton 149
Concholepas 120
concinnum, Gyrineum 22
conditus, Murex 41
confinis, Triton 137
constricta
Distorsia 87
Distorsio 19, 21,
 25, 28, 80, **84**, 85-87, 89, 92-94, 99, 366; Pl. 13, Figs 4-5, 9
 (Rhysema) 84, 90
floridana, Distorsio 92
constrictus
Distorsio 84, 86, 90, 92
simillimus, Distorsio 97
Triton 84, 86-87, 90, 92
contabulatum, Tritonium 141
Conus 211
coosense, Argobuccinum (Fusitriton) 106-107
corbiculata, Ranella (Priene) 106
corbiculatum, Gyrineum 106
mediocre var. 106-107
cornuta, Cassis 23, 210-211, 220-224
cornutum, Buccinum 210
cornutus, Monoplex 151
coronadoi
Bathygalea 242
Cassis 242
corrugata
Biplex 45, 47-48
Bursa 19, 21-22, 24-25, 27-30, 34, **45-49**, 52-53, 55, 64-
 65, 176, 186, 342, 345; Pl. 1, Figs 11-13; Pl. 2, Figs 1-4, 6-7
 (Colubrellina) 45
Cassis 248, 250, 482; Pl. 71, Figs 2, 6
corrugata, Bursa 45
 (Colubrellina) 45
lineata, Bursa 48, 50
ponderosa, Bursa (Colubrellina) 45
pustulosa, Bursa (Colubrellina) 45
Ranella (Lampas) 45
corrugatum
amictum, Cymatium 143
 (Monoplex) 143, 158
krebsii, Cymatium
 (Monoplex) 157
 (Septa) 157
tremperi, Cymatium 143
 (Monoplex) 143
 var. *krebsii, Triton (Simpulum)* 157
corrugatus, Monoplex 22, 25, 29, 55, 143-144, 158-159, 171
cossmanni, Cancellaria 81-82
costatum
Cymatium 156-157, 167
 (Cabestana) 167
 (Monoplex) 167
Lotorium 166
Triton (Lampusia) 166
Tritonium 166
costatus
Murex 156, 166, 168
Triton (Simpulum) 166
costulatus, Murex 166, 168
costulifera, Cassis
 . . 17, 20, 24, 27, 213-**214**, 215, 217, 232, 453; Pl. 56, Figs 2, 4-6
corturnix, Cadus 268
cowlitzi, Gyrinopsis 111
crassa
bowdenensis, Bursa 72-73, 358; Pl. 9, Figs 7-8
Bursa 72
caribbaea, Bursa 72
Charonia 120
colombiana, Bursa 72, 358; Pl. 9, Figs 3, 5
proavus, Bursa 72-73, 358; Pl. 9, Fig. 14
Ranella 72
crassicornatum, Crassicymatium
 112, **128**-130, 401; Pl. 30, Figs 3-5, 8
Crassicymatium **128**
crassicornatum 112, **128**-130, 401; Pl. 30, Figs 3-5, 8
crassilabris, Malea 260-261
crassum
Gyrineum 72
Triton 121
crassus, Murex 72-73, 361; Pl. 10, Figs 1-2
craticulata, Semicassis 23
crenulum, Dolium 264
cretaceum, Dalium 239
crispus, Triton 138-139
cristinae, Bufonaria 22
Crossata **68**
californica 68
californica 68
sonorana 68
ventricosa 17, 19,
 21, 26-28, 33, 43, 59, 62, **68**-71, 107, 134, 354, 357-358,
 442; Pl. 7, Figs 1, 5; Pl. 8, Figs 1-7; Pl. 9, Fig. 2; Pl. 51, Fig. 7
 (Crossata), Bursa
californica 68
ventricosa 68
crosseanum
Dolium 253
Eudolium 6, 22-25, 253
cruzana, Cymatium pileare var. 145, 147
cruentata
Bursa 22, 43-44, 66-67
Lampadopsis 43
Ranella 43-44

- (Lampas)* 66
(Lampas), var. *rhodostoma* 57
cruentatum, *Gyrineum* 57
crumena, *Bufonaria* 22
Cryotritonium 104
 murrayi 104
 magellanicus 104
(Cryotritonium), *Tritonium murrayi* 105
cryptocentrus, *Amphychthus*
 94, 152, 173, 183, 192, 197, 225, 230, 270
cubaniana
 Bursa 48
 (Colubrellina) 48
 granularia 49
 granularis 45, 48
 granularis 48
 Gyrineum affine var. 48
 intermedia, *Bursa* 48, 50
 Ranella 48-49, 436; Pl. 3, Figs 1, 3
cubaniana, *Gyrineum*
 affine var. 48
 afine var. 48
cumingiana, *Bursa* 48-50
cumingi, *Tonna* 23
cutacea, *Cabestana* 22, 118, 140, 175
cutaceum
 Cymatium 141
 (Linatella) 140
 Tritonium 118
cutaceus
 Aquillus 118
 Cabestana 118
 Dolarium 118
 Fusus 140-141
 Neptunella 118
Cymatiella **208**
 eburnea 210
 fennemai 209
 gaimardi 210
 lesueuri 210
 parvula 208
 pratti 210
 pumilio 23, 208
 quoyi 208
 sexcostata 210
 tritonea 209
 verrucosa 210
 vokesorum 13, 15, 27, 209-**210**, 449; Pl. 54, Figs 1-10
Cymatiinae **118**
Cymatilesta spengleri 118
Cymatium **130**
 adairense 194-195, 438; Pl. 49, Fig. 10
 amictodeum 143-144
 amictum 143
 andoi 140, 170-171
 aquatile 134, 145, 164, 170
 bayeri 145, 187-188
 (Cabestana)
 costatum 167
 felipponei 119
 labiosum 195
 parthenopeus 167
 tenuiliratum 197
 tenuiliratus 197
 caribbaeum 181-183, 195
 caudatum 140
 cecilianum 147-148
 cingulatum 140-141
 comptum 149, 177, 184
 amphiatlanticum 149, 151
 corrugatum amictum 143, 158
 costatum 156-157, 167
 cutaceum 140-141
 (Cymatriton) nicobaricum 164
 cynocephalum 181
 domingense 193
 echo 167
 elsmerense 186
 exaratum 152
 felipponei 119
 femorale 14, 19, 21-22, 24-25, 27, 130-**131**,
 132-135, 401-402; Pl. 30, Figs 6-7, 9-12; Pl. 31, Figs 2, 5-7
 ficoideis 175
 (Gelagna) succinctum 137
 gemmatum 162-163
 gracile 149, 151, 188
 (Gutturium)
 amictodeum 143-144
 amictum 143
 bayeri 187
 muricinum 138
 pfeifferianum 187
 ritteri 172-173
 jobbernsi 202-204
 krebsii 145
 labiosum 192, 195
 (Lampusia)
 aquatilis 145
 bayeri 177
 chlorostoma 164
 pileare 170, 197
 martinianum 170
 var. *borneana* 177
 var. *martiniana* 170
 vestitum 178
 lignarium 160
 (Linatella)
 cingulatum 140
 peninsululum 140-141
 clandestinum 137
 cutaceum 140
 cynocephalum 179
 floridanum 140-142
 krenkeli 140-141
 poulsenii 140
 succinctum 137
 tranquebaricum 179
 valentinei 167-168
 wiegmanni 179
 lineatum 157, 187
 martinianum 145, 170
 (Monoplex)
 amictum 143
 aquatile 145
 cercadicum 148
 comptum 149, 154

<i>corrugatum</i>					<i>kugleri</i>	160
<i>amictum</i>	158				<i>mohorterae</i>	184
<i>krebsii</i>	157				<i>mohorteri</i>	183-184
<i>tremperi</i>	143				<i>moritinctum caribbaeum</i>	182
<i>costatum</i>	167				<i>muricinum</i>	138
<i>doliarium</i>	167				<i>nicobaricum</i>	164
var. <i>minor</i>	167				<i>pfeifferianum</i>	188
<i>echo iwakawanum</i>	167				<i>pyrum</i>	184
<i>exaratum</i>	152				<i>rehderi</i>	184
<i>gemmatum</i>	163				<i>rehderi</i>	184
<i>keenae</i>	156				<i>sarcostoma</i>	182
<i>krebsii</i>	157				<i>sarcostomum</i>	152
<i>lignarium</i>	160				<i>tenuilirata</i> var. <i>nodocostata</i>	202
<i>macrodon</i>	162				<i>testudinarium rehderi</i>	184
<i>martinianum</i>	170				<i>ranzanii</i>	22, 131, 132
<i>mundum</i>	163				<i>rehderi</i>	184
<i>nicobaricum</i>	164				<i>remotum</i>	202-204
<i>parthenopaeum</i>	167, 176				(<i>Reticutriton</i>)	
<i>parthenopeum</i>	156, 167				<i>elsmerense</i>	186
<i>echo</i>	167				<i>lineatum</i>	187
<i>keenae</i>	156				<i>pfeifferianum</i>	188
<i>parthenopeum</i>	167				<i>tenuiliratum</i>	197
<i>pharcidum</i>	197				<i>ridleyi</i>	184
<i>pileare</i>	170				<i>ritteri</i>	172
<i>tenuiliratum</i>	197				<i>rubeculum occidentale</i>	190
<i>thersites</i>	177				<i>sarcostomum</i>	182
<i>tranquebaricum</i>	174				(<i>Septa</i>)	
var. <i>linatelloides</i>	174				<i>amictum</i>	143
<i>trigonum</i>	175				<i>tremperi</i>	143
<i>turtoni</i>	176				<i>aquatile</i>	145
<i>valentinei</i>	167				<i>beui</i>	191-192
<i>vespaceum</i>	177				<i>comptum</i>	149
<i>vestitum</i>	178				<i>corrugatum krebssii</i>	157
<i>wiegmanni</i>	179				<i>gemmatum</i>	149, 162
<i>moritinctum</i>	182				<i>henicum</i>	158
<i>caribbaeum</i>	182				<i>krebsii</i>	157, 197
<i>mundum</i>	163				<i>labiosum</i>	196
<i>muricinum</i>	138				<i>lignarium</i>	160
<i>nicobaricum</i>	164				<i>lineatum</i>	187
<i>occidentale</i>	149, 177, 191				<i>martinianum</i>	170
<i>olearium</i>	166				<i>mundum</i>	163
<i>parthenopeum</i>	156, 167, 170				<i>nicobaricum</i>	164
<i>keenae</i>	156				<i>occidentale</i>	191
<i>pfeifferianum</i>	187				<i>ogygium</i>	192
<i>pharcidum</i>	197				<i>parthenopeus</i>	167
<i>pileare</i>	134, 145, 159, 162, 170				<i>parthenopeum</i>	167
<i>macrodon</i>	162				<i>parthenopum</i>	167
<i>martinianum</i>	170				<i>pfeifferianum</i>	188
<i>orientale</i>	171				<i>pileare</i>	145, 162, 170
var. <i>borneana</i>	177				<i>henicum</i>	157-158
var. <i>cruzana</i>	145, 147				<i>martinianum</i>	145, 170
<i>poulsenii</i>	140				<i>orientalis</i>	170
<i>praefemorale</i>	13-14, 16-17, 24, 27, 131-132, 133, 402, 406; Pl. 31, Fig. 3; Pl. 33, Figs 1-9				<i>pileare</i>	170
<i>problematicum</i>	174				<i>rubeculum occidentale</i>	190
<i>raderi</i>	14, 21, 24, 27-28, 131-133, 134-135, 402, 405; Pl. 31, Figs 1, 4; Pl. 32, Figs 1-3				<i>tenuiliratum</i>	197
(<i>Ranularia</i>)					<i>tranquebaricum</i>	174
<i>aegrotum</i>	183				<i>trigonum</i>	175
<i>caribbaeum</i>	181-182, 195				<i>turtoni</i>	176
<i>caudatum</i>	140				<i>vespaceum</i>	149, 177
<i>cynocephalum</i>	182				<i>vestitum</i>	178
<i>gallinago</i>	183				(<i>Septa</i>)	
					<i>carlotae</i>	186
					<i>chlorostomoides</i>	149

- infelix* 155
succinctum 137
tenuiliratum 197
testudinarium rehderi 184
tigrinum . . 21, 25, 28, 39, 130-132, **135**-136, 409; Pl. 34, Figs 1, 4
tigrinus 135-136
tranquebaricum 158, 173-174
 forma problematicum 174
trigonum 175
 (*Tritoniscus*)
 labiosum 195
 labiosus 195
tuberosum 138
 (*Turritriton*)
 comptum 149
 domingense 193
 exaratum 152
 exaratum 152
 kiiense 152
 gibbosum 194
 gibbosum 194
 indomelanicum 177
 labiosum 195
 lignarium 160
 pharcidum 197
 tenuiliratum 197
 vespaceum 177
vespaceum 151, 177
vestitum 156, 162, 178
 insulare 170-171
wiegmanni 156, 179
zimara 152-153
 (*Cymatium*)
 Cymatium
 etcheversi 134
 femorale 131, 133
 praefemorale 133
 raderi 134
 tigrinum 135
 Lotorium kiiense 151, 153
 Triton
 femorale 131
 tigrinum 135
 tigrinus 135
 Tritonium femorale 131-132
Cymatoma kampyla 202
Cymatona 198
 kampyla 202
 jobbernsi 202
 kampyla 202
 tomlini 202
Cymatriton nicobaricum 164
cymocephala
 Gelagna 137
 Lampusia 181
cymocephalum
 Cymatium 181
 (*Linatella*) 179
 (*Ranularia*) 182
 Ranularia 21-
 25, 27, 32, 34, 181-**182**, 183, 191, 430; Pl. 45, Figs 4-6, 8-9
 Triton 137, 179, 181-182
 (*Gutturium*) 181
 Tritonium 181
cymocephalus
 Triton 181
 (*Gutturium*) 181
Cypraecassis **225**
 cantaurana 20, 27, 29,
 175, **225**, 226-229, 466, 469; Pl. 63, Figs 3-7; Pl. 64, Figs 5, 9
 chipolana 20, 25, 27-
 28, 35, 173, **226**-227, 457, 465; Pl. 58, Figs 2-3; Pl. 62, Fig. 7
 coarctata 21, 28,
 225-**227**, 230, 245, 465-466; Pl. 62, Fig. 2; Pl. 63, Figs 1-2
 rufa 23, 225
 tenuis 21,
 28-29, 225-**227**, 228, 457-458; Pl. 58, Fig. 4; Pl. 59, Fig. 3
 testiculus 13, 16, 20,
 22, 24, 27, 216, 224, 226-**228**, 229, 465; Pl. 62, Figs 4-6, 8-10
 senegalica 22, 230
 testiculus 228
 wilmae . . . 20-21, 25, 28, 35, 225-227, **230**, 465; Pl. 62, Figs 1, 3
Cypraecassis (Levenia) coarctata 227, 230
 (*Cypraecassis*), *Cassis*
 tenuis 228
 testiculus 228
Dalium **238**
 cretaceum 239
 dalli
 13, 15, 24, 26-27, 29, 238-**239**, 240, 469; Pl. 64, Figs 1-3, 5-6
 ecuadoriana 240
 ecuadorianum 20, 24-26, 28, 239-**240**, 469; Pl. 64, Figs 7-8
 ecuadorium 240
 solidum 14, 22, 24-26, 29, 35, 238-240
dalli
 Bathygalea (Miogalea) 243
 Cassis (Phalium) 242-243
 Dalium
 13, 15, 24, 26-27, 29, 238-**239**, 240, 469; Pl. 64, Figs 1-3, 5-6
 Galeodea 242
 Trachydolium 242
dautzenbergi
 Lotorium 320
 Triton (Argobuccinum) 319-320
dautzenbergi
 Triton 320
 (*Argobuccinum*) 319-320
 Urosalpinx (sensu lato) 319-320
 Xymene 320
davidboschi, Bursa 22
decrensensis, Cassis (Hypocassis) bicarinata var. 211
decussata
 Distorsio 13, 16-19, 21, 24, 26-28, 33, 80-81, 83-
 87, 88-92, 94-98, 369-370; Pl. 14, Figs 1-9; Pl. 15, Figs 1-5, 9
 gatumensis
 Distorsio 16, 81, 84-85, 87-89
 (*Rhysema*) 84, 86-87, 90
 Distortrix 84
 simillima, Distorsio (Rhysema) 97
 decussatum
 Phalium 23
 Tritonium 81, 87-88, 90
 decussatus, Distorsio 87, 94
 ringens 95
 simillimus 87, 93, 97

- delta*, *Cassis* 20, 27, **215**-216, 222
densecostata
Malea 20, 27, 35, **257**-260, 263, 489; Pl. 74, Figs 4, 8
Tonna (Malea) ringens 257
dentatum, *Dolium* 260
(Malea) 260
depressa, *Aspa* 66
deshayesii, *Tonna* 23
dharmai, *Septa* 190
Diadema antillarum (echinoid) 223
Diconoficus gayana 312
dimidiata, *Liobindsia* 109-110
Dissentoma prima 167-168
Distorsia constricta 87
Distorsio **79**
acuta occidentalis 81
anus 23, 79
biangulata
. 19, 24, 27, **80**-81, 385; Pl. 22, Figs 4, 7; Pl. 51, Figs 4-5
burgessi 23, 79
cancellina 81, 99-100
clathrata 13, 16-19, 21, 24,
26-28, 33, **80**-**81**, 82-87, 89, 92, 95, 365; Pl. 12, Figs 1-10
clathratus gatunensis 81, 83, 87
constricta 19,
21, 25, 28, 80, **84**-87, 89, 92-94, 99, 366; Pl. 13, Figs 4-5, 9
floridana 92-93
mcgintyi 92
mcgintyi 92
constrictus 84, 86, 90, 92
constrictus simillimus 97
decussata 13, 16-19, 21, 24, 26-28, 33, 80-81, 83-
87, 88-92, 94-98, 369-370; Pl. 14, Figs 1-9; Pl. 15, Figs 1-5, 9
gatunensis 16, 81, 84-85, 87-89
decussatus 87, 94
ringens 95
simillimus 87, 93, 97
euconstricta 23
floridana
. 13, 19, 24, 27-28, 81-82, **89**-90, 370; Pl. 15, Figs 6-8, 10-12
graceiellae 23, 44
grasi 99
habei 23
horrida 94
jenniernestae
. 19, 21, 28, 80, 84-86, **90**, 92, 94, 374; Pl. 17, Figs 1-3
jungi 19, 24, 26, 37, 81, 85, 87,
90-92, 97-98, 173, 373-374; Pl. 16, Figs 1-11; Pl. 17, Figs 4-5, 7
kurzi 23
mcgintyi 92
mcgintyi 13, 16-19, 21, 25, 27-28, 80, 85-87, 89, 91-
92, 93-94, 108, 366, 374, 377-378; Pl. 13, Figs 2-3, 6-8;
Pl. 17, Figs 6, 8; Pl. 18, Figs 1-2, 4-5, 7-9; Pl. 19, Figs 1, 4
minoruohishii
. 19, 21, 28, 80, 84-87, 90-**94**, 378; Pl. 19, Figs 2-3, 10, 12
muehlhaeusseri 23
muricina 138-139
parvimpedita 23, 82
perdistorta . 21-24, 27, 32, 80, 82, **94**-95, 378; Pl. 19, Figs 5-9, 11
perdistorta 94
(Personella)
grasi 99
nucleoides 201
reticularis 23, 73, 82
reticulata 92
(Rhysema)
clathrata 81
constricta 84
mcgintyi 92
decussata
gatunensis 84, 86-87
simillima 97
floridana 81
gatunensis 87
horrida 94-95
mcgintyi 92
robinsoni 81-82
ridens 81-82, 87, 90, 98-99
ringens 26, 91-92, **95**-97, 112, 203, 381; Pl. 20, Figs 1-5, 7
robinsoni 81-82
simillima . 13, 16-17, 24, 26, 27, 29, 83-88, 91-93, **97**-98, 381-382,
385; Pl. 20, Figs 6, 8-10; Pl. 21, Figs 1-8; Pl. 22, Figs 1-2, 6, 8-9
simillimus 84, 97
smithi 22, 81, 83, **98**-99, 118, 385; Pl. 22, Figs 3, 5
smithii 99
somalica 23
thersites 95
ventricosa 23
Distorsionella
lewisi 23
pseudaphera 23
Distorsomina pusilla 23
Distorta
anus 79
rotunda 79
Distortio
reticularis var. *clathratus* 81
reticulatus 81
Distortrix
anus 79
gatunensis 84, 87-88
reticulare 81
reticulata 81, 87, 97
var. *clathratus* 81, 92
var. *reticulata* 81
ridens 98
simillima 81, 87, 97
doliare, *Murex* 166, 168
doliarium
Cabestana 118
Cymatium (Monoplex) 167
var. *minor*, *Cymatium (Monoplex)* 167
doliata
Cassis 247
Neptunea 137
Doliopsis 253
Dolium
album 266, 268
antillarum 264, 266
var. *brasiliiana* 264-265, 267, 494; Pl. 77, Fig. 1
crenulatum 264
crosseanum 253
dentatum 260
(Endolium) 251
galea 259, 263-265
latilabre 260

- losariense* 140-141
 (Malea)
 camura 260
 dentatum 260
 ringens 260
pennatum 266, 268
perdix 266-267
 occidentale 266-267
 var. *brasiliiana* 266
personatum 260-261
plicosum 260-261
plumatum 267, 494; Pl. 77, Figs 5-6
ringens 260
sagrae 264
tenuis 264
dolium, *Tonna* 23
domingensis, *Turritriton* 13-14, 16-17, 20, 24, 27, 154, 192-193, 194, 438; Pl. 49, Figs 1-4, 8
domingense
 Cymatium 193
 (*Turritriton*) 193
 Tritonium (*Ranularia*) 193
donghaiensis, *Pisanianura* 23
dorae, *Semicassis* 23
Dulcerana
 granularis 42, 48
 jabick 48
 versigranulata 48
 (*Dulcerana*), *Colubrellina granularis* 48
dunkeri
 Ranularia 23, 181, 185
 Tonna 23
durbanensis, *Monoplex* 152-153
durietzii, *Verrucaria* (lichen) 202
eburnea, *Cymatiella* 210
echinata, *Bufonaria* 22
echinoids, prey of *Cassis tuberosa* 223
 Arbacia, *Cassidulus cariboeorum*, *Clypeaster roscaeus*, *C. subdepressus*,
 Diadema antillarum, *Echinometra lucunter*, *Echinonius*, *Leodia*
 sexiesperforata, *Lytechinus variegatus*, *Mellita quinquiesperforata*, *Meoma*,
 Moira, *Plagiobrissus grandis*, *Tripneustes eculentus*, *T. ventricosus*
Echinometra lucunter (echinoid) 223
Echinonius (echinoid) 223
Echinophora 230
echinophora
 Cassidaria 230
 Galeodea . . 13, 15, 22, 24, 27, 230-231, 232, 477; Pl. 68, Figs 4, 7
 Morio 230
Echinophoria 242
 andersoni 242-244
 bituberculosa 23
 carnosa 23
 famulans 20, 27, 242-244
 hadra 1, 13, 15-18, 20, 22, 24, 27, 35, 41, 242-243, 244, 477, 482; Pl. 68, Figs 3, 5; Pl. 71, Fig. 4
 monilifera 4
 pilsbryi 21, 26, 244
 woodringi 20, 28, 244, 477; Pl. 68, Figs 1-2
 uyvillei 23, 224
 (*Echinophoria*)
 Phalium
 andersoni 243
 hadrum 243
 woodringi 244
 Semicassis apenes 228
echinophorum, *Buccinum* 231
Echinora tuberculata 230
echo
 Cymatium 167
 (*Monoplex*) *parthenopeum* 167
 iwakawanum, *Cymatium* (*Monoplex*) 167
 Monoplex 167
 parthenopeum 167
ecuadoriana
 Dalium 240
 Neosconsia 318, 334, 474; Pl. 67, Figs 4, 6
ecuadorianum, *Dalium* . 20, 24-26, 28-29, 239-240, 469; Pl. 64, Figs 7-8
ecuadorium, *Dalium* 240
edentatum, *Tritonium* (*Lagena*) 46, 65
effusa, *Litiopa* 169, 171
Eione inflata 66-67, 442; Pl. 51, Figs 1-3
elevata, *Oocorys* 21, 316-317, 470; Pl. 65, Figs 6-7, 9
elliptica, *Malea* 13, 16-17, 27, 255-257, 258, 260-262, 485, 489; Pl. 72, Figs 5, 7-9; Pl. 74, Figs 1-3, 6
 camura var. 257
elongatum, *Tritonium* (*Ranularia*) 177
elongatus, *Triton* 176
elsmerense
 Cymatium 186
 (*Reticutriton*) 186
 Gyrineum 186
elsmerensis, *Reticutriton* 24, 28, 107, 130, 186-187, 434; Pl. 47, Figs 2-4, 6-8
emilyae, *Argenthina* 319
encaustica, *Ranularia* 23
 (*Endolium*), *Dolium* 251
eogassinense
 Eutritonium 114
 Ranella 111
 Triton 114
erinaceus
 Casmaria 23
 Murex 318
 Ocenebra 318
esculentus, *Tripneustes* (echinoid) 223
etcheversi, *Cymatium* (*Cymatium*) 131, 134
etchuensis, *Shichiheia* 242
euclia
 Cabestanomorpha 152-153
 Charonia 121
 instructa, *Charonia* 121, 123
 Triton lampas var. 121, 123
euclioides, *Charonia capax* 121, 123
euconstricta, *Distorsio* 23
Eucorys
 barbouri 22
 bartschi 22
Eudolium 253
 antiquum 253
 bairdii 6, 22-24, 253-254
 crosseanum 6, 22-25, 153
 fasciatum 265-266
 (*Galeodolium*) *subfasciatum* 253
 marylandicum 254
 pyriforme 25
 (*Simplicodolium*) *fasciatum* 264

- subfasciatum* 24, 27, 173, **253**, 482; Pl. 71, Figs 8, 11
Eugyrina
 gemnifera lepta 113
 gigantea 114
Eupleura 194-195
Euspinacassis pollens 242
Eutriton (Simpulum) problematicum 173-174
Eutritonium
 eogassinense 114
 pileare 170
 salbriacense 121
 (*Sassia*) *aperturale* 121
exarata, Cabestanomorpha 143, 152
exaratum
 Cymatium 152
 (*Monoplex*) 152
 (*Turritriton*) 152
 exaratum, Cymatium (Turritriton) 152
 kiiense, Cymatium (Turritriton) 152
 Phalium bandatum 23
 Triton 151
exaratus
 Monoplex 4, 6, 21, 23-24,
 32, 143, 150-**151**, 152-153, 169, 174, 202, 414; Pl. 37, Figs 1-4
 Triton 143
exiguum, Tritonium 117, 205-206
exilis, Ranularia 23
famulans
 Bathygalea (Miogalea) 242
 Echinophoria 20, 27, **242**, 243-244
fasciata
 Morio 264
 Pyrula 263-265
 Simplicodolium 263
fasciatum
 Eudolium 265-266
 (*Simplicodolium*) 264
 Faurotis faurotis 244
faurotis
 Faurotis 244
 Semicassis 23, 244
felipponei
 Cabestana 21, **119**-120, 168, 397; Pl. 28, Figs 5, 8
 Cymatium 119
 (*Cabestana*) 119
 Lotorium 119
femorale
 Cymatium 14, 19, 21-22, 24-25, 27, 130-**131**,
 132-135, 401-402; Pl. 30, Figs 6-7, 9-12; Pl. 31, Figs 2, 5-7
 Lotorium 131
 Murex 130-133
 Nyctilochus 131
 Triton 131-132, 135
 (*Cymatium*) 131
 (*Lotorium*) 131
 Tritonium 131-132
 (*Cymatium*) 131-132
femoralis, Triton 131-132
fennemai
 Cymatiella 209
 Triton 209
fernandesi
 Bursina 22
 Semicassis 23
Ficidae **311**
Ficoidea 311
ficoides
 Cymatium 158, 175
 Sympulum 175
 Triton 175
 (*Simpulum*) 175
 Tritonium 175
Ficula ficus 312
Ficus
 bernardi **312**-313, 315, 498; Pl. 79, Figs 1, 4-5, 7
 carbacea 313-315
 communis 314-315
 ficus 312
 gayana 312
 gibsonsmithi 312-**313**, 314-316, 497; Pl. 78, Figs 4-5, 7-9
 lisselongata **315**, 498; Pl. 79, Figs 2-3, 6, 8
 papyratia 313-314
 pilsbryi 312-313, **315**-316, 497; Pl. 78, Figs 1-3, 6
 subintermedia 312
 variegata 312
ficus
 Bulla 312
 Ficula 312
 Ficus 312
 Murex 312
 Pirula 312
 Pyrula 312
 Sycotypus 312
fijiensis, Bursina 22
filipponei, Tritonium 119
fimbria, Phalium 23
fimbriata, Cassis 23, 311
 (*Hypocassis*) 211
finlayi, Bursa 52-54, 56
 (*Colubrellina*) 52
fitikau, Turritriton 22, 192, 293
flintensis, Cassis **217**-218, 221
flammea, Cassis 20, 22, 24,
 27, 34, 39, 212-**216**, 217, 220-221, 224, 462; Pl. 61, Figs 1-2
 (*Goniogalea*) 216
flammeum, Buccinum 216
flammiferum, Phalium 23
flaveola, Septa 23
flexibilis, Akibumia 23
floridana
 Distorsio . 13, 19, 24, 27-28, 81-82, **89**-90, 370; Pl. 15, Figs 6-8, 10-12
 (*Rhysema*) 81-82
 Personella 81-82, 89, 92
 floridanum, Cymatium (Linatella) 140-141
 floridensis, Cassis . 24, 27, 214-215, **218**-219, 221-222, 454; Pl. 57, Figs 2-3
 ketteri, Cassis 219
 foliata, Bufonaria 22
 Foratidolium 263
 fossatum, Triton 166
 fosteri, Bursa 22, 42
freyi
 Bursa (Marsupina) 75
 Marsupina 24, 28, **75**-76, 361; Pl. 10, Figs 6, 8-9
Fusitriton **104**
 algoensis 105-106
 brasiliensis **104**

- cancellatum* 105
cancellatus 105
 murrayi 105
futuristi 105
galea 22, 106-107
izumozakiensis 104, 106
kampylum 202
laudandum 105
laudandus 105
laudanum 105
magellanicus 4, 6, 21, **104**-107, 202-203, 208, 386; Pl. 23, Figs 2, 4, 6
 laudandus 105
 magellanicus 105
 murrayi 105
 retiolus 105
midwayensis 23, 55
multinodosa 114
murrayi 104-105
oregonensis 5, 21, 28, 40, 105-**106**, 107
retiolus 105
takedai 104, 107
(Fusitriton)
 Argobuccinum
 cancellatum
 cancellatum 105
 retiolus 105
 oregonense 106
 coosense 106-107
 laudandum 105
 magellanicum 105
 murrayi 105
 oregonensis 106
 Priene
 cancellatus 104
 oregonensis 106
fusoides
 Buccinum 122
 Siphonalia 122
Fusus
 cancellatus 104
 cinereus 319
 cutaceus 140
 oregonensis 106
 plebeius 319
 sowerbyanus 208
 voigtii 140-141
 wiegmanni 179
futuristi, *Fusitriton* 105
gabbi, *Sconsia laevigata* var. 233-235
gaimardi, *Cymatiella* 240
Galea 263
galea
 abbotti, *Tonna* 265-266
 brasilianna, *Tonna* 265, 494; Pl. 77, Fig. 1
 Buccinum 263-265
 Cadium 264
 Cadus 264
 Dolium 259, 263-264
 Fusitriton 22, 106-107
 galea, *Tonna* 265-266
 Tonna 13, 16, 20, 22, 25, 27, 253, 262, **264**-265, 268, 493-494; Pl. 76, Figs 3-7; Pl. 77, Fig. 1
Galeodaria 254
Galeodea **230**
 alcocki 23
 allani 231-232
 bituminata 23
 (*Caliagaleodea*) *californica* 231
 californica 231
 dalli 242-243
 echinophora . 13, 15, 22, 24, 27, 230-**231**, 232, 477; Pl. 68, Figs 4, 7
 (*Gomphopages*) *turneri* 231
 hoarai 23
 keyteri 23
 leucodoma 23, 231
 maccamleyi 23, 241
 (*Mambrinia*) *planotecta* 231
 planotecta 231
 tuberculiformis 210
 rugosa 22, 232
 (*Taieria*) *allani* 231-232
Galeodia hodgii 235
Galeodocassis 211
 (*Galeodocassis*), *Cassis*
 anceps 211
 saccoi 211
Galeodolium muticum 253
 (*Galeodolium*), *Eudolium subfasciatum* 253
Galeodosconsia striatula 232, 234
Galeocorys leucodoma 231
gallinago
 Cymatium (*Ranularia*) 183
 Ranularia 21, 23-24, 27, 31-32, 34, 113, 182-**183**, 184, 433; Pl. 46, Figs 1-5, 8
 Triton 183-184
 (*Gutturium*) 183
gatunensis
 Distorsio 16, 84, 87-89
 clathratus 81, 83, 87
 decussatus 84, 87, 90, 96
 (*Rhysema*) 87
 decussata 84, 86
 Distortrix 84
gatunicus, *Monoplex* 17, 27, **153**-154, 414, 417, 446; Pl. 37, Figs 11, 15-17, 19-20; Pl. 38, Figs 6-7; Pl. 53, Figs 9-12
gayana
 Diconoficus 312
 Ficus 312
Gelagna **137**
 clandestina 137
 cyncephala 137
 pallida 22, 137
 succincta 21-22, 24, 27, 32, **137**-138, 409; Pl. 34, Fig. 5
 (*Gelagna*)
 Cymatium succinctum 137
 Linatella succincta 137
 Tritonium clandestinum 137
gemma, *Afrocanidea* 138-39
gemmatum
 Cymatium 162
 (*Monoplex*) 163
 (*Septa*) 149, 162
 Tritonium 163
gemmatus
 Monoplex 23, 150, 163, 177

- Triton* 149, 154, 162-163
 (*Simpulum*) 162
- gemmellari*
 Semiranella 120
 Triton (*Semiranella*) 120-121
- gemmafera*
 Argobuccinum (*Eugyrina*) 113
 Ranella . . 21, 24, 27, 32, 101, 111, **113**-114, 390; Pl. 25, Figs 7-9, 11
 australasia 113
- gemmaferum*
 Argobuccinum 113
 (*Mayena*) *australasium* 113
 Tritonium 113
 var. *minor*, *Tritonium* 113
- gemmafera* var. *lepta*, *Eugyrina* 113
- gibba*
 abbreviata, *Semicassis* 245, 248
 Cassis (*Semicassis*) 248
 inflata, *Semicassis* 245
 Semicassis 245, 248
- gibbosa*
 Bursa 72-73, 361; Pl. 10, Figs 1-2
 Cabestana 194
- gibbosum*
 Cymatium 194
 (*Turritriton*) 194
 gibbosum, *Cymatium* (*Turritriton*) 194
- gibbosus*
 Triton 192, 194
 (*Gutturnium*) 194
 Tritonium 194
 Turritriton 17, 21, 25, 27-28, 143, 186, 192-**194**,
 195-196, 434, 438; Pl. 47, Figs 13-14; Pl. 49, Figs 6-7, 10-13
- gibbum*, *Buccinum* 248-249, 482; Pl. 71, Figs 2, 6
- gibbonsmithi***, *Ficus* 312-**313**, 314-316, 497; Pl. 78, Figs 4-5, 7-9
- gigantea*
 Eugyrina 114
 Gyrina 114
 Ranella 111, 114-115
 (*Apollon*) 114
 (*Argobuccinum*) 114
 var. *atlantica*, *Ranella* 114
- giganteus*, *Apollon* 114
- glabra*, *Tritonium nodiferum* var. 124
- glabrata*, *Semicassis* 23
- glabrum*, *Tritonium* 121
- glans*, *Austrofusius* 205
- glaucum*, *Phalium* 23
- globulus*, *Cassis* 248-249, 482; Pl. 71, Figs 2, 6
- gnorima*, *Bursina* 22
- goliath*, *Malea* 13, 16-17, 27, 256,
 258-259, 263, 486, 490; Pl. 73, Figs 1-4; Pl. 75, Figs 1-2, 5
 (*Gomphopages*), *Galeodea turneri* 231
- Gondwanula tumida* 100-101
- (*Goniogalea*), *Cassis*
 flammea 216
 madagascariensis 210, 219
 tuberosa 223
- graceiellae*, *Distorsio* 23, 44
- gracile*
 Cymatium 149, 151, 188
 Gutturnium 159
 Lampusia 149, 187
- Triton* 150
 var. *gurabonicum*, *Gutturnium* 154-155
- gracilis*, *Triton* 149, 187-188
- grandimaculata*, *Lotoria* 23
- grandis*
 Oocorys 22-23
 Plagiobrissus (echinoid) 223
- granifera*, *Ranella* 48-49
 (*Lampas*) 48
- granosum*, *Triton* 199
- granulare*, *Tritonium* 42, 48-49
- granularia*, *Bursa* (*Colubrellina*) 49
- granularis*
 Bursa 5, 21-22, 24-25,
 27-28, 32, 42-43, 45-46, **48**-50, 52-55, 346; Pl. 3, Figs 1, 3
 (*Bufoariella*) 49
 (*Colubrellina*) 49
 Colubrellina 48
 (*Dulcerana*) 48
 Dulcerana 48
- granularis*
 affinis, *Bursa* 48
 granularis cubaniana, *Bursa* 48
 (*Colubrellina*) 48
- granulata*
 Cassis (*Semicassis*) 247
 Ranella 72-73, 361; Pl. 10, Figs 1-2
 Semicassis 15-17, 20, 22, 24-25, 27, 29, 33, 35, 245-**248**,
 249-251, 481-482; Pl. 70, Figs 4, 6; Pl. 71, Figs 2, 5-7, 9-10
 (*Tylocassis*) 247-248
- granulata loxahatcheensis*, *Semicassis* 250
- granulatum*
 abbreviata var. *centiquadrata*, *Phalium* 248
 Buccinum 248
 centiquadratum
 Phalium (*Tylocassis*) 247
 Semicassis 247
 forma cicatricosum, *Phalium* (*Tylocassis*) 248
 granulatum, *Phalium* (*Tylocassis*) 248
 loxahatcheensis, *Phalium* 248
 Phalium 248
 (*Semicassis*) 248
 (*Tylocassis*) 248
 reclusum, *Phalium* (*Tylocassis*) 251
 Semicassis 248
- granulosa*
 Cassidea 248-251, 482; Pl. 71, Figs 2, 6
 Cassis 248-249
- grasi*
 Distorsio 99
 (*Personella*) 99
 Persona 99
 Personopsis 21-22, 24, **99**-100, 377; Pl. 18, Figs 3, 6
 Triton 99-100
- grayana*, *Bursa* . 12-13, 16-17, 27, 45, **50**-51, 57-58, 346; Pl. 3, Figs 2, 4-9
- grayi*, *Sconsia* 7, 15-18, 20, 22,
 26-28, 34-35, **232**-238, 473-474; Pl. 66, Figs 6-7; Pl. 67, Figs 1, 3, 5
- grimaldii*, *Pisanianura* 22-23
- grundensis*, *Turritriton* 25, 192-193, 195
- guichimerri*, *Charonia* 120
- gurabonicus*, *Monoplex*
 13-14, 24, 27, 151, **154**-155, 193, 413; Pl. 36, Figs 12-13, 15-17
- gurabonicum*, *Gutturnium gracile* var. 154

- gutturium, Ranularia* 23, 181
Gutturium **138**
 gracile 154
 var. *gurabonicum* 154-155
 muricinum 21-22, 24, 27, 32, **138-139**, 409; Pl. 34, Figs 2-3
 (*Gutturnium*)
 Cymatium
 amictoideum 143-144
 amictum 143
 bayeri 187
 muricinum 138
 pfeifferianum 187
 ritteri 172-173
 Ranularia tuberosa 138
 Triton
 amictus 143
 antillarum 139
 cynocephalum 181
 cynocephalus 181
 gallinago 183
 gibbosus 194
 orientalis 195
 pfeifferianus 187
 tenuiliratus 197
 trilineatum 183
 vespaceum 176
 vespaceus 177
 Tritonium tuberosum 138
gutturium, Tudicla 181
Gyrina
 gigantea 114
 maculata 111, 114-115
gyrinata, Ranella 138-139
Gyrineum
 (*Aspa*) *marginatum* 66
 atlanticum 108
 affine 48
 var. *cubaniana* 48
 afine var. *cubaniana* 48
 (*Bechtelia*) *strongi* 71, 78-79
 bituberculare 22
 concinnum 22
 corbiculatum 106
 crassum 72
 cruentatum 57
 elsmerense 186
 gyrinum 22, 71, 78
 hirasei 22
 lacunatum 22
 longicaudatum 22
 louisae 107-108
 mediocre 100-101
 var. *corbiculatum* 106-107
 natator 22
 pusillum 22
 roseum 22
 strongi 60, 78-79
 sylviaensis 106-107
 wilmerianum 22
gyrinum, Gyrineum 22, 71, 78
gyrinoides
 Charonia 121
 Murex 120, 123
 rubicunda, Charonia 121
 Triton 121
 var. *sauliae, Charonia* 121
Gyrinopsis cowlitzi 111
habei, Distorsio 23
hadra
 Bathygalea (Miogalea) 243
 Echinophoria 1, 13, 15-18, 20, 22, 24, 27, 35, 41, 242-**243**, 244, 477, 482; Pl. 68, Figs 3, 5; Pl. 71, Fig. 4
 hadrum, Phalium (Echinophoria) 243
 haemastoma
 Triton 169, 171
 (*Simpulinus*) 178
 Halgyrineum **107**
 Halgyrineum louisae 19, 22, 24, 27, 34, 107-**108**, 109, 389; Pl. 24, Figs 4, 7-10
 hawaiiensis, Tonna 23
 hedleyi, Xenophalium 244
Helix
 sulfurea 266-268
 sulphurea 266-268
 henicum, Cymatium (Septa) 158
 pileare 157-158, 417; Pl. 38, Figs 10, 12
 hepatica, Septa 23, 191
 hirasei, Gyrinem 22
 hirsutum, Tritonium 166, 168
 hoarai, Galeodea 23
hodgii
 Cassis 235-236
 Galeodia 235
 Sconsia 27, **235-238**
horrida, Distorsio 94
 (*Rhysema*) 94-95
humilis, Bursa 22
(Hypocassis), Cassis
 bicarinata var. *decrensensis* 211
 fimbriata 211
 ignobilis, Bursina 22
 imbricata, Triton 126
 incerta, Ranella 114
infelix
 Cymatium (Septa) 155
 Monoplex 24, 149, **155**, 180
 Simpulum 155
inflata
 Cassis 247-248
 (*Semicassis*) 248
 Eione 66-67, 442; Pl. 51, Figs 1-3
 monilifera, Cassis 251
 Semicassis 248
 gibba 245
 waltonensis
 Semicassis 251
 (*Tylocassis*) 248, 251
inflatum
 Buccinum 248
 Phalium (Tylocassis) 248
inornata, Semicassis 23
instructa, Charonia euclia 121, 123
insulare, Cymatium vestitum 170-171
intercostalis, Ranella 111
intermedia
 Bursa cubaniana 48, 50

- Cassis* 242
Echinophoria 242
intermedius
Monoplex 23, 44, 145-146
Murex 166, 168
Ipunina vladimiri 316-317, 470; Pl. 66, Figs 2, 4-5, 8
iwakawanum, *Cymatium* (*Monoplex*) *echo* 167
izumozakiensis, *Fusitriton* 104, 106
jabick
Colubrellina 48
Dulcerana 48
Tritonium 48-49
jabik, *Bursa pustulosa* var. 45, 47
jackwinorum, *Monoplex* . . 19, 24, 27, 155-156, 414; Pl. 37, Figs 6-9
jamanensis, *Bursa nana* 76-77
jameshoubrieki, *Cassis* 215, 218-219, 221
japonica
Cassis 244
Semicassis 244
jenniernestae, *Distorsio*
. 19, 21, 28, 80, 84-86, 90, 92, 94, 374; Pl. 17, Figs 1-3
jobbernsi
Cymatium 202-204
Cymatona kampyla 202
judensis, *Marsupina* . . 24, 28, 33, 42, 75-76, 361; Pl. 10, Figs 4, 7, 10
jungi, *Distorsio* 19, 24, 26, 37, 81, 85, 87,
90-92, 97-98, 173, 373-374; Pl. 16, Figs 1-11; Pl. 17, Figs 4-5, 7
Kahua 241-242
kaiparaensis, *Ranella* 111-112
kalosmodix, *Casmaria* 23
Kalydon plebeius 319
kampyla
Charonia (*Negyrina*) 202
Cymatoma 202
Cymatona 202
jobbernsi, *Cymatona* 202
kampyla
Cymatona 202
Sassia 202
Nassaria 198, 202-203
Sassia
. 6, 24, 96, 201-202, 203-204, 208, 270, 441; Pl. 50, Figs 3-4
tomlini
Cymatona 202
Sassia 202
kampylum, *Fusitriton* 202
katherineae, *Ranella* 111
keenae
Cymatium parthenopeum 156
Cymatium (*Monoplex*) *parthenopeum* 156-157
Monoplex 19, 21, 25, 28-30, 35, 156-
157, 168, 178-179, 186, 227, 422; Pl. 41, Figs 3, 6-7
Septa (*Monoplex*) *parthenopea* 156
ketteri, *Cassis* 24, 27, 213-215, 219, 454; Pl. 57, Figs 1, 4
floridensis 219
kewi
Ameranella 116
Nyctilochus 116
keyteri, *Galeodea* 23
kiiense
Cymatium (*Turritriton*) *exaratum* 152
Lotorium (*Cymatium*) 151
kiiensis
Lotorium 152-153
Turritriton 152
kingii, *Ranella* 101, 103
kobelti, *Turritriton* 22, 25, 118, 192-195
kowiensis, *Bursa* 48-50
krebsii
Cymatium 157
(*Monoplex*) 157
corrugatum 157
(*Septa*) 157, 197
corrugatum 157
Monoplex 13-
14, 16-19, 21, 24-25, 27-28, 108, 143-145, 147-148, 157-159,
173, 175, 180, 417, 434; Pl. 38, Figs 1-5, 8-12; Pl. 47, Fig. 15
Triton
(*Lampusia*) 157-158, 197
(*Simpulum*) *corrugatum* var. 157
kreipli, *Cassis* 23, 211
krenkeli, *Cymatium* (*Linatella*) 140-141
kugleri, *Cymatium* (*Ranularia*) 160, 414; pl. 37, Fig. 12
kurzi, *Distorsio* 23
labiata
Cassis 223-224
Semicassis 6, 23, 202
labiosa
Cabestana 195
Lampusia 195
labiosum
Cymatium 192, 195
(*Cabestana*) 195
(*Septa*) 196
(*Tritoniscus*) 195
(*Turritriton*) 195
Triton (*Cabestana*) 195
Tritonium 195
labiosus
Cymatium (*Tritoniscus*) 195
Murex 192, 195-196
Triton 195
(*Cabestana*) 195
(*Simpulum*) 195
Tritoniscus 195
Turritriton 6, 15, 20-25, 27-28, 167,
192-195, 196, 243, 438, 446; Pl. 49, Figs 5, 9; Pl. 53, Fig. 7
lactea, *Cassis* 247
(*Semicassis*) 248
lacunatum, *Gyrineum* 22
laevigata
Aspa 66
Cassidaria 236-237
Cassis 248-249
laevigata, *Sconsia* 236
Ranella 65-66, 442; Pl. 51, Figs 1-3
(*Aspa*) 66-67
Sconsia 13, 15-16, 20, 24, 27, 35, 173, 226,
233, 236-238, 473-474; Pl. 66, Figs 1-5, 8-10; Pl. 67, Fig. 2
sublaevigata, *Sconsia* 233
var. *gabbi*, *Sconsia* 233-235
Lagena 137
Clandestinum 137
Succinctus 137
(*Lagena*)
Leucozonia smaragdula 233

- Ranularia*
clandestinus 137
rostratus 140
wiegmanni 179
- Triton*
cancellatum 104
clandestinum 137
magellanicus 104
wiegmanni 179
- Tritonium edentatum* 65
- lamarckii*, *Bursa* 22
- Lampadopsis* 41
cruentata 43
rhodostoma 57
- (*Lampadopsis*)
Bursa
calcipicta 59-60, 68, 70, 357; Pl. 8, Figs 3-4
thomae 57
- Ranella thomae* 57
- (*Lampas*)
Bursa
austriaca 55
ranelloides var. *tenuisculpta* 54, 56
- Ranella*
californica 68
corrugata 45
cruentata 66
var. *rhodostoma* 57
granifera 48
thomae 57
ventricosa 68
- lampas*
capax, *Charonia* 121-122
Charonia 4, 6, 13-14, 19, 21-22, 24, 27, 32, 113, 115-116, **120**-123, 126-128, 132, 153, 169, 202, 398; Pl. 29, Figs 1-6
lampas, *Charonia* 121-122
macilenta, *Charonia* 121
Murex 120, 123, 132
pustulata, *Charonia* 121-122
rubicunda, *Charonia* 121-122
saulliae, *Charonia* 121-122
weisbordi, *Charonia* 121, 123-124, 398; Pl. 29, Figs 4, 6
var. *euclia*, *Triton* 121, 123
- Lampasopsis* 41
- (*Lampasopsis*), *Bursa*
amphitrites 42, 60
rhodostoma 57
thomae 57
- (*Lampresia*), *Triton*
aquatilis 145
chlorostomus 164
pileare 170
tranquebaricus 173
tuberosum 138
- Lampusia*
chlorostoma 164
cynocephala 181
gracile 149, 187-188
labiosa 195
murrayi 104-105
nodocostata 202-203
olearium 166
pharcida 197, 426; Pl. 43, Fig. 1
- pilearis* 142, 169-170
(*Priene*) *murnayi* 104
- (*Lampusia*)
Cymatium
aquatilis 145
bayeri 177
chlorostoma 164
pileare 170, 197
var. *borneana* 177
var. *martiniana* 170
martinianum 170
vestitum 178
- Lotorium*
rada 318-319
usurpator 320
- Triton*
chlorostomum 164
var. *pumilio* 164
costatum 166
krebsii 156
martinianum 170
rubecula occidentale 149, 177, 190-191
vestitum 162
Tritonium lineatum 157
- landaui**, *Septa*
. 13-14, 24, 27, **189**-190, 200, 437; Pl. 48, Figs 1-2, 4-7, 10
- latilabre*, *Dolium* 260
latilabris, *Malea* 254, 260-261
latis, *Triton martinianum* 170
latitudo, *Bursa* 12, 22, 25, 42, 52-53
natalensis 52
(*Bufo*) *nariella* 52
(*Colubrellina*) 52
- Laubierinidae* 8, 22-23, 41
- laudandum*, *Fusitriton* 105
laudandus, *Fusitriton* 105
magellanicus 105
laudandum, *Fusitriton* 105
Leodia sexiesperforata (echinoid) 223
lepta, *Eugyrina gemnifera* 113
lessonae race *occidentalis*, *Bursa* 55
lesueuri, *Cymatiella* 210
leucodoma
Galeodea 23, 231
Galeoocorys 231
- leucostoma*
Ranella 113
Septa 113
var. *nigromaculata*, *Triton* 113
var. *peocilostoma*, *Ranella* 113
- leucostomoides*
Sassia 106, 202-204, **207**-208, 445; Pl. 52, Figs 8, 11
Triton 104, 202, 207-208
- Leucozonia* (*Lagena*) *smaragdula* 233, 235
(*Levenia*) 225
- Cassis*
coarctata 225, 227
coarctatus 227
Cypraeocassis coarctata 227, 230
- lewisi*
Distorsionella 23
Sassia 22, 24-25, 28, 37, 199-**200**, 201, 441; Pl. 50, Fig. 9
- lichens

- Caloplaca sublobulata* 302
Rinodina peloleuca 302
Verrucaria durietzii 302
- lignarium*
Cymatium 160
 (Monoplex) 160
 (Septa) 160
 (Turritriton) 160
Tritonium 160
- lignarius*
Monoplex 19,
 21, 24, 26-28, 33, 153-154, **160**, 414; Pl. 37, Figs 10, 12-14, 18
Triton 160
 (Simpulum) 160
- limonensis*, *Arcobelia* 265
limpui, *Microconsia* 23
- Linatella* **140**
caudata 6, 17, 19, 21-28, 33-34, **140**-142,
 148, 166, 174, 179, 409, 466; Pl. 34, Figs 6-10; Pl. 63, Figs 8, 11
cingulata 141
 (Gelagna) *succincta* 137
neptunia 140-141
succincta 137
wiegmanni 140, 179
- (*Linatella*)
Cymatium
caudatum 140
cingulatum 140
peninsulum 140-141
clandestinum 137
cutaceum 140
cyncephalum 137
floridanum 140-142, 409; Pl. 34, Fig. 6
krenkeli 140-141
poulsenii 140
succinctum 137
tranquebaricum 174
valentinei 167-168, 422; Pl. 41, Fig. 2
wiegmanni 179
- Triton*
clandestinus 137
poulsenii 140-141
rostratum 140
tranquebaricum 173
tranquebaricus 173
wiegmanni 179
- linatelloides*, *Cymatium* (*Monoplex*) *tranquebaricum* var. 174
lindae, *Sconsia* 7, 233-235
lindneri, *Sassia* 198
lineata, *Bursa corrugata* 48, 50
- lineatum*
Cymatium 157, 187
 (*Reticutriton*) 187
 (*Septa*) 187
Tritonium (*Lampusia*) 157-158
- lineatus*
Reticutriton 21, 24-25, 28, 186-**187**, 188, 434; Pl. 47, Figs 1, 5
Triton 187
 (*Simpulum*) 187
- linteria*, *Sconsia* 236-238
Liobindsia dimidiata 109-110
Liracassis 241-242
lischkeana, *Tonna* 23
- lisselongata*, *Ficus* **315**, 498; Pl. 79, Figs 2-3, 6, 8
- Litiopa*
effusa 169, 171
melanostoma 6, 317
obesa 138-139
- livida*, *Ranella* 48-50
- loebbeckei*
Triton 152, 195-196
Turritriton 152
- longicaudatum*, *Gyrineum* 22
- longispira*, *Monoplex* 13-14, 27, 147, **161**, 413; Pl. 36, Figs 3, 5
- loroisii*
Triton 192, 195-196
Tritoniscus 192
- losariense*, *Dolium* 140-141
- lotor*, *Lotorium* 130-132, 401; Pl. 30, Figs 11-12
- Lotoria*
armata 23
grandimaculata 23
lotoria 5, 21, 23, 31-32, 113, 130
perryi 23
- lotoria*, *Lotoria* 5, 21, 23, 31-32, 113, 130
- Lotorium*
costatum 166
 (*Cymatium*) *kiiense* 151, 153
dautzenbergi 319
dautzenbergi 320
femorale 131
felipponei 119
kiiensis 152-153
 (*Lampusia*)
rada 318-319
usurpator 320
- lotor* 130-132
morgani 206
nodocostatum 202
obliteratum 319
prae-femorale 132-133
ranelloides 54
rubicundum 121
- (*Lotorium*)
Triton
femorale 131
tigrinum 135
tigrinus 135
Tritonium bicegoi 117, 205
- lotorium*
Murex 131
Triton 131-132
- louellae*, *Ranella* 111
- louisae*, *Bursa caelata* 45, 47
- louisae*
Gyrineum 107-108
Halgyrineum
 . 19, 22, 24, 27, 34, 107-**108**, 109, 389; Pl. 24, Figs 4, 7-10
- loxahatcheensis*
Phalium 248
granulatum 248, 250
Semicassis granulata 250
- lucaensis*, *Bursa* 22
- lucrativa*, *xenogalea* 248
- lucunter*, *Echinometra* (echinoid) 223
- luteostoma*

- Bursa* 22
Tonna 23
Luterium 130
Lytechinus variegatus (echinoid) 223
maccamleyi, *Galeodea* 23, 240
Macgillivrayia pelagica 263
macgintyi, *Distorsio* 92
macilenta, *Charonia*
lampas 122
sauliae 121, 123
macra, *Urosalpinx* 320
macrodon
Cymatium
(Monoplex) 162
pileare 162
Monoplex
. . 21, 25, 28, 35, 146, **162**, 171, 227, 417; Pl. 38, Figs 13-16
Triton 162
maculata, *Gyrina* 111, 114-115
maculosa
Cominella 267
mareana, *Tonna* (*Cadus*) 267-268
Tonna 266-268
(Cadus) 267
maculosum, *Buccinum* 266-268
madagascarensis, *Cassis* 220
madagascariensis
Cassis 20, 22, 24, 27, 210, 213-216,
218-**219**, 220-224, 457-458; Pl. 58, Figs 1, 5; Pl. 59, Figs 1, 4
(Goniogalea) 210, 219
spinella, *Cassis* 218, 220-221
magellanica
Neptunea 104, 386; Pl. 23, Figs 2, 6
Priene 104
magellanicus
Argobuccinum (*Fusitriton*) 105
Fusitriton . 4, 6, 21, **104**-107, 202-203, 208, 386; Pl. 23, Figs 2, 4, 6
laudandus, *Fusitriton* 105
magellanicus, *Fusitriton* 105
Murex 104
murrayi, *Fusitriton* 105
retiolus, *Fusitriton* 105
Triton (*Lagena*) 104
Tritonium (*Cryotritonium*) 105
Malea **254**
camura . . 13, 16, 20, 24, 27, **255**-261, 263, 485; Pl. 72, Figs 1-4, 6
var. *elliptica* 257
crassilabris 260-261
densecostata 20, 27, 35, **257**-260, 263, 489; Pl. 74, Figs 4, 8
elliptica 13, 16-17, 27, 255-**257**,
258, 260-262, 485, 489; Pl. 72, Figs 5, 7-9; Pl. 74, Figs 1-3, 6
goliath 13, 16-17, 27, 256,
258-259, 263, 486, 490; Pl. 73, Figs 1-4; Pl. 75, Figs 1-2, 5
latilabris 254, 260-261
mareana 20, 27, 257, **259**-260
orbiculata 255
petiti 262, 265-266
pomum 6, 22-24, 26, 32, 255-256, 258
ringens 17-18, 20-21, 24, 26-28, 34, 254-
259, **260**-263, 498, 490; Pl. 74, Figs 5, 7; Pl. 75, Figs 3-4
mareana 259
springi 27, 255, 259, **262**-263, 265
(Malea)
Dolium
camura 260
dentatum 260
ringens 260
Tonna ringens densecostata 257
maleaformis, *Semicassis* (*Tylocassis*) 20, 251
malum, *Cassis* 248-249, 482; Pl. 71, Figs 2, 6
(Mambrinia), *Galeodea planotecta* 231
mammata, *Bursa* 57
mammillaris, *Cassis* 211
(Mangkalia), *Cassis martini* 211
mareana
Malea 20, 27, 257, **259**-260
ringens 259
Tonna (*Cadus*) *maculosa* 267-268
marerubra, *Septa* 23, 191
margaritula, *Bufonaria* 22, 66, 75
marginata
Aspa 6, 19, 22, 24-25, 27, 41, 63, **66**-68,
354, 362, 442; Pl. 7, Fig.2; Pl. 11, Fig. 3; Pl. 51, Figs 1-3
Bufonaria 66
(Aspa) 66
Bursa 64, 66
Cassis 66
Murex 67
Ranella 66
(Aspa) 66
marginatus, *Apollon* 66
marginatum
Buccinum 65-67
Gyrineum (*Aspa*) 66
Mariacassis caelatura 242
marmorata, *Cassis* 216
marmoratum
Buccinatorium 126
Triton 125-127
(Buccinatorium) 126
Marsupina **71**
bufo 12-13, 15-19, 21, 25, 27, 33, 35, 42, 60, 62, **72**-73, 75,
77, 123, 268, 358, 361; Pl. 9, Figs 1, 3-15; Pl. 10, Figs 1-3, 5
freyi 24, 28, **75**-76, 361; Pl. 10, Figs 6, 8-9
judensis 24, 28, 33, 42, **75**-76, 361; Pl. 10, Figs 4, 7, 10
nana 19, 21-22, 24-25, 28, 33, 35, 60, 72, **75**-**76**,
77-78, 270, 361-362; Pl. 10, Figs 11-12; Pl. 11, Figs 1-2, 5, 7-8
strongi 24, 28, **78**-79, 362; Pl. 11, Figs 3-4
(Marsupina)
Bufonaria nana 77
Bursa
albofasciata boussingaulti . . 43, 59-61, 352, 355; Pl. 5, Fig. 14
bufo 72
freyi 75
proavus 72
bowdenensis 72
spadicea 72
martini
Cassis (*Mangkalia*) 211
Sconsia 232
Turbinella 211
martiniana, *Cymatium* (*Lampusia*) *pileare* var. 170
martinianum
Cymatium 145, 168, 170
(Lampusia) pileare 170
(Monoplex) 170

- pileare* 170
(Septa) 170
pileare 145, 170
laticor, Triton 170
Triton 145, 169, 171
(Lampusia) 170
Tritonium 169
martinianus, Monoplex 146-147, 170-171
massenae, Cassis 227-228, 457-458; Pl. 58, fig. 4; Pl. 59, Fig. 3
matthewsi, Siphonalia 205-206, 445; Pl. 52, Fig. 5
Mauicassis 241
mauritium, Tritonium 162-163
Mayena
australasia 111-113
multinodosa 114-115
(Mayena), Argobuccinum australasium gemmiferum 113
mcgintyi, Distorsio 13, 16-19, 21, 25, 27-28, 80, 85-87, 89, 91-92, 93-94, 108, 366, 374, 377-378; Pl. 13, Figs 2-3, 6-8; Pl. 17, Figs 6, 8; Pl. 18, Figs 1-2, 4-5, 7-9; Pl. 19, Figs 1, 4
Mediargo mediocris 100-101
mediocre
Argobuccinum 107
Gyrineum 100-101
Mediargo 100-101
var. corbiculatum, Gyrineum 106-107
mediocris, Mediargo 100-101
mediterraneum, Tritonium 121, 123
melanostoma
Litiopa 6, 317
Tonna 23
meleagris, Cadus 268
Mellita quinquiesperforata (echinoid) 223
melpangi, Sassia 23, 199
menthafons, Phalium (Menthafontia) 210
Menthafontia 210
(Menthafontia), Phalium menthafons 210
Meoma ventricosa (echinoid) 223
metae, Sconsia 236
mexicana, Bursa 45, 47, 341; Pl. 1, Fig. 12
Microsconsia limpusi 23
microstoma, Semicassis 23
midwayensis
Fusitriton 55
Nesiocypraea 55
Sassia 23, 55
minae, Personopsis 100
minor
Bufonaria scrobiculator var. 62
Cymatium (Monoplex) doliarium var. 167
Tritonium
gemmiferum var. 113
sequenzae var. 125
minoruohmishii, Distorsio 19, 21, 28, 80, 84-87, 90-94, 378; Pl. 19, Figs 2-3, 10, 12
minuta, Cassis 248-249, 482; Pl. 71, Figs 2, 6
(Miogalea), Bathygalea
dalli 242-243
famulans 242
hadra 242
mirabilis
Charonia 121, 123
nodiferum 121
Tritonium (Charonia) nodiferum 121
mixta, Septa 23, 191
mohorterae
Cymatium (Ranularia) 184
Ranularia 184
mohorteri
Cymatium (Ranularia) 183-184
Ranularia 184
Moiria (echinoid) 223
monilifera
Cassis 251-252
inflata 251
Echinophoria 4
Ranularia 23
moniliferum
Cassis (Phalium) 251
Phalium 251
monitata, Bursa 41
Monoplex 142
amicus 19, 21, 25, 28-29, 44, 107, 144-145, 158, 405, 410; Pl. 32, Figs 4-5; Pl. 35, Figs 1-5, 7
aquaticus 17, 19, 21-25, 27-28, 145-149, 155, 158, 161-162, 169-172, 178, 191, 410, 413; Pl. 35, Figs 6, 8-16; Pl. 36, Figs 1-2
australasiae 142, 166, 168
cecilianus 147-148, 413; Pl. 36, Fig. 4
cercadicus 13-14, 16-17, 19, 24-25, 28, 37, 148-149, 155-156, 161, 173, 179-180, 413, 434; Pl. 36, Figs 6-9, 11; Pl. 47, Fig. 16
chlorostomoides 164
comptus 14, 19, 21-25, 27, 32, 149-152, 154, 177, 188, 413; Pl. 36, Figs 10, 14
cornutus 151
corrugatus 22, 25, 29, 55, 143-144, 158-159, 171
durbanensis 152-153
echo 167
exaratus 4, 6, 21, 23-24, 32, 143, 150-151, 152-153, 169, 174, 202, 414; Pl. 37, Figs 1-4
gatunicus 17, 27, 153-154, 414, 417, 446; Pl. 37, Figs 11, 15-17, 19-20; Pl. 38, Figs 6-7; Pl. 53, Figs 9-12
gurabonicus 13-14, 24, 27, 151, 154-155, 193, 413; Pl. 36, Figs 12-13, 15-17
infelix 24, 149, 155, 180
intermedius 23, 44, 145-146
jackwinorum 19, 24, 27, 155-156, 414; Pl. 37, Figs 6-9
keenae 19, 21, 25, 28-30, 35, 156-157, 168, 178-179, 186, 227, 422; Pl. 41, Figs 3, 6-7
krebsii 13-14, 16-19, 21, 24-25, 27-28, 108, 143-145, 147-148, 157-159, 173, 175, 180, 417, 434; Pl. 38, Figs 1-5, 8-12; Pl. 47, Fig. 15
lignarius 19, 21, 24, 26-28, 33, 153-154, 160, 414; Pl. 37, Figs 10, 12-14, 18
longispira 13-14, 27, 147, 161, 413; Pl. 36, Figs 3, 5
macrodon 21, 25, 28, 35, 146, 162, 171, 227, 417; Pl. 38, Figs 13-16
martinianus 146-147, 170-171
mundus 21, 23-24, 27-28, 32, 113, 139, 162-163, 418, 421-422; Pl. 39, Figs 14, 16-17; Pl. 40, Figs 4, 6; Pl. 41, Figs 1, 5
norai 23, 250
nicobaricus 5, 21, 23-25, 27, 32, 139, 163-165, 366; Pl. 13, Fig. 1
oboesus 181
panamensis 17, 19, 24, 27-28, 33, 165-166, 175, 421; Pl. 40, Figs 1, 3, 5, 7
parthenopeum echo 167-168
parthenopeus 4-6, 13-14, 16-19, 21-25, 27-30, 35, 115, 124, 142, 146, 148, 153,

- 156-157, 161, **166**-167, 169, 172, 176, 179-180, 202, 227, 421-422, 425; Pl. 40, Figs 2, 8-9; pl. 41, Figs 2, 4; Pl. 42, Figs 1, 5, 7
penniketi 23, 250
pilearis 13-14, 19, 21-23, 25, 27-28, 32, 35, 140, 142, 145-147, 149, 153, 155, 162-163, 168-**169**, 170-172, 180-181, 227, 418; Pl. 39, Figs 1-13, 15, 18
ritteri 19, 24, 27, **172**-173, 426; Pl. 43, Figs 2-4
thersites 23, 177
tranquebaricus 6, 19, 21-22, 27, 118, 158, 166, **173**-175, 179, 426; Pl. 43, Figs 5-7, 9-14
trigonus . 6, 21-22, 27, 48, 113, 160, **175**-176, 429; Pl. 44, Figs 1-2
turtoni 24, **176**, 425; pl. 42, Figs 2-4, 6, 8
vespaceus 21, 23-24, 27, 32, 113, 149-152, 164, **176**, 179, 429; Pl. 44, Fig. 5
vestitus 19, 21, 25, 28-30, 156-157, 162, **178**, 186, 429; Pl. 44, Figs 3-4, 6-12
wiegmanni 14, 19, 21, 24-26, 28, 34, 148, 157, 166, **179**-180, 182, 430; Pl. 45, Figs 1-3, 7
williamsi 24, 149, **180**
 (Monoplex), *Cymatium*
amictum 143
aquatile 145
cercadicum 148
comptum 149, 154
corrugatum
amictum 143, 158
krebsii 157
tremperi 143
costatum 167
doliarium 167
 var. *minor* 167
echo iwakawanum 167
exaratum 152
gemmatum 163
krebsii 157
lignarium 160
macrodon 162
martinianum 170
mundum 163
nicobaricum 164
parthenopaeum 167
parthenopeum 167
 echo 167
 keanae 156
 parthenopeum 167
pharcidum 197
pileare 170
tenuiliratum 197
thersites 177
tranquebaricum 174
 var. *linatelloides* 174
trigonum 175
turtoni 176
valentinei 167
vespaceum 177
vestitum 178
wiegmanni 179
morgani
Lotorium 206
Sassia . . 205-**206**, 207, 445-446; Pl. 52, Figs 7, 9-10; Pl. 53, Fig. 4
Tritonium 206
Morio
echinophora 232
fasciata 264
Morionassa amplectens 232, 303
moritincta, *Ranularia* 182
moritinctum
Cymatium 182
Tritonium 181, 183
moritinctum caribbeaum, *Cymatium* 182
 (Ranularia) 182
moritinctus, *Triton* 181-183; 430; Pl. 45, Fig. 4
morrisoni, *Tonna* 23
muangmani, *Phalium* 23
muehlhaeuseri, *Distorsio* 23
multinodosa
Fusitriton 114
Mayena 114-115
mulus, *Murex* 75
mundum
Cymatium 163
 (Monoplex) 163
 (Septa) 163
Triton 162
Tritonium 162
mundus, *Monoplex* 21, 23-24, 27-28, 32, 113, 139, **162**-163, 418, 421-422; Pl. 39, Figs 14, 16-17; Pl. 40, Figs 4, 6; Pl. 41, Figs 1, 5
munsteri, *Tritonium* 141
Murex
anus 79
argus 101-102, 179, 386; Pl. 23, Figs 5, 8
bufo 71-73, 361; Pl. 10, Figs 1-2
bufonius 41, 57
clandestinus 137
clavator 181
conditus 41
costatus 156, 166, 168
costulatus 166, 168
crassus 72-73, 361; Pl. 10, Figs 1-2
cutaceus 118-119
doliare 166, 168
erinaceus 318
femorale 130-133, 401; Pl. 30, Figs 6-7, 9-12
ficus 312
gyrinoides 120, 123
intermedius 166, 168
labiosus 192, 195-196
lampas 120, 123, 132
lotorium 131
magellanicus 104
marginata 67
mulus 73
nerei 121, 123
nodosus 62
olearium 111, 114-115, 166, 169
parthenopeus 142, 166, 176
pileare 169, 171
rana var. 62
reticulatus 81, 92, 94, 98, 114
rubecula 189
scrobiculator 62
scrobilator 62, 64
succinctus 137
trigonus 175
tritoni 120, 125-127
williamsi 180

- Muricidae 318-320
muricina, Distorsio 138-139
muricinum
 Cymatium 138
 (*Gutturium*) 138
 (*Ranularia*) 138
 Gutturium . . . 21, 22, 24, 27, 32, **138**-139, 409; Pl. 34, Figs 2-3
 Ranularia (*Gutturium*) 139
murrayi
 Argobuccinum (*Fusitriton*) 105
 Cryotritonium 104
 Fusitriton 104-105
 cancellatus 105
 magellanicus 105
 Lampusia 104-105
 (*Priene*) 104
 Phalium (*Tylocassis*) 246
 Semicassis 246
 Tritonium (*Cryotritonium*) 105
mutica, Cassidaria 253
muticum, Galeodolium 253
nana
 albofasciata, Bursa (*Colubrellina*) 77
 Bufonaria (*Marsupina*) 77
 Bursa 72, 75, 77
 Cassis 23, 211
 (*Nannocassis*) 211
 jamanensis, Bursa 7, 77
 Marsupina 19, 21-22, 24-25, 28, 33, 35, 60, 72, 75-76,
 77-78, 270, 361-362; Pl. 10, Figs 11-12; Pl. 11, Figs 1-2, 5, 7-8
 Ranella 60, 72, 76-78
Nassaria kampyla 198, 202-203
nassariformis, Sassia 23, 199
natalensis, Bursa
 . . . 12, 19, 21, 25, 37, 42-43, **52**-54, 56, 63, 346; Pl. 3, Figs 10-13
 (*Bufonariella*) *latitudo* 52
 (*Colubrellina*) 52-53
 (*Colubrellina*) *latitudo* 52
 latitudo 52
natator, Gyryneum 22
Negyrina subdistorta 198
(Negyrina), Charonia
 alfredensis 121
 kampyla 202
Neosconsia ecuadoriana **318**, 334, 474; Pl. 67, Figs 4, 6
nephele, Sconsia 22, 234, 237
Neptunea
 doliata 137
 magellanica 104, 386; Pl. 23, Figs 2, 6
 szukouensis 140-141
Neptunella cutaceus 118
neptunia, Linatella 140-141
neri, Murex 121, 123
Nesiocypraea midwayensis 55
new species, Akibumia 22-23
nicobaricus
 Cymatium 164
 (*Cymatriton*) 164
 (*Monoplex*) 164
 (*Ranularia*) 164
 (*Septa*) 164
 Cymatriton 164
 Tritonium 163
 nicobaricus, Monoplex
 5, 21, 23-25, 27, 32, 139, **163**-165, 366; Pl. 13, Fig. 1
 nigrita, Tutufa (*Tutufella*) 22
 nigromaculata, Triton leucostoma var. 113
 nipponensis, Casmaria 23
 nobile
 Buccinatorium 120
 Triton 120
nobilis
 Bursina 22, 44
 Charonia 127
 tritonis 127
 tritonis var. 127
 Septa tritonis var. 127
 Triton 126-127
 (*Buccinatorium*) 126
 tritonis var. 127
 Tritonium tritonis var. 127
nodifer, Triton 121
nodifera, Charonia 121
nodiferum
 Simpulum 121
 Triton 121, 123
 Tritonium 121
 (*Charonia*) 121
nodiferum
 mirabilis, Tritonium (*Charonia*) 121
 var. *glabra, Tritonium* 124
nodiferus, Triton 121
nodocostata
 Cymatium (*Ranularia*) *tenuilinata* var. 202
 Lampusia 202-203
nodocostatum, Lotorium 202
nodosa
 Bursa 63
 (*Bufonariella*) 63
 scrobiculata 62
 Ranella 62
 (*Apollon*) 62
 Siphonalia 205
nodosocincta, Siphonalia 205-206
nodosum, Tritonium 179-180
nodosus, Murex 62
nodulus
 Tritonium 138-139
 (*Ranularia*) 138
norai
 Cassis 7, 22-25, 27, 213, 215-216, **221**, 450; Pl. 55, Figs 4-5
 Monoplex 150
nucleoides
 Distorsio (*Personella*) 201
 Sassia 201
Nyctilochus
 alfredensis 121, 123
 femorale 131
 kewi 116
 obesa, Litiopa 138-139
 oblita, Ranularia 23
 obliteratum, Lotorium 319
 obliteratus, Xymene 319-320
 oboesa, Ranularia 23
 Obscuranella papyrodes 104, 253
 obscurus, Triton 151-153

- occidentale*
Cymatium 149, 177
rubeculum 190
 (Septa) 191
Dolium perdix 266-267
Triton
rubeculum 149, 177, 190-191
 (Lampusia) *rubecula* 149, 177, 190-191
 (Simpulum)
aquatile 145, 147
thersites 149
- occidentalis*
Bursa lessonae race 55
Distorsio acuta 81
Dolium perdix 266
 Septa . . 20-25, 27, 189-**190**, 191-192, 437; Pl. 48, Figs 3, 8-9, 11-12
Ocenebra erinaceus 318
oentoengi, *Tonna* 23
olearia, *Ranella* 114
olearium
Argobuccinum (*Ranella*) 114
Buccinum 264-265
Cymatium 166
Lampusia 166
Murex 111, 114-115, 166, 169
Ranella . . . 4, 6, 21, 22, 24, 27, 111-112, **114**-116, 124, 202, 393-394, 397; Pl. 26, Fig. 5; Pl. 27, Figs 1, 3, 5; Pl. 28, Figs 1, 3, 7
Triton 166
 (Simpulum) 166
Tritonium 169
Tonna 266
olearium barcellosi, *Ranella* 114
Olequahia washingtoniana 31
Oocorys **240**
bartschi 241, 317
clericus 241
clericus 17, 22, 27, **241**, 317, 470; Pl. 65, Figs 1, 3
elevata 21, 316-317, 470; Pl. 65, Figs 6-7, 9
grandis 22-23
rotunda 21
sulcata 21-24, 240, 317
verilli 22-24
Oocorythinae **238**
opis, *Tritonium* 120, 123
orbiculata, *Malea* 255
oregonense
Argobuccinum (*Fusitriton*) *cancellatum* 106
Triton 106-107
oregonensis
Argobuccinum (*Fusitriton*) 106
Fusus 106
Fusitriton 5, 21, 28, 40, 105-**106**, 107
Priene (*Fusitriton*) 106
Ranella 106
 (Priene) 106
 var. *angelensis*
Priene 106-107
Ranella (Priene) 106
orientalis
Akibumia 22-23
Cymatium (Septa) *pileare* 170
Triton 195-196
 (Gutturnium) 195
- ostenfeldi*, *Ranella* 114-115
Ostrea cochlear 100
Otus reticulatus 312
Orthaulax pugnax 65
oyamai, *Tutufa* (*Tutufella*) 22
pacifica
Argobuccinum (Priene) 106-107
Ranella (Priene) 106
pacomoni, *Bursa* (*Bursa*) 50-51
palmeri, *Sassia* 23
panamensis, *Monoplex*
 . 17, 19, 24, 27-28, 33, **165**-166, 175, 421; Pl. 40, Figs 1, 3, 5, 7
papillosum, *Simpulum* 54, 56, 350; Pl. 5, Figs 1, 4
papyratia
Ficus 313-314
Pyrrula 313
papyrodes, *Obscuranella* 104, 253
paraense, *Phalium* 251
paralaevigata, *Sconsia* 20, 27, 173, 226, **238**
Paralagena 137
parfaiti, *Talisman* 41
parkinsonia
Austrosassia 198
Sassia 198
Septa 198
parthenopaeum, *Cymatium* 167
 (Monoplex) 167, 176
parthenopea
keenae, *Septa* (Monoplex) 156
parthenopea, *Septa* (Monoplex) 167
parthenopeum
Cymatium 156, 167, 170
 (Monoplex) 156, 167
 (Septa) 167
echo
Cymatium (Monoplex) 167
 Monoplex 167-168
keenae, *Cymatium* (Monoplex) 156
parthenopeum
Cymatium
 (Monoplex) 167
 (Septa) 167
Triton 166
parthenopeus
Cymatium (Septa) 167
 Monoplex 4-
 6, 13-14, 16-19, 21-25, 27-30, 35, 115, 124, 142, 146, 148, 153, 156-157, 161, **166**-167, 169, 172, 176, 179-180, 202, 227, 421-422, 425; Pl. 40, Figs 2, 8-9; pl. 41, Figs 2, 4; Pl. 42, Figs 1, 5, 7
Murex 166
parthenopum, *Cymatium* (Septa) 167
parthenopus, *Cymatium* (*Cabestana*) 167
parthi, *Ranularia* 23
Particymatium 143
labiosus 192
strangei 192, 195
partschii, *Tritonium* 121, 123
parvimpedita, *Distorsio* 23, 82
Parvitonna perselecta 264
parvula, *Cymatiella* 208
parvulum, *Triton* 208
patamakanthini, *Cassis* 23, 211
paucirugis, *Semicassis* 23

- paulucciana*, *Ranella* 57-58
peasei, *Septa* 23, 44, 190-191
pelagica, *Macgillivrayia* 263
peloleuca, *Rinodina* (lichen) 202
pelouatensis
 Bursa 43-55
 Ranella 44
peninsulium, *Cymatium* (*Linatella*) *cingulatum* 140-141
pennata, *Tonna* 13, 16-17, 20, 22,
 25, 27, 265-266, 267-269, 490, 493; Pl. 75, Fig. 6; Pl. 76, Figs 1-2
pennatum, *Dolium* 266, 268
penniketi, *Monoplex* 23, 250
perca, *Biplex* 22
perdistorta
 Distorsio 21-24, 27, 32, 80, 82, 94-95, 378; Pl. 19, Figs 5-9, 11
 (*Rhysema*) 94
Perdix reticulatus 263, 268
perdix
 Buccinum 263, 268
 Cadium 263
 Cadus 263
 Dolium 266-267
 occidentale, *Dolium* 266-267
 Tonna 23, 25, 265-268, 494; Pl. 77, Figs 5-6
 var. *brasiliiana*, *Dolium* 266
peregrinatrix, *Akibumia* 22
perelegans, *Bufonaria* 22
perficus, *Saginafusus pricei* 170-171
perforatus, *Triton* 179
peridistorta, *Distorsio* (*Rhysema*) 94
peristephes, *Semicassis cicatricosa* 245, 248, 250
perrugata, *Urosalpinx* 320
perryi
 Casmaria 22-23
 Lotoria 23
perselecta, *Parvitorina* 264
Persona 79
 anus 79
 clathrata 81
 grasi 99
 simillima 81, 97
 smithi 98-99
personatum
 Dolium 260-261
 Triton 100
Personella
 floridana 81-82, 89, 92
 septemdentata 201
(Personella), *Distorsio*
 grasi 99
 nucleoides 201
Personidae 79
Personopsis 99
 beui 100
 grasi 21-22, 24, 99-100, 377; Pl. 18, Figs 3, 6
 minae 100
 purpurata 23
 trigonaperta 23
pesleonis, *Bufonaria* 62, 64
petiti, *Malea* 262, 265-266
pfeifferianum
 Cymatium 187
 (*Gutturium*) 187
 (*Ranularia*) 187
 (*Reticutriton*) 188
 (*Septa*) 188
Reticutriton 187
pfeifferianus
 Reticutriton 21, 23-25, 27,
 32, 113, 150-151, 186-187, 188-189, 434; Pl. 47, Figs 10, 12
Triton 145, 149, 186-188
 (*Gutturium*) 187
 (*Simpulum*) 187
Phaliinae 241
Phalium
 alligator 248, 250
 areola 23
 bandatum
 bandatum 23
 exaratum 23
 (*Bezoardica*) *sulcosum* var. *abbreviatum* 247
 cicatricosum 248-249
 decussatum 23
 (*Echinophoria*)
 andersoni 243
 hadrum 243
 woodringi 244
 fimbria 23
 flammiferum 23
 glaucum 23
 granulatum 248
 abbreviata var. *centiquadrata* 247
 loxahatcheensis 248, 250
 loxahatcheensis 248
 (*Menthafontia*) *menthafons* 210
 moniliferum 251
 muangmani 23
 paraense 251
 (*Semicassis*)
 cicatricosum 248
 granulatum 245, 248
 strigatum 224
 (*Tylocassis*)
 aldrichi 246
 cicatricosum 248
 granulatum 248
 centiquadratum 245, 247
 forma cicatricosum 248
 granulatum 245, 248
 reclusum 251
 undulatum 245
 inflatum 248
 murrayi 246
 reclusa 251
 sulcosum senni 252
 waltonensis 248
(Phalium)
 Cassis
 aldrichi 246
 dalli 242-243
 moniliferum 251
 Phanozesta remensa 198
pharcida, *Lampusia* 197, 426; Pl. 43, Fig. 1
pharcidum, *Cymatium* 197
 (*Monoplex*) 197
 (*Turritriton*) 197

- philomelae*
Sassia 24, 202-**204**, 207-208, 441; Pl. 50, Figs 6-7, 10
Triton 202, 204
- pileare*
Cymatium 134, 145, 159, 162, 170
 (*Lampusia*) 145, 170
 (*Monoplex*) 170
 (*Septa*) 145, 162, 170
Eutritonium 170
henicum, *Cymatium* (*Septa*) 157-158
Lampusia 170, 197
macrodon, *Cymatium* 162
martinianum, *Cymatium* 170
 (*Lampusia*) 170
 (*Septa*) 145, 170
Murex 169, 171
orientalis, *Cymatium* (*Septa*) 170-171
pileare, *Cymatium* (*Septa*) 170
Simpulum 170
Triton 169
 (*Lampresia*) 170
 (*Simpulum*) 145
Tritonium 157, 169
 var. *borneana*, *Cymatium* (*Lampusia*) 177
 var. *cruzana*, *Cymatium* 145, 147
 var. *martinianum*, *Cymatium* (*Lampusia*) 170
- pilearis*
Aquillus 170
Lampusia 169-170
Monoplex 13-14, 19, 21-23,
 25, 27-28, 32, 35, 140, 142, 145-147, 149, 153, 155, 162-163,
 168-**169**, 170-172, 180-181, 227, 418; Pl. 39, Figs 1-13, 15, 18
Murex 143, 157, 162, 170-171, 197
Septa 170
 var. *aquatilis*, *Tritonium* (*Simpulum*) 145
- pilsbryi*
Echinophoria 21, 26, 244
Ficus 312-313, **315**-316, 497; Pl. 78, Figs 1-3, 6
Pirula ficus 312
Pisanianura
 breviaxis 23
 donghaiensis 23
 grimaldii 22-23
Plagiobrissus grandis (echinoid) 223
planotecta
 Cassidaria 231
 Galeodea 231
 (*Mambrinia*) 231
Plaxiphora aurata 202
pleurotoma, *Buccinum* 66-67
plicata, *Cassis* 223
plicatum, *Buccinum* 217, 223-224
plicosum, *Dolium* 260-261
pliniae, *Triton* 121, 123
plumatum, *Dolium* 267, 292; Pl. 77, Figs 5-6
poecilostoma
 Charonia 113
 Ranella leucostoma var. 113
Polia scabra 109
(Polytropia), *Purpura bantamensis* 140
polyzonalis, *Ranella* 101-102, 386; Pl. 23, Figs 5, 8
pomum
 Buccinum 255
- Malea* 6, 22-24, 26, 32, 255-256, 258
Quimalea 255
- ponderosa*
 Bursa (Colubrellina) corrugata 45
 Ranella 45, 47, 342; Pl. 1, Figs 11, 13
 ponderosa, *Casmaria* 23
 unicolor, *Casmaria* 23
poppei, *Tonna* 23
poulsenii
 Cymatium 140
 (*Linatella*) 140
 Triton (Linatella) 140-141
powelli, *Charonia* 121, 123
praefemorale
 Cymatium 13-14, 16-17,
 24, 27, 131-**132**, 133, 402, 406; Pl. 31, Fig. 3; Pl. 33, Figs 1-9
 Lotorium 132-133
pratti, *Cymatiella* 210
 prey species (echinoids), *Cassis tuberosa* 223
pricei perficus, *Saginafus* 170-171
Priene **109**
 (*Fusitriton*)
 cancellatus 104
 oregonensis 106
 magellanic 104
 oregonensis var. *angelensis* 106
 retiolium 105
 rude 109
 scaber 109
 scabra 109
 scabrum 21, 105, **109**-110, 134, 203, 389-
 390, 442; Pl. 24, Figs 5-6; Pl. 25, Figs 2-3, 5-6; Pl. 51, Figs 6, 8
 (*Priene*)
 Argobuccinum
 pacifica 106-107
 rude 109-110
 scaber 109
 scabrum 109
 Lampusia murrayi 104-105
 Ranella
 corbiculata 106
 oregonensis 106
 var. *angelensis* 106-107
 pacifica 106
 tugaruensis 106-107
 Triton
 cancellatus 104
 rudis 109
 Tritonium
 cancellatus 106
 rude 109
 scaber 109
prima, *Dissentoma* 167-168
proavus
 bowdenensis, *Bursa (Marsupina)* 72
 Bursa
 crassa 72-73, 358; Pl. 9, Fig. 14
 (*Marsupina*) 72
problematicum
 Cymatium 174
 tranquebaricum forma 174
 Eutriton (Simpulum) 173-174
prodiata

- Bursa* (Apollon) 101
Ranella (Apollon) 101
proditor
Argobuccinum 101-102, 116
ranelliforme 101, 114
Bursa (Apollon) 101-102
Ranella (Apollon) 101-103
productum, *Triton* 138-139
prolongata, *Sconsia* 27, 238
Proxicharonia arthritica 198
pseudaphera, *Distorsionella* 23
Pseudobursa 41
Pseudogaleodea tricarinata 231
pugnax, *Orthaulax* 65
pulchella, *Biplex* 22
pulchellus, *Triton* 164
pulchra
Biplex 22, 76
Ranella 76-78
Sconsia 232
pumilio
Charonia 208
Cymatiella 23, 208
Triton (*Lampusia*) *chlorostomum* var. 164
Vernotriton 208
Purpura (*Polytropa*) *bantamensis* 140-141
purpurata, *Personopsis* 23, 100
pusilla, *Distorsomina* 23
pusillum, *Gyrineum* 22
pustulata
Charonia 121
lampas 121-122
Tritonium 121, 123
pustulosa
Bursa 29, 45, 48
(*Colubrellina*) *corrugata* 45
Ranella 45, 47, 345; Pl. 2, Figs 6-7
var. *jabik*, *Bursa* 45, 47
pustulosum
Argobuccinum 4, 6, 21, 101-103, 111,
114, 202, 386, 389; Pl. 23, Figs 1, 3, 5, 7-9; Pl. 24, Figs 1-3
Buccinum 100-103
ranelliforme, *Argobuccinum* 102
tumidum, *Argobuccinum* 102
Pycnodonte cochlear 100
pygmaea, *Bursa* 54-56
pyriformis, *Triton* 138-139
Pyrula
carbasea 313
fasciata 263-265
ficus 312
papyratia 313
pyrula, *Ranularia* 23
pyrum
Cassis 244
Cymatium (*Ranularia*) 184
Ranularia 23, 181-182, 185
rehderi, *Cymatium* (*Ranularia*) 184
Semicassis 23, 245
Xenogalea 244
quercina, *Apollon* 62, 64
Quimalea pomum 255-256
quinquiesperforata, *Mellita* (echinoid) 223
quirihorai, *Bursa* 23
quoyi, *Cymatiella* 208
rada
Lotorium (*Lampusia*) 318-319
Ocenebra 318-319
raderi, *Cymatium* 14, 21, 24,
27-28, 131-133, 134-135, 402, 405; Pl. 31, Figs 1, 4; Pl. 32, Figs 1-3
radialis
Austrotriton 198
Sassia 198
Triton 198
rana
Bufonaria 22
var., *Murex* 62
Ranella 111
affinis 48-50
albifasciata 77
albofasciata 60, 77-78, 362; Pl. 11, Figs 1-2
ampullacea 101-103
(*Apollon*)
argus 101
caelata 45
gigantea 114
nodosa 62
prodita 101
proditor 101-103
vexillum 101
(*Argobuccinum*)
argus 101
gigantea 114
argus 101-102
(*Aspa*)
laevigata 66
marginata 66
australasia 4, 22, 111-112
gemmifera 113
bergeri 57-58
brocchii 66
bronni 114
(*Bursa*)
affinis 48
thomae 57
calata 45
caelata 45, 47, 345; Pl. 2, Figs 1, 3
californica 68-70, 109, 357; Pl. 8, Fig. 7
chilena 111-112, 393; Pl. 26, Figs 1-4, 6-8
coriacea 62-64
crassa 72
caudata 175
cubaniana 48-49, 346; Pl. 3, Figs 1, 3
eogassinense 111
gemmifera
. . . 21, 24, 27, 32, 101, 111, 113-114, 390; Pl. 25, Figs 7-9, 11
gigantea 111, 114-115
var. *atlantica* 114
granifera 48-49
granulata 72-73
gyrinata 138-139
incerta 114
intercostalis 111
kaiparaensis 111-112
katherineae 111
kingii 101, 103

- laevigata* 65-67, 442; Pl. 51, Figs 1-3
(*Lampas*)
- californica* 68
- corrugata* 45
- cruentata* 66
- cruentata* var. *rhodostoma* 57
- granifera* 48
- ranelloides* var. *tenuisculpta* 54, 56
- thomae* 57
- ventricosa* 68
- (*Lampasopsis*) *thomae* 57
- leucostoma* 113
- var. *peocilostoma* 113
- louellae* 111
- marginata* 66
- nana* 60, 72, 76-78
- olearia* 114
- olearium* 4, 6, 21-22, 24, 27, 111-112, **114**-116, 124, 202, 393-394, 397; Pl. 26, Fig. 5; Pl. 27, Figs 1, 3, 5; Pl. 28, Figs 1, 3, 7
- var. *barcellosi* 114
- ostenfeldi* 114-115
- paulucciana* 57-58
- pelouatensis* 44
- polyzonalis* 101-102, 386; Pl. 23, Figs 5, 8
- ponderosa* 45, 47, 342; Pl. 1, Figs 11, 13
(*Priene*)
- corbiculata* 106
- oregonensis* 106
- var. *angelensis* 106
- pacifica* 106-107
- tugaruensis* 106-107
- pustulosum* 45, 47, 345; Pl. 2, Figs 6-7
- ranelloides* 56
- reticularis* 114
- rhodostoma* 41, 49, 57-58
- var. *xantosotoma* 57-58
- rugosa* 59-61, 68, 350; Pl. 5, Figs 9, 13
- scabra* 109
- scrobiculata* 55, 62
- scrobiculator* 62
- semigranosa* 45, 47-48, 345; Pl. 2, Fig. 4
- spadicea* 72
- tenuis* 68, 70
- thomae* 57-58, 350; Pl. 5, Fig. 5
- tristanensis* 101
- tuberculata* 62
- tuomeyi* 111
- ventricosa* 68-70, 357; Pl. 8, Figs 1-2, 6
- venustula* 57-58
- verrucosa* 42
- vexilla* 101
- vexillum* 101-103, 386; Pl. 23, Figs 3, 9
- washingtoniana* 111
- yasumurai* 111
(*Ranella*)
- Bursa*
- amphitrites* 59
- rhodostoma* 58
- Tritonium verruculosum* 117
- Ranellidae **100**
- ranelliforme
- Argobuccinum* 101-102
- argus* 101
- pustulosum* 102
- proditor*, *Argobuccinum* 101, 113-114
- ranelliforme*, *Argobuccinum* 101
- Triton* 102, 121
- tumidum*, *Argobuccinum* 101
- ranelliformis*, *Triton* 101
- ranelliformis*, *Argobuccinum* 101
- tumidum*, *Argobuccinum* 101
- Ranellinae **100**
- ranelloides*
- benvegnuae*
- Bursa* 54-55
- (*Bufonariella*) 54-55
- (*Colubrellina*) 54
- Bufonariella* 54
- Bursa* 17-18, 22, 24, 27, 31-32, 34, 42, 53-54, 55-57, 349; Pl. 4, Figs 1-9; Pl. 5, Figs 1-4, 6, 8
- (*Colubrellina*) 54
- (*Tritonoranella*) 54
- Lotorium* 54
- Ranella* 56
- ranelloides*, *Bursa* 54
- (*Bufonariella*) 54
- (*Colubrellina*) 54
- tenuisculpta*, *Bursa* 54
- (*Bufonariella*) 54
- (*Colubrellina*) 54
- Triton* 42, 54, 56-57
- Tritonoranella* 42, 54
- Tutufa* 57
- var. *tenuisculpta*, *Bursa* (*Lampas*) 54, 56
- Ranula* 181
- Ranularia* **181**
- andamanensis* 23
- arthuri* 23
- boschi* 23
- caudata* 23, 140
- clavator* 181
- cynocephalum* 21-25, 27, 32, 34, 181-**182**, 183, 191, 430; Pl. 45, Figs 4-6, 8-9
- dunkeri* 23, 181, 185
- encaustica* 23
- exilis* 23
- gallinago* 21, 23-24, 27, 31-32, 34, 113, 182-**183**, 184, 433; Pl. 46, Figs 1-5, 8
- gutturina* 23, 181
(*Gutturium*)
- muricinum* 139
- tuberosa* 138
(*Lagena*)
- clandestinus* 137
- rostratus* 140
- wiegmanni* 179
- longirostra* 181
- mohorterae* 184
- mohorteri* 184
- monilifera* 23
- moritincta* 182
- oblita* 23
- oboesa* 23
- parthi* 23
- pyrula* 23
- pyrum* 23, 181-182, 184-185

- rehderi* . . . 21, 27-28, 32, 151, 181-182, **184**-185, 433; Pl. 46, Figs 6-7
sarcostoma 23, 182
sinensis 23
springsteeni 23
testudinaria 23, 181, 185
trilineata 23, 181
tripa 23
tuberosa 138
(Ranularia)
Cymatium
aegrotum 183
caribbaeum 181, 195
caudatum 140
cynocephalum 182
gallinago 183
kugleri 160, 414; Pl. 37, Fig. 12
mohorterae 184
morhorteri 184
moritinctum caribbaeum 182
muricinum 138
nicobaricum 164
pfeifferianum 188
pyrum 184
rehderi 184
rehderi 184
sarcostoma 182
sarcostumum 152
tenuilirata var. *nodocostata* 202
testudinarium rehderi 184
Tritonium
domingense 193
nodulus 138
ranzani, *Cymatium* 23, 131-132
reclusa
Cassis 251-252
Semicassis 13, 15-16, 20, 24, 27, 35, 246, 250-
251, 252, 478, 481; Pl. 69, Figs 3-10; Pl. 70, Figs 1-3, 5, 7-10
(Tylocassis) 248, 252
reclusum, *Phalium* (*Tylocassis*) *granulatum* 251
recurvirostrum
Buccinum 248-249, 482; Pl. 71, Figs 2, 6
Cassis 248
rehderi
Cymatium 184
(Ranularia) 184
pyrum 184
testudinarium 184
testudinarium 184
Ranularia
. . . 21, 27-28, 32, 151, 181-182, **184**-185, 433; Pl. 46, Figs 6-7
remensa
Phanozesta 198
Sassia 23, 198-199
remotum, *Cymatium* 202-204
reticulare
Distortrix 81
Tritonium 81
reticularis
Distorsio 23, 73, 82
Murex 81, 92, 94, 98, 114
Ranella 114
var. *clathratus*, *Distortio* 81
reticulata
Distorsio 92
Distortrix 92
var. *clathratus*, *Distortrix* 81, 92
reticulatus
Distortio 92
Otus 312
Perdix 263, 268
Reticutriton **186**
carlottae 24-25, 27, **186**, 188-189
elsmerensis . . . 24, 28, 107, 130, **186**-187, 434; Pl. 47, Figs 2-4, 6-8
lineatus 21, 24-25, 28, 186-**187**, 188, 434; Pl. 47, Figs 1, 5
pfeifferianus 21, 23-25, 27,
32, 113, 150-151, 186-**187**, 188-189, 434; Pl. 47, Figs 10, 12
pfeifferianum 187
tenuiliratus 197
(Reticutriton), *Cymatium*
elsmerense 186
lineatum 187
pfeifferianum 188
tenuiliratum 197
retiolus
Argobuccinum 105
(Fusitriton) *cancellatum* 105
Priene 105
retiolus, *Fusitriton* 105
magellanicus 105
Retusum 181
oboesus 181
retusum 181
rhodostoma
Bursa 18-19, 22, 24-25,
27, 41, 49-52, **57**-58, 59, 173, 350; Pl. 5, Figs 5, 7, 10-12, 15
Lampadopsis 57
Ranella 41, 49, 57-58
(Lampas) *cruentata* var. 57
rhodostoma, *Bursa* 57
thomae, *Bursa* 57
var. *xantostoma*, *Ranella* 57-58
Rhysema 79
(Rhysema), *Distorsio*
clathrata 81, 99
constricta 84, 90
mcgintyi 92
macgintyi 92
decussata 87
gatunensis 84, 86-87, 90, 97
simillima 97
floridana 81-82
gatunensis 87
horrida 94-95
mcgintyi 92
perdistorta 94
robinsoni 81-82
ridens
Distorsio 87, 90, 99
Distortrix 98
Triton 81-82, 87, 90, 98-99
ridleyi
Cymatium 184
Triton 149, 151, 184
ringens
Buccinum 260-261
Cassis 254-255, 260

- densecostata*, *Tonna* (*Malea*) 257
- Distorsio* 26, 91-92, **95**-96, 97, 112, 203, 381; Pl. 20, Figs 1-5, 7
- decussatus* 95
- Dolium* 260
- (*Malea*) 260
- Malea* 17-18, 20-21, 24, 26-28, 34, 254-
 260, 261-263, 490, 498; Pl. 74, Figs 5, 7; Pl. 75, Figs 3-4
- Tonna* (*Malea*) 260
- Tritonium* 95-96
- Rinodina peloleuca* (lichen) 202
- ritteri*
- Cymatium* 172
- (*Gutturium*) 172-173
- Monoplex* 19, 24, 27, **172**-173, 426; Pl. 43, Figs 2-4
- robinsoni*, *Distorsio*
- clathrata* forma 81
- (*Rhysema*) 81-82
- rosa*, *Bursa* 23
- rosaceus*, *Clypeaster* (echinoid) 223
- rosemaryae*, *Tonna* 23
- roseum*, *Gyrineum* 22
- rostratum*, *Triton* (*Linatella*) 140
- rostratus*, *Ranularia* (*Lagena*) 140
- rotunda*
- Distorta* 79
- Oocorys* 21
- rotundata*, *Cassiss* 219-220
- royana*
- Cassidea* 23, 244
- Semicassis* 23
- royanum*, *Xenophalium* 244
- rubecula*
- Murex* 189
- occidentale*, *Triton* (*Lampusia*) 149, 177, 190-191
- Septa* 23, 143, 190-191
- rubeculum*
- Cymatium* (*Septa*) 190
- occidentale*
- Cymatium* 190
- (*Septa*) 190
- Triton* 190
- rubeta*, *Tutufa* (*Tutufella*) 22
- rubicola*, *Biplex* 48-49
- rubicunda*
- Charonia* 121
- gyrinoides* 121
- lampas* 121
- Septa* 121-123
- rubicundum*, *Lotorium* 121
- rude*
- Argobuccinum* 109
- (*Priene*) 109
- Priene* 109
- Tritonium*
- (*Argobuccinum*) 109
- (*Priene*) 109
- rudis*, *Triton* 109-110, 442; Pl. 51, Fig. 6
- (*Priene*) 109
- rufa*, *Cypraeacassis* 23, 225
- rufum*, *Buccinum* 225
- rugosa*
- Bursa* 12, 16-19, 21-22, 24, 26-28, 33, 42-45, **59**-62, 68-69,
- 160, 186, 242, 350, 353; Pl. 5, Figs 9, 13-14; Pl. 6, Figs 1-10
- Galeodea* 22, 232
- Ranella* 59-61, 68, 350; Pl. 5, Figs 9, 13
- rutilum*, *Tritonium* 195-196
- saburon*, *Semicassis* 22, 245, 249
- saccoi*
- Cassis* 210
- (*Galeodocassis*) 210
- Cassissoma* 210
- Saginafusus pricei perficus* 170-171
- sagrae*, *Dolium* 264
- salbriacense*, *Eutritonium* 121
- sarcostoma*
- Cymatium* (*Ranularia*) 182
- Ranularia* 23, 182
- Triton* 152, 181
- sarcostomum*, *Cymatium* 182
- (*Ranularia*) 152, 181
- Sassia* **198**
- abbotti* 205
- apenninica* 6, 15, 20,
- 22, 27, 198-**199**, 200-202, 208, 242, 317, 441; Pl. 50, Fig. 1
- armata* 112,
- 117, **205**-207, 445-446; Pl. 52, Figs 1-6, 12; Pl. 53, Figs. 3, 5-6
- arthritica* 199
- bicegoi* 117, 205
- kampyla* 6, 24, 96, 201-**202**, 203-204, 208, 270, 441; Pl. 50, Figs 3-4
- kampyla* 202
- tomlini* 202
- leucostomoides* 106, 202-204, **207**-208, 445; Pl. 52, Figs 8, 11
- lewisi* 22, 24-25, 28, 37, 199-**200**, 201, 441; Pl. 50, Fig. 9
- lindneri* 198
- melpangi* 23, 199
- midwayensis* 23, 55
- minima* 204-205, 207
- morgani* 205-**206**, 207, 445-446; Pl. 52, Figs 7, 9-10; Pl. 53, Fig. 4
- nassariformis* 23, 199
- nucleoides* 201
- palmeri* 23
- parkinsonia* 198
- philomelae* 24, 202-**204**, 207-208, 441; Pl. 50, Figs 6-7, 10
- radialis* 198
- remensa* 23, 198-199
- semitorta* 23, 199
- subdistorta* 198
- tatei* nom. nov. 205
- warreni* 13, 15,
- 27, **200**, 441, 466; Pl. 50, Figs 2, 5, 8, 11-13; Pl. 63, Figs 9-10
- zealta* 204-205, 207
- (*Sassia*)
- Charonia apenninica* 199
- Eutritonium aperturale* 121
- sauliae*
- Charonia* 121
- gyrinoides* var. 121
- lampas* 121-122
- Triton* 121, 123
- sauliae macilenta*, *Charonia* 121, 123
- saundersi*, *Bursa* 41
- scaber*
- Argobuccinum* (*Priene*) 109

- Priene* 109
Triton 109-110
Tritonium
 (*Argobuccinum*) 109
 (*Priene*) 109
- scabra*
 Polia 109
 Priene 109-110
 Ranella 109
- scabrum*
 Argobuccinum 109
 (*Priene*) 109
 Priene 21, 105, **109**-110, 134, 203, 389-390,
 442; Pl. 24, Figs 5-6; Pl. 25, Figs 2-3, 5-6; Pl. 51, Figs 6, 8
- schnireli*, *Cassis* 218-219
- Sconsia* **232**
 alexarthuri 22, 32, 211, 234
 barbudensis 233-235
 bocasensis 233-235
 grayi 7, 15-18, 20, 22, 26-28, 34-
 35, **232**-238, 473-474; Pl. 66, Figs 6-7; Pl. 67, Figs 1, 3, 5
 hodgii 27, **235**-238
 laevigata 13, 15-16, 20, 24, 27, 35, 173, 226,
 233, **236**-238, 473-474; Pl. 66, Figs 1-5, 8-10; Pl. 67, Fig. 2
 laevigata 236
 sublaevigata 233
 var. *gabbi* 233-234
 lindae 7, 233-235
 lintea 237-238
 martini 232
 metae 236
 nephele 22, 234, 237
 paralaevigata 20, 27, 173, 226, **238**
 prolongata 27, **238**
 pulchra 232
 striata 232-235, 237
 sublaevigata 233
 sublaevigata 233-234, 236
 (*Sconsia*), *Cassidaria striata* 233
 scrobiculata, *Bursa* (*Bufonariella*) 62
- scrobiculator*
 Bufonaria 62
 Bursa 62
 (*Bufonariella*) 62
 Murex 62
 nodosa, *Bursa* (*Bufonariella*) 62
 Ranella 62
 Triton 62
 Tritonium 62
- scrubulator*, *Bursa* 63
- seguenzae*
 Charonia 22, 25, **124**-125, 127-128
 Triton 125
 Tritonium 125
 var. *minor*, *Tritonium* 125
- Semicassis* **244**
 aldrichi 20, 24, 27, 173, **246**-247, 477; Pl. 68, Figs 6, 8
 angasi 23
 bisulcata 23, 244-245
 bondarevi 23
 bulia 23
 canaliculata 23
 centiquadrata 20, 22,
 25, 28-29, 33, 35, 186, **247**, 250-251, 478; Pl. 69, Figs 1-2
 cicatricosa 245, 248, 250
 peristephes 245, 248, 250
 craticulata 23
 dorae 23
 (*Echinophoria*) *apenes* 228
 faurotis 23, 244
 fernandesi 23
 gibba 245, 248
 abbreviata 245, 248
 inflata 245
 glabrata 23
 granulata 15-17, 20, 22, 24-25, 27, 29, 33, 35, **245**-**248**,
 249-251, 481, 482; Pl. 70, Figs 4, 6; Pl. 71, Figs 2, 5-7, 9-10
 granulata 248
 centiquadrata 247
 loxaharcheensis 250
 granulatum 248
 inflata 248
 waltonensis 251
 inornata 23
 japonica 244
 labiata 2, 23, 202
 microstoma 23
 monilifera 251-252
 murrayi 246
 paucirugis 23
 pyrum 244-245
 reclusa 13, 15-16, 20, 24, 27, 35, 246, 250-
 251, 252, 478, 481; Pl. 69, Figs 3-10; Pl. 70, Figs 1-3, 5, 7-10
 royana 23, 244
 saburon 22, 245, 249
 senni 20, 27, 251-**252**, 482; Pl. 71, Figs 1, 3
 sophia 23
 thomsoni 23
 (*Tylocassis*)
 aldrichi 246
 granulata 247-248
 inflata waltonensis 248
 maleaformis 20, 251
 reclusa 248, 251
 umbilicata 23
 undulata 22, 245-250
 westralis 23
- (*Semicassis*)
 Cassis
 abbreviata 248
 centiquadrata 247
 cicatricosa 248
 gibba 248
 granulata 248
 granulatus 247
 inflata 248
 lactea 248
 tegalensis 140-141

- undulata* 248
Phalium
cicatricosum 245, 248
granulatum 248
semigranosa
Colubrellina 48
Ranella 45, 47-48
semigranosum, Antephalium 245
Semiranella gemmellari 120
(Semiranella), Triton
gemmellari 120-121
valrovinensis 121
semitorta, Sassia 23, 199
senior, Triton vestitus var. 178
senni
Phalium (Tylocassis) sulcosa 251-252
Semicassis 20, 27, 251-252, 482; Pl. 71, Figs 1, 3
Septa 189
bibbeyi 23, 191
blacketi 190-191, 437; Pl. 48, Fig. 9
closeli 23, 191
dharmai 190
flaveola 23, 191
gemmata 162
hepatica 23, 191
leucostoma 113
landaui . 13, 14, 24, 27, 189-190, 200, 437; Pl. 48, Figs 1-2, 4-7, 10
marerubra 23, 191
mixta 23, 191
(Monoplex) parthenopea
parthenopea 167
keenae 156
occidentalis 20-25, 27, 189-190, 191-192, 437; Pl. 48, Figs 3, 8-9, 11-12
ogygia 192
parkinsonia 198
peasei 23, 44, 190-191
pilearis 170
rubecula 23, 143, 190-191
rubicunda 120-121, 123
spengleri 118, 179
triangularis 131-132, 401; Pl. 30, Figs 11-12
tritonia 126
tritonis 126
var. nobilis 127
(Septa), Cymatium
amicum 143
tremperi 143
aquatile 145
beui 191
comptum 149
corrugatum krebsii 157
gemmatum 149, 162
henicum 158
krebsii 157
labiosum 196
lignarium 160
lineatum 187
martinianum 170
mundum 163
nicobaricum 164
occidentale 191
ogygium 192
parthenopeum 167
parthenopeus 167
pfeifferianum 188
pileare 170
henicum 157-158, 417; Pl. 38, Figs 10, 12
martinianum 170
orientalis 170
pileare 170
rubeculum occidentale 190
tenuilatum 197
trigonum 175
tranquebaricum 174
turtoni 176
vespaceum 149, 177
vestitum 178
septemdentata, Personella 201
(Septra), Cymatium
carlotae 186
chlorostomoides 149
infelix 155
setosa, Cassidaria 179
sexcostata, Cymatiella 210
sexiesperforata, Leodia (echinoid) 223
Shichiheia etchuensis 242
simillima
Distorsio . 13, 16-17, 24, 26-27, 29, 83-88, 91-93, 97-98, 381-382, 385; Pl. 20, Figs 6, 8-10; Pl. 21, Figs 1-8; Pl. 22, Figs 1-2, 6, 8-9
(Rhysema) decussata 97
Distortrix 87, 97
Persona 97
simillimus
Distorsio 84, 97
constrictus 97
decussatus 87, 93, 97
Distortia 97
Triton 81, 87, 97
Simplicodolium fasciata 263, 265
(Simplicodolium), Eudolium fasciatum 264
(Simpulinus), Triton haemastoma 178
Simpulum
antillarum 148
var. cercadicum 148
carlottae 186
chlorostomoides 149
infelix 155
nodiferum 121
papillosum 46, 54, 350; Pl. 5, Figs 1, 4
pileare 170
(Simpulum)
Eutriton problematicum 173-174
Triton
acclivis 166, 168
ficoides 175
gemmatum 162
labiosus 195
lignarius 160
pfeifferianus 187
pileare 145
thersites occidentale 149
tranquebaricum 173
tranquebaricus 173
Tritonium pilearis var. *aquatilis* 145
sinensis, Ranularia 23, 185

- sinuosum*, *Antephalium* 245
- Siphonalia*
- fusoides* 122
- matthewsi* 205-206
- nodosa* 205
- nodosocincta* 205-206
- smaragdula*, *Leucozonia* (*Lagena*) 233, 235
- smithi*
- Distorsio* 22, 81, 83, **98-99**, 118, 385; Pl. 22, Figs 3, 5
- Persona* 98-99
- smithii*, *Distorsio* 99
- solidum*, *Dalium* 14, 22, 24-26, 29, 35, 238-240
- solitarium*, *Tritonium* 121
- somalica*, *Distorsio* 23
- sonorana*
- Bursa* 68, 70
- californica* 68-69
- Crossata californica* 68
- sophia*, *Semicassis* 23
- sowerbyanus*, *Fusus* 208
- spadicea*
- Bursa* 72
- (*Bufonaria*) 72
- (*Marsupina*) 72
- Ranella* 72
- spadiceus*, *Buffo* 71-73, 361; Pl. 10, Figs 1-2
- sp. A, *Bursa* (*Colubrellina*) 59-60
- spengleri*
- Cabestana* 118-119
- Cymatilesta* 118
- Septa* 118, 179
- spinella*
- Cassis* 218
- madagascariensis* 218, 220
- spinosa*, *Calcarella* 79
- springi*, *Malea* 27, 255, 259, **262-263**, 265
- springsteeni*, *Ranularia* 23
- strangei*
- Particymatium* 192, 195
- Triton* 192, 195-196
- striata*
- Cassidaria* 232, 235
- Cassis* 233-234
- Sconsia* 232-235, 237
- striata sublaevigata*, *Sconsia* 233
- striatula*
- Cassidaria* 232
- Cassis* 232
- striatum*, *Buccinum* 223-224
- strigatum*, *Phalium* 224
- Strombus* 267
- strongi*
- Bechtelia* 71, 78-79
- Gyrineum* 60, 71, 78
- (*Bechtelia*) 78-79
- Marsupina* 24, 28, **78-79**, 362; Pl. 11, Figs 3-4
- subcolubrinum*, *Triton* 121
- subcutaceum*, *Tritonium* 118
- subcutaceus*, *Murex* 118
- subdepressus*, *Clypeaster* 223
- subdistorta*
- Charoniella* 198
- Negyryna* 198
- Sassia* 198
- subdistortus*, *Triton* 198
- subfasciatum*, *Eudolium* 24, 27, 173, **253**, 482; Pl. 71, Figs 8, 11
- (*Galeodolium*) 253
- subgranulata*, *Aspa* 66
- subintermedia*, *Ficus* 312
- sublaevigata*
- Cassidaria* 233-235
- Sconsia* 233-234, 236
- laevigata* 233
- striata* 233
- sublobulata*, *Caloplaca* (lichen) 202
- subtuberosa*, *Cassis* 34, 216-217
- succincta*
- Gelagna* 21-22, 24, 27, 32, **137-138**, 409; Pl. 34, Fig. 5
- Linatella* 137
- (*Gelagna*) 137
- succinctum*
- Argobuccinum* 137
- Cymatium* 137
- (*Gelagna*) 137
- (*Linatella*) 137
- Triton* 166, 168
- succinctus*
- Murex* 137
- Triton* 166
- sufflatum*, *Antephalium* 245
- sulcata*, *Oocorys* 22-23, 240, 317
- sulcifera*
- Cassidea* 221
- Cassis* 13, 15, 20, 24, 27, 213-217, **221-222**, 223, 458, 461; Pl. 59, Fig.2; Pl. 60, Figs 1-8
- sulcosa*
- Tonna* 23, 264
- senri*, *Phalium* (*Tylocassis*) 251-252
- sulcosum* var. *abbreviatum*, *Phalium* (*Bezoardica*) 247
- sulfurea*, *Helix* 266-268
- sulphurea*, *Helix* 266-267
- Sycotypus ficus* 312
- sylviaense*, *Argobuccinum* 106
- sylviaensis*, *Gyrineum* 106-107
- Sympulum tranquebaricum* 173
- szukouensis*, *Neptunea* 140-141
- tabulata*
- Cabestana* 119
- Cabestanimorpha* 152
- Taieria allani* 231-232
- (*Taieria*), *Galeodea allani* 231-232
- takedai*, *Fustritron* 104, 107
- Talisman parfaiti* 41
- tankervillii*, *Tonna* 23
- tatei** nom. nov., *Sassia* 205
- tegalensis*, *Cassis* 140-141
- (*Semicassis*) 140-141
- tenebrosa*, *Tonna* 23
- tenue*, *Dolium* 264-265
- tenuigranosa*, *Tutufa* (*Tutufa*) 22
- tenuilirata* var. *nodocostata*, *Cymatium* (*Ranularia*) 202
- tenuiliratum*
- Cymatium* 197
- (*Monoplex*) 197
- (*Reticutriton*) 197
- (*Turritriton*) 197

- Turritriton* 197
tenuilatus
Cymatium (Cabestana) 197
Reticutriton 197
Triton 197
(Gutturium) 197
Turritriton
 22-23, 27, 143, 153, 192-194, 197-198, 426; Pl. 43, Figs 1, 8
tenuis
Cassis 227-228
(Cassidea) 228
(Cypraecassis) 228
Cypraecassis
 21, 28-29, 225-227, 228, 457-458; Pl. 58, Fig. 4; Pl. 59, Fig. 3
Ranella 67, 70
tenuisculpta
Bursa
(Bufonariella) ranelloides var. 54
(Colubrellina) 54
ranelloides var. 54
ranelloides 54
Ranella (Lampas) ranelloides var. 54, 56
terrysmithae, Ameranella 116
tessellata
Cassis 22, 214, 219, 248, 250, 267
Tonna 23, 264
tessellatum, Buccinum 248
testiculus
Buccinum 228-229
Cassidea 228
Cassis 228-229
(Cassidea) 228
(Cypraecassis) 228
Cypraecassis 13, 16, 20,
 22, 24, 27, 216, 224, 226-228, 229, 465; Pl. 62, Figs 4-6, 8-10
senegalica, Cypraecassis 229-230
testiculus, Cypraecassis 228-229
tetudinaria, Ranularia 23, 282, 285
tetudinarium rehderi, Cymatium 184
(Ranularia) 184
tetleyi, Cabestana 118-119
tetracotula, Tonna 23
Thalassocyron 312
Thalassocyronidae 312
thersites
Bufonaria 20, 23
Cymatium (Monoplex) 177
Distorsio 95
Monoplex 23, 150, 177
thersites occidentale, Triton (Simpulum) 149
Triton 96, 177
Tritonium 95-96, 203
(Distorsio) 95
thomae
Bursa 50, 57
(Lampasopsis) 57
(Lampas) 57
rhodostoma 57-58
Ranella 57-58, 350; Pl. 5, Fig. 5
(Bursa) 57
thomsoni, Semicassis 23
tigrinum
Cymatium 21, 25, 28, 39, 130-132, 135-136, 409; Pl. 34, Figs 1, 4
Nyctilochus 130
Triton 135
(Cymatium) 135
(Lotorium) 135
tigrinus
Cymatium 135-136
Triton
(Cymatium) 135
(Lotorium) 135
tomlini
Cymatona 202-203, 441; Pl. 50, Fig. 4
kampyla 202
Sassia kampyla 202
Tonna 263
alanbeui 23
allium 23, 260
ampullacea 23
berthae 23
boucheti 23
(Cadus)
maculosa 267
mareana 267-268
canaliculata 23, 265, 267
cerevisina 23
chinensis 23
cumingi 23
deshayesii 23
dolium 23
dunkeri 23
galea 13, 16, 20, 22, 25, 27, 253,
 262, 264-265, 268, 493-494; Pl. 76, Figs 3-7; Pl. 77, Fig. 1
abbotti 265-266
brasiliiana 265, 494; Pl. 77, Fig. 1
hawaiiensis 23
lischkeana 23
luteostoma 23
maculosa 266-267
(Malea)
ringens 260
densecostata 257
melanostoma 23
morrisoni 23
oentoengi 23
olearium 266
pennata 13, 16-17, 20-22, 25,
 27, 265-266, 267-269, 490, 493; Pl. 75, Fig. 6; Pl. 76, Figs 1-2
perdix 23, 25, 265-268, 494; Pl. 77, Figs 5-6
poppei 23
rosemaryae 23
sulcosa 23, 264
tankervillii 23
tenebrosa 23
tessellata 23, 264
tetracotula 23
variegata 23
zonata 23, 25, 253, 265-266
Tonnidae 252
Tonnoidea 41
torva, Cassis 23, 211
Trachydolium dalli 242
tranquebaricum
Cymatium 152, 158, 173
(Linatella) 174

(<i>Monoplex</i>)	174	<i>marmoratum</i>	126
(<i>Septa</i>)	174	<i>nobilis</i>	120, 126
<i>forma problematicum, Cymatium</i>	174	(<i>Buccinum</i>) <i>cancellatum</i>	106
<i>Sympulum</i>	173	(<i>Cabestana</i>)	
<i>Triton</i>	158, 173-174	<i>labiosum</i>	195
(<i>Linatella</i>)	173	<i>labiosus</i>	195
(<i>Simpulum</i>)	173	<i>cancellatum</i>	104
var. <i>linatelloides, Cymatium (Monoplex)</i>	174	<i>cancellatus</i>	104-106, 386; Pl. 23, Figs 2, 6
<i>tranquebaricus</i>		<i>caudatus</i>	175
<i>Monoplex</i>	6, 19, 21-22, 27, 118,	<i>chemnitzii</i>	141, 173, 179
158, 166, 173-174, 175, 179, 426; Pl. 43, Figs 5-7, 9-14		<i>chlorostoma</i>	164
<i>Triton</i>	173	<i>chlorostomum</i>	163-164
(<i>Lampresia</i>)	173	var. <i>pumilio</i>	164
(<i>Linatella</i>)	173	<i>chlorostomus</i>	163
(<i>Simpulum</i>)	173	<i>clandestinum</i>	137
<i>tremperi, Cymatium</i>		<i>clandestinus</i>	137
<i>corrugatum</i>	143	<i>clathratum</i>	79, 81-82, 92
(<i>Monoplex</i>) <i>corrugatum</i>	143-144, 410; Pl. 35, Figs 2-3	<i>commutatus</i>	126
(<i>Septa</i>) <i>amictum</i>	143	<i>comptus</i>	149, 151
<i>triangularis</i>		<i>confinis</i>	137
<i>Cassis</i>	223-224	<i>constrictus</i>	84, 86-87, 92
<i>Septa</i>	131-132, 401; Pl. 30, Figs 11-12	<i>crassum</i>	121
<i>tricarinata, Pseudogaleodea</i>	231	<i>crispus</i>	138-139
<i>trigonaperta, Personopsis</i>	23, 100	(<i>Cymatium</i>) <i>femorale</i>	131
<i>trigonum, Cymatium</i>	175	<i>cynocephalum</i>	137, 179-182
(<i>Monoplex</i>)	175	<i>cynocephalus</i>	181
(<i>Septa</i>)	175	<i>dautzenbergi</i>	319-320
<i>trigonus</i>		<i>domingensis</i>	154, 157-158
<i>Monoplex</i>		<i>elongatus</i>	176-177
. . . 6, 21-22, 27, 48, 113, 160, 175-176, 429; Pl. 44, Figs 1-2		<i>eogassinense</i>	114
<i>Murex</i>	175	<i>exaratum</i>	151
<i>trilineata, Ranularia</i>	23, 181	<i>femorale</i>	131-132, 135-136
<i>trilineatum, Triton (Gutturnium)</i>	183	<i>femoralis</i>	131-132
<i>tripa, Ranularia</i>	23	<i>fennemai</i>	209
<i>Tripneustes (echinoid)</i>		<i>ficoides</i>	175
<i>esculentus</i>	223	<i>fossatum</i>	166
<i>ventricosus</i>	223	<i>gallinago</i>	183-184
<i>tristanense</i>		<i>gemmatus</i>	149, 154, 162-163
<i>Argobuccinum</i>	101-102	<i>gibbosus</i>	192, 194
<i>Argobuccinum proditor</i>	101, 103	<i>gracile</i>	150
<i>tristanensis</i>		<i>gracilis</i>	149, 187-188
<i>Argobuccinum</i>	102	<i>granosum</i>	199
<i>Ranella</i>	101	<i>grasi</i>	99-100
<i>Tritocurrus amphytidris</i>	39, 130, 135-136	(<i>Gutturnium</i>)	
<i>Triton</i>		<i>amictus</i>	143
<i>abbreviatus</i>	166	<i>antillarum</i>	138
<i>aegetus</i>	183-184, 433; Pl. 46, Figs 4, 8	<i>cynocephalus</i>	181
<i>albocingulatus</i>	138-139	<i>gallinago</i>	183
<i>americanum</i>	166, 168, 422; Pl. 41, Fig. 4	<i>gibbosus</i>	194
<i>amictum</i>	143-144	<i>orientalis</i>	195
<i>antillarum</i>	138-140	<i>pfeifferianus</i>	187
<i>apenninicum</i>	198-199	<i>tenuiliratus</i>	197
<i>aquatilis</i>	145, 147, 169-170	<i>trilineatum</i>	183
(<i>Argobuccinum</i>) <i>dautzenbergi</i>	319-320	<i>vespaceum</i>	176
<i>armatum</i>	205	<i>vespaceus</i>	177
<i>armatus</i>	205, 445; Pl. 52, Figs 1-2	<i>gyrinoides</i>	121
<i>atlantica</i>	126-127	<i>haemastoma</i>	170-171, 178
<i>australe</i>	121, 123	<i>imbricata</i>	126
<i>australis</i>	121	<i>labiosus</i>	195
<i>balteatus</i>	173	(<i>Lagena</i>)	
<i>barthelemyi</i>	119, 179	<i>cancellatum</i>	104
<i>brasilianum</i>	166, 168	<i>clandestinus</i>	137
(<i>Buccinatorium</i>)		<i>magellanicus</i>	104

- wiegmanni* 179
lampas var. *euclia* 121, 123
 (Lampresia)
aquatilis 145
chlorostomus 164
pileare 170
tranquebaricus 173
tuberosum 138
 (Lampusia)
chlorostomum 164
 var. *pumilio* 164
costatum 166
krebsii 157
martinianum 170
rubecula occidentale 190
vestitum 162
leucostoma var. *nigromaculata* 113
leucostomoides 104, 202, 207-208
lignarius 160
 (Linatella)
clandestinus 137
poulsenii 140-141
rostratum 140
tranquebaricum 173-174
tranquebaricus 173
wiegmanni 179
lineatus 187
loebbeckei 192, 195-196
loroisii 192, 195-196
 (Lotorium)
femorale 131
tigrinum 135
tigrinus 135
lotorium 131-132
macrodon 162
marmoratum 125-127
martinianum
 . 145, 169-171, 410, 418; Pl. 35, Figs 8, 10; Pl. 39, Figs 5, 10
 latior 170
moritinctus 181-183, 430; Pl. 45, Fig. 4
mundum 162-163
nobile 120
nobilis 127
nodifer 121
nodiferum 121, 123
nodiferus 121
obscurus 151-153
olearium 166
orientalis 195-196
parthenopeum 166, 168
parvulum 208
perforatus 179
personatum 100
pfeifferianus 145, 149, 187-188
philomelae 202, 204
pileare 169-170
pilearis 169
pliniae 121, 123
 (Priene)
cancellatus 104
rudis 109
productum 138-139
pyriformis 138-139
quoyi 208
radialis 198
ranelliforme 101-102, 121
ranelliformis 101-102
ranelloides 42, 54, 56-57
retusum 181
ridens 81-82, 87, 98-99
ridleyi 149, 151, 184
rudis 109-110, 442; Pl. 52, Fig. 6
samier 175
sarcostoma 152, 181
sauliae 121, 123
scaber 109-110
scrobiculator 62
seguenzae 109-110
 (Semiranella)
gemmellari 120-121
valrovinensis 121
 (Simpulinus) *haemastoma* 178
 (Simpulum)
acclivis 166, 168
aquatile occidentale 145, 147
chlorostomum 164
chlorostomus 164
corrugatum var. *krebsii* 157
costatus 166
ficoides 175
gemmatus 162
labiosus 195
lignarius 160
lineatus 187
olearium 188
pfeifferianus 187
pileare 145
pilearis 170
 var. *aquatilis* 145
thersites occidentale 149
tranquebaricus 173
strangei 192, 195-196
subcolubrinum 121
subdistortus 198
succinctum 166, 168
succinctus 166
tenuiliratus 197
thersites 96, 177
tigrinum 130-131, 135-136
tranquebaricum 158, 173-174
tranquebaricus 173
tritonis 120, 125, 127
 var. *nobilis* 127
tuberosum 138-139
tuberosus 138
turtoni 176
undosum 140
variegatum 120, 126-127
variegatus 126
veliei 170-171
ventricosum 121
verrucosus 208
verruculosum 117
verruculosus 117, 205
vespaceum 149, 176-177
vestitus 162, 169-170, 178

- var. *senior* 178
tritonia, *Cymatiella* 209
Tritonellium 120
tritonia, *Septa* 126
tritonis
 Charonia 21-22, 24-25, 28, 31-32, 113, 120, 122, **125**-128
 Eutritonium 120
 Lampusia 126
 Murex 120, 126-127
 Septa 126
 Triton 120, 125, 127
 tritonis, *Charonia* 126
 Tritonium 125, 127
 var. *nobilis*
 Charonia 127
 Septa 127
 Triton 127
 variegata, *Charonia* 125
Tritonium 127
Tritoniscus
 labiosus 192, 195
 loroisii 192
 (*Tritoniscus*), *Cymatium*
 labiosum 195
 labiosus 195
Tritonium
 adansonii 173
 americanus 166
 aquatile 145
 argo-buccinum 101-102, 386; Pl. 23, Figs 5, 8
 (*Argobuccinum*)
 rude 109
 scaber 109
 australe 121
 beccarii 171
 bicegoi 205-206, 445; Pl. 52, Figs 6, 12
 (*Cabestana*) *verbeeki* 140-141
 (*Charonia*) *nodiferum* 121
 (*Charonia*) *nodiferum mirabilis* 121
 (*Cryotritonium*) *murrayi* 105
 commutatum 59
 contabulatum 141
 costatum 166
 cutaceum 118
 (*Cymatium*) *femorale* 131
 cynocephalum 181
 decussatum 81, 87-88, 90
 (*Distorsio*) *thersites* 95
 edentatum 46, 65
 exiguum 117, 205-206
 femorale 131
 filipponei 119
 gibbosus 194
 gemmatum 163
 gemmiferum 113
 var. *minor* 113
 glabrum 121
 granulare 42, 48-49
 (*Gutturnium*) *tuberosum* 138
 hirsutum 166, 168
 jabick 48-49
 labiosum 195
 (*Lagena*) *edentatum* 65
 lignarium 160
 (*Lotorium*) *bicegoi* 117, 205
 martinianum 169
 mauritanum 162-163
 mediterraneum 121, 123
 morgani 206-207
 moritinctum 181, 183
 mundum 162
 munsteri 141
 nicobaricum 143, 163-164
 nodiferum 121
 var. *glabra* 124
 nodosum 179-180
 nodulus 138-139
 olearium 169
 opis 120, 123
 partschii 121, 123
 pileare 157, 169
 (*Priene*)
 cancellatus 106
 rude 109
 scaber 109
 pustulata 121, 123
 (*Ranella*) *verruculosum* 117
 (*Ranularia*)
 domingense 193
 elongatum 177
 nodulus 138
 vespaceum 177
 reticulare 81
 rutilum 195-196
 scrobiculator 62
 seguenzae 125
 var. *minor* 125
 (*Simpulum*)
 beccarii 170
 pilearis 170
 var. *aquatilis* 145
 solitarium 121
 subcutaceum 118
 thersites 95-96, 203
 tritonis 127
 var. *nobilis* 127
 verruculosum 117, 205-206
 vestitum 169-170, 178
Tritonocauda caudata 181
Tritonoranella ranelloides 42, 54
 (*Tritonoranella*), *Bursa ranelloides* 54
tuberculata, *Echinora* 230
tuberculiformis, *Galeodea* 210
tuberosa
 Cassidea 223
 Cassis 15, 20, 22,
 24-25, 27, 212-217, 219-**223**, 224-225, 462; Pl. 61, Figs 4-5
 (*Goniogalea*) 223
 Ranularia 138
 (*Gutturnium*) 138
tuberosissima, *Bursa* 22
tuberosum
 Buccinum 221, 224
 Cymatium 138
 Triton 138-139
 (*Lampresia*) 138

- tuberosus*, *Triton* 138
Tudicla gutturnium 181
tugaruensis, *Ranella* (*Priene*) 106-107
tumida
 Bursa 100-103, 386; Pl. 23, Figs 1, 7
 Gondwanula 101
tumidum, *Argobuccinum* 101-102
 argus 101
 pustulosum 101
 ranelliforme 101
 ranelliformis 101
tuomeyi, *Ranella* 111
Tuberculodolium antiquum 253
Turbinella martini 211
turneri, *Galeodea* (*Gomphopages*) 231
Turritella 74, 83, 195
Turritriton **192**
 domingensis 13-14, 16-17, 20, 24, 27, 154, 192-**193**, 194, 438; Pl. 49, Figs 1-4, 8
 fitikau 22, 192-193
 gibbosus 17, 21, 25, 27-28, 143, 186, 192-**194**, 195-196, 434, 438; Pl. 47, Figs 13-14; Pl. 49, Figs 6-7, 10-13
 grundensis 25, 192-193, 195
 kiiensis 152
 kobelti 22, 25, 192-195, 228
 labiosus 6, 15, 20-25, 27-28, 167, 192-**195**, 196, 243, 438, 446; Pl. 49, Figs 5, 9; Pl. 53, Fig. 7
 loebbeckei 152, 195
 pharcidus 193, 197
 tenuiliratum 197
 tenuiliratus 22-23, 27, 143, 153, 192-194, **197**-198, 426; Pl. 43, Figs 1, 8
 vespaceus 177
(Turritriton), *Cymatium*
 comptum 149
 domingense 193
 exaratum 152
 exaratum 152
 kiiense 152
 gibbosum 194
 indomelanicum 177
 labiosum 195
 lignarium 160
 pharcidum 197
 tenuiliratum 197
 vespaceum 177
turtoni
 Cymatium
 (*Monoplex*) 176
 (*Septa*) 176
 Monoplex 24, **176**, 425; pl. 42, Figs 2-4, 6, 8
 Triton 176
Tutufa
 bubo 22
 nanelloides 57
 (*Tutufella*)
 bardeyi 22
 bubo 22, 123, 132
 bufo 22
 tenuigranosa 22
 (*Tutufella*)
 boholic 22
 nigrita 22
 oyamai 22
 rubeta 22
 (*Tutufella*), *Tutufa*
 boholic 22
 nigrita 22
 oyamai 22
 rubeta 22
 (*Tylocassis*)
 Phalium
 aldrichi 246
 cicatricosum 245, 248
 granulatum 245, 248
 centiquadratum 247
 granulatum 248
 reclusum 251
 undulatum 245
 var. *cictricosum* 248
 inflatum 245, 248
 murrayi 246
 reclusa 251
 sulcosum senni 251-252
 Semicassis
 aldrichi 246
 granulata 247-248
 inflata waltonensis 248, 250-251
 maleaformis 251
 reclusa 245, 251
 umbilicata, *Semicassis* 23
 undosum
 Buccinum 140
 Triton 140
 undulata
 Cassis (*Semicassis*) 248
 Semicassis 22, 245-246, 248-250, 252
 undulatum, *Phalium* (*Tylocassis*) *granulatum* 245
 unicolor, *Casmaria ponderosa* 22
Urosalpinx
 archipatagonica 320
 dautzenbergi 320
 macra 320
 perrugata 320
 usurpator, *Lotorium* (*Lampusia*) 320
valentinei, *Cymatium*
 (*Linatella*) 167-168, 422; Pl. 41, Fig. 2
 (*Monoplex*) 167
valrovinensis, *Triton* (*Semiranella*) 121
variegata
 Charonia 13-14, 16-17, 19, 21-22, 24, 24, 27, 59, 122, 124-**126**, 127-128, 401; Pl. 30, Figs 1-2
 tritonis 125
 Ficus 312
 Tonna 23
 variegatum
 Buccinatorium 120
 Triton 120, 126-127
 variegatus
 Lytechinus 223
 Triton 126
 veliei, *Triton* 170-171
 ventricosa
 Bursa 68
 (*Crossata*) 68
 Cassis 248

- Charonia* 120
Crossata 17,
 19, 21, 26-28, 33, 43, 59, 62, **68-71**, 107, 134, 354, 357-358,
 442; Pl. 7, Figs 1, 5; Pl. 8, Figs 1-7; Pl. 9, Fig. 2; Pl. 51, Fig. 7
Distorsio 23
Meoma 223
Ranella 68
 (*Lampas*) 68
ventricosus, *Triton* 121
ventricosus, *Tripneustes* (echinoid) 223
venustula
Bursa 58
Ranella 57-58
Vernotriton pumilio 208
verrillii, *Oocorys* 22-24
Verrucaria durietzii (lichen) 202
verrucosa
Annaperenna 42
Bursa 22
Cymatiella 209-210
Ranella 42
verrucosus, *Triton* 208
verruculosa, *Ameranella* 113, **117-118**, 206, 390, 394, 397;
 Pl. 25, Figs 1, 4, 10, 12; Pl. 27, Figs 2, 4, 6; Pl. 28, Figs 2, 4, 6
verruculosum
Triton 117
Tritonium 117, 205-206
 (*Ranella*) 117
verruculosus
Cymatium 117
Triton 117, 205
versigranulata, *Dulcerana* 48
vespaceum
Cymatium 149, 151, 164, 177
 (*Septa*) 149, 177
 (*Monoplex*) 177
 (*Turritriton*) 177
Triton 149, 164, 176-177
 (*Guttarium*) 176
Tritonium (*Ranularia*) 177
vespaceus
Monoplex 21,
 23-24, 27, 32, 113, 149-152, 164, **176**, 179, 429; Pl. 44, Fig. 5
Triton (*Guttarium*) 177
Turritriton 177
vestitum
Cymatium 156, 162, 178
 (*Lampusia*) 178
 (*Monoplex*) 178
 (*Septa*) 178
Triton (*Lampusia*) 162
Tritonium 169
vestitus
Monoplex 19, 21, 25,
 28-30, 156-157, 162, **178**, 186, 429; Pl. 44, Figs 3-4, 6-12
Triton 170, 178
Tritonium 170, 178
 var. *senior*, *Triton* 178
veterior, *Charonia* 120
vexilla, *Ranella* 101
vexillum
Argobuccinum 101
Ranella 101-103, 386; Pl. 23, Figs 3, 9
 (*Apollon*) 101
vibexmexicana, *Casmaria* 21, 26
victrix, *Bursa* 46, **65**, 345; Pl. 2, Fig. 5
vladimiri, *Ipunina* **316-317**, 470; Pl. 65, Figs 2, 4-5, 8
voigtii, *Fusus* 140-141
vokesorum, *Cymatiella* . . 13, 15, 27, 209-**210**, 449; Pl. 54, Figs 1-10
waltonensis
Phalium 248
Semicassis
inflata 251
 (*Tylocassis*) *inflata* 248, 250-251
warreni, *Sassia* 13,
 15, 27, **200**, 441, 466; Pl. 50, Figs 2, 5, 8, 11-13; Pl. 63, Figs 9-10
washingtoniana
Cassidaria 31
Olequahia 31
Ranella 111
weisbordi, *Charonia lampas* 121-124, 398; Pl. 29, Figs 4, 6
westralis, *Semicassis* 23
wiegmanni
Cymatium 156, 179
 (*Linatella*) 179
 (*Monoplex*) 179
Fusus 141, 179
Linatella 140, 179
Monoplex 14, 19, 21, 24-26,
 28, 34, 148, 157, 166, **179-180**, 182, 430; Pl. 45, Figs 1-3, 7
Ranularia (*Lagena*) 179
Triton (*Lagena*) 179
williamsi
Monoplex 24, 149, 180
Murex 180
wilmae, *Cypraeacassis*
 20-21, 25, 28, 35, 225-227, **230**, 465; Pl. 62, Figs 1, 3
wilmerianum, *Gyrineum* 22
woodringi
Echinophoria 20, 28, **244**, 477; Pl. 68, Figs 1-2
Phalium (*Echinophoria*) 244
wyvillei, *Echinophoria* 23, 224
xantostoma, *Ranella rhodostoma* var. 57-58
Xenogalea
lucrativa 248
pyrum 244
Xenophalium
hedleyi 244
royanum 244
Xymene dautzenbergi 320
yasila, *Marsupina* 72, 75
yasumurai, *Ranella* 111
zelebori, *Bursa* 101
zimara, *Cymatium* 152-153
zonata, *Tonna* 23, 25, 253, 265-266

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