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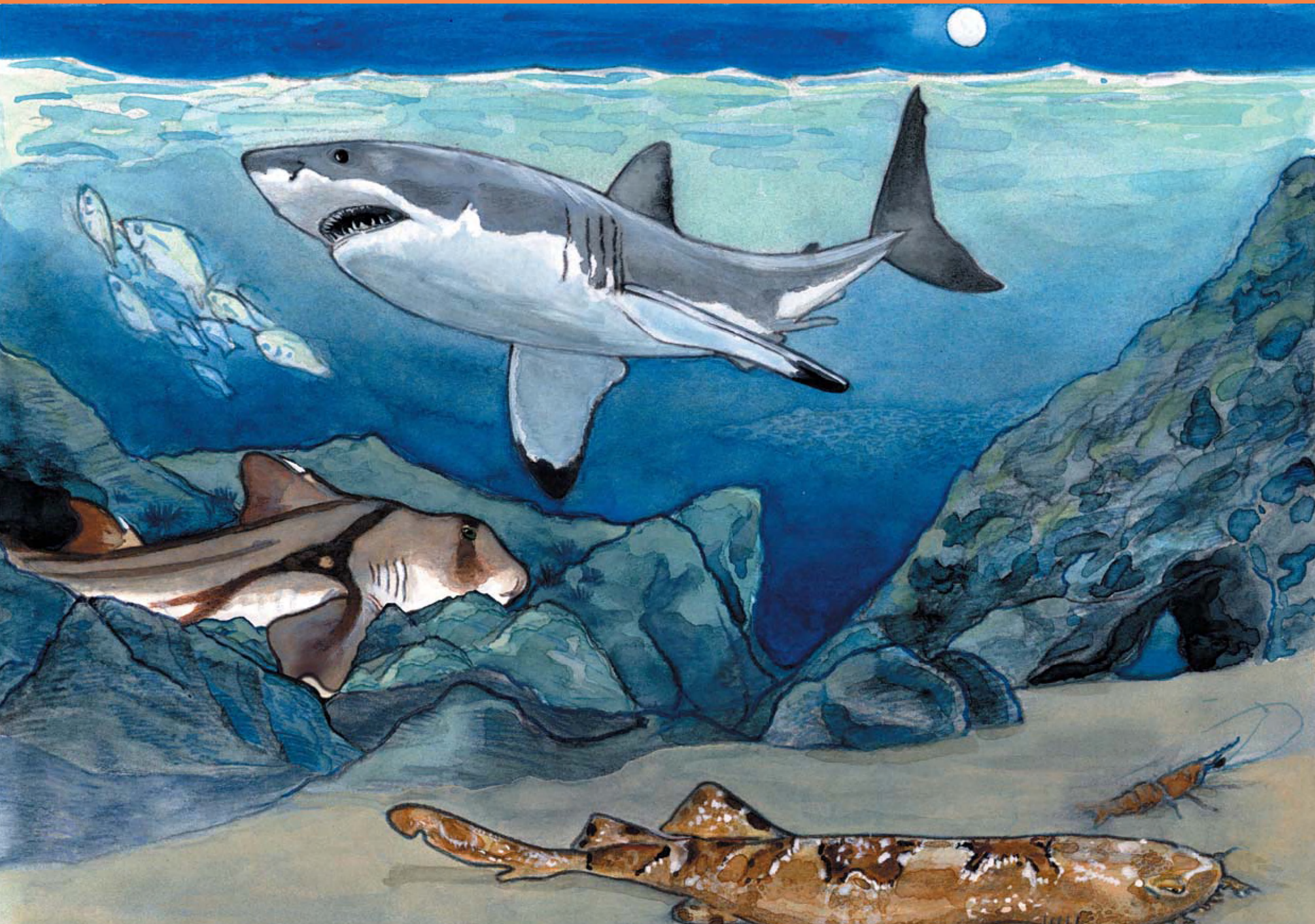
SHARKS OF THE WORLD

AN ANNOTATED AND ILLUSTRATED CATALOGUE OF SHARK SPECIES KNOWN TO DATE

Volume 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes)



Food
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Volume 2

Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes)

by

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FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
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PREPARATION OF THIS DOCUMENT

This document was prepared in FAO under a special programme made possible thanks to a generous Trust Fund (GCP/INT/643/JPN) from the Government of Japan. The present publication is the second installment of the updated version of the original FAO Catalogue of Sharks of the World (Compagno 1984), and constitutes volume two of the first number in a new series: *FAO Species Catalogue for Fishery Purposes*. Up until now, FAO Species Catalogues had existed as a far too lengthy series of volumes within *FAO Fisheries Synopsis No. 125*. But given the importance and size of that series and the continuing need for this type of publication in the foreseeable future, the species catalogues have grown out as an independent series starting with the present three-volume work. In order to preserve the continuity of the species catalogues, the new series will maintain the trademark orange-coloured cover of the old series as well as most of its format. As the new Catalogue has grown apace with new information and revisions, it is being published as three free-standing volumes, each with separate pagination, introduction, terminology, systematic sections, glossary, list of species by FAO Statistical Areas, and a dedicated bibliography. This will allow readers to independently use each volume without having to consult the other volumes for technical terms and measurements or bibliographic purposes, as was the case in the old catalogue. We hope that this added flexibility will be received as an improvement.

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ABSTRACT

This is the second volume of an extensively rewritten, revised, and updated version of the original FAO Catalogue of Sharks of the World. The present volume reviews all 15 families 25 genera and 57 species of living bullhead, mackerel and carpet sharks (orders Heterodontiformes, Lamniformes and Orectolobiformes), that is, the non-carcharhinoid galeomorph sharks, including certain well-established but currently undescribed species mainly from Australia. It gives accounts for all orders, families and genera and all keys to taxa are fully illustrated. Information under each species account includes: valid modern names and original citation of the species (or subspecies); synonyms; the English, French, and Spanish FAO Names for the species; a lateral view and often other useful illustrations; field marks; diagnostic features; distribution, including a GIS map; habitat; biology; size; interest to fisheries and human impact; local names when available; a remarks section when necessary; and literature. The volume is fully indexed and also includes sections on terminology and measurements including an extensive glossary, a list of species by FAO Statistical Areas, an appendix on shark preservation, and a dedicated bibliography.

Distribution

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It is hard to summarize the large number of people that have helped me over the course of preparing the 1984 shark catalogue and its current revision; several are no longer living, but I salute the memories of the dead as with the living, and make no distinction here. I apologize beforehand if I have forgotten anybody, which will inevitably happen.

I would especially like to thank W.I. (Bill) Follett, of the California Academy of Sciences, San Francisco, California, for encouragement on my initial checklists and interest in shark systematics many, many years ago. Especial thanks go to five of my research colleagues, Shelton P. (Shelly) Applegate (Los Angeles County Museum and Instituto de Geologia, Ciudad Universitaria, Mexico City), J.A.F. (Jack) Garrick (Department of Zoology, Victoria University, Wellington, New Zealand), Stewart (Stew) Springer (National Marine Fisheries Service, USA, and Mote Marine Laboratory, Sarasota, Florida), Warren C. Freihofer (Division of Systematic Biology, Stanford University, California Academy of Sciences and Tiburon Center for Environmental Studies) and Sid F. Cook (Argus-Mariner Consulting Scientists, Portland, Oregon), all of whom were extremely helpful and inspirational over the years. Special thanks for my wife, Martina Roeleveld (South African Museum) for her support.

The 1984 catalogue owed an enormous amount to the untiring and titanic efforts of Dr Walter Fischer, formerly Marine Resources Department, FAO Fisheries Division, who inspired me to make it a far more useful work than would have been my inclination as a professional systematist. This was not entirely a painless process, but I learned an enormous amount while writing it. Special thanks go to Dr Bernard Zahuranec, of the US Office of Naval Research, for providing support for the writing of the catalogue over three years in the form of a research contract to the writer at the Tiburon Center for Environmental Studies, San Francisco State University, Tiburon, California, and for arranging funding for a circumglobal research trip in 1982. Thanks also to Dr Samuel E. Gruber (University of Miami) and the American Elasmobranch Society for support for the publication of the 1984 catalogue in the United States. Dr Cornelia E. Nauen, formerly of the Marine Resources Department, FAO Fisheries Division, was extremely helpful in the organization of the final version of the 1984 catalogue, which went through several changes in format during the past five years. Thanks also to the staff of Dr W. Fischer’s Species Identification and Data Programme (SIDP) at FAO for their efforts, particularly for the fine artistic work of Emanuela D’Antoni, Pier Luigi Isola, Paolo Lastrico, and Oliviero Lidonnici in translating often difficult material from the literature as well as the writer’s research drawings and maps into the illustrations in this catalogue; and to Giulia Sciarappa-Demuro for typing the final manuscript. Mrs Paula Smith, Ms Barbara Nabors, and Ms Dale White of the Tiburon Center for Environmental Studies helped in the typing and copying of versions of the manuscript and the organization of the bibliography.

The present revised Catalogue was made much easier on the writer’s side by powerful personal computers, slide and flatbed scanners, OCR and digital graphics programmes, and electronic communications, which eliminated the need to spend part of the time at Rome to produce the Catalogue. A very large thanks to Dr Ramón Bonfil (Fisheries Centre, University of British Columbia), who served as grand coordinator of production and editor for the Catalogue at SIDP, as well as peer reviewer, user-friendliness tester, and contributor to the work; a massive task, but from this side not thankless! Thanks to Dr Pere Oliver, Dr Kent Carpenter, Mr Jascha Minow, Ms Michèle Kautenberger, Ms Emanuela D’Antoni, Ms Nicoletta De Angelis and Ms Guilia Sciarappa at SIDP, and Mr Fabio Carocci at FAO, for their outstanding work during various stages of the project that helped to make it possible.

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1. INTRODUCTION

This is the second volume of an extensively rewritten, revised, and updated version of the original FAO Catalogue of Sharks of the World (Compagno, 1984). It covers all the described species of living sharks of the orders Heterodontiformes, Lamniformes, and Orectolobiformes, including their synonyms as well as certain well-established but currently undescribed species (primarily Australian species mentioned by Last and Stevens, 1994). It includes species of major, moderate, minor, and minimal importance to fisheries (Compagno, 1990c) as well as those of doubtful or potential use to fisheries. It also covers those species that have a research, recreational, educational, and aesthetic importance, as well as those species that occasionally bite and threaten people in the water and the far more numerous species that are 'bitten' and threatened by people through exploitation and habitat modification. The Catalogue is intended to form part of a comprehensive review of shark-like fishes of the world in a form accessible to fisheries workers as well as researchers on shark systematics, biodiversity, distribution, and general biology. It also caters to other researchers that need comparative information on sharks, people who encounter sharks during the course of work or play in the sea or in fresh water, and the general public. This Catalogue builds on a progressive increase in our knowledge of shark biology over the past two decades, and addresses an exponential increase in popular interest in sharks and a growing concern over their burgeoning conservation problems.

The term *Shark* is used here in the broad sense of the FAO International Plan of Action for the Conservation and Management of Sharks (FAO 1999). Sharks include rays or batoids and chimaeroids as well as 'nonbatoid' or 'typical' sharks, which are the subject of the original shark catalogue and of the present volume. A problem with sharks is that most researchers, much less the general public, are unaware of their diversity and tend to focus on the larger, toothy, nonbatoids. There are approximately 1 200 *known* living and valid species of shark-like fishes, cartilaginous fishes, or chondrichthyans, which form the class Chondrichthyes. These include at least 50 species of ghost sharks, silver sharks, elephant fish, chimaeras or ratfish (order Chimaeriformes), over 600 species of batoids, flat sharks, or winged sharks (order Rajiformes), and nearly 500 species of nonbatoid, ordinary or traditional sharks. The living shark-like fishes are included in 10 orders, 60 families, and 186 genera. Diversity of all cartilaginous fishes, living and extinct, is far greater, with at least 140 valid families, 600 valid genera, and at least 3 700 valid species (from databases prepared by the writer).

The living cartilaginous fishes are divided into two sister-groups with a long separate, pre-Devonian history, the chimaeroids, Holocephali (with a single living order Chimaeriformes), and the sharks and rays proper or Elasmobranchii, with the surviving group subcohort Neoselachii or modern sharks including all of the living species. There is a traditional concept in the taxonomic literature that divides the living Neoselachii into sharks, Selachii or Pleurotremata, and rays or batoids, Batoidea or Hypotremata. Modern cladistic classifications rank the batoids as an order Rajiformes of the squalomorph sharks (superorder Squalomorphii), and a sister-group of the sawsharks (order Pristiophoriformes) (Fig.1). Hence the batoids are highly modified, highly diverse, and extremely successful sharks that outnumber all other cartilaginous fishes in species. Chimaeroids are the closest evolutionary cousins to elasmobranchs within the Chondrichthyes, and may find a higher profile as silver sharks or ghost sharks. Considering them as 'sharks' brings batoids and chimaeroids out of the perceptual dark. The batoids and chimaeras tend to receive far less attention than nonbatoid sharks in most places. Some of the batoids currently are as important for fisheries or more so than nonbatoid sharks or chimaeroids, and some are under severe threat from overexploitation and habitat modification (i.e. sawfishes, freshwater stingrays). The batoid sharks will hopefully be the subject of a forthcoming and much overdue FAO Catalogue of Batoids of the World; likewise for the chimaeroids.

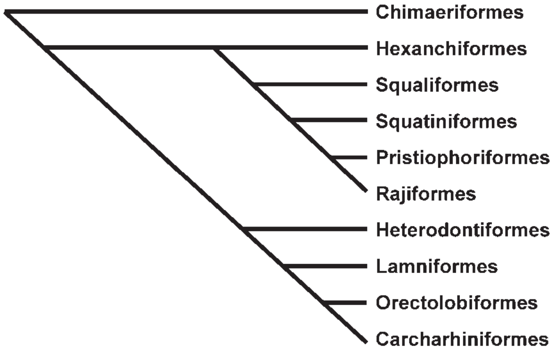


Fig. 1 Cladogram showing interrelationships of the orders of living cartilaginous fishes

The original 1984 FAO Shark Catalogue was in one volume in two parts, with pagination across both parts and with a single bibliography. As the new Catalogue has grown apace with new information and revisions, it is being published as three free-standing volumes, each with separate pagination, introduction, terminology, systematic sections, glossary, list of species by FAO Statistical Areas, and a dedicated bibliography. This will allow readers to independently use each volume without having to consult the other volumes for technical terms and measurements or bibliographic purposes, as was the case in the old catalogue. We hope that this added flexibility will be received as an improvement. A larger general introduction to the whole catalogue appears on the first volume and appendices on shark encounters and shark conservation are confined to the third volume. Readers are also encouraged to consult the addenda section included in the last volume of the catalogue. The present and second volume reviews all the species of living bullhead, mackerel and carpet sharks (orders Heterodontiformes, Lamniformes and Orectolobiformes), that is, the noncarcharhinoid galeomorph sharks (see Plan of the Catalogue below). The first volume covers the nonbatoid squalomorph sharks (orders Hexanchiformes, Squaliformes, Squatiniformes and Pristiophoriformes), and the third volume reviews the carcharhinoid galeomorphs (order Carcharhiniformes).

Apparently sharks are extremely popular at present with conservationists, fisheries managers, the news and entertainment media, and the general public, and are likely to stay that way for the foreseeable future. Negative concepts of sharks were reflected in the 1984 catalogue, sometimes embarrassingly so in hindsight, and partially due to the negative shark milieu of the times. Hopefully the present version departs from this perspective and portrays sharks as a major group of biologically interesting, poorly known vertebrates with over 400 million years of unqualified success as predators and survivors of mass extinctions. Sharks were then and are now challenged by the ultimate and most terrible of predators, *Homo sapiens* ('man, prudent or wise' as optimistically named by Linnaeus, 1758); but unlike former times the human superpredator is apparently aware of the problems and is taking some steps (at last!) to solve it. One can hope that those efforts are successful.

1.1 Plan of the Catalogue

This Catalogue is based on original work on various groups of sharks as well as my interpretation of data in the literature. Original descriptions of shark species and other taxa were consulted if at all possible; when not, various authoritative works were consulted for consensus on citations. Some of the arrangements of families, genera and species used here disagree with those of previous workers including those in my own papers, but in such cases the disagreements are discussed or reference is made to discussions of such problems in the literature. Nonsystematists may not appreciate changes to classification and nomenclature wrought by systematic studies, and often consider them as annoyances, but shark systematics evolves as does any other science and changes are inevitable. Hopefully they are producing increased stability as knowledge improves in a former backwater of systematic ichthyology.

Classification and systematic arrangement used here. The present arrangement has evolved from my earlier works (Compagno, 1973, 1977, 1979, 1982, 1984, 1988, 1999), which initially divided the nonbatoid sharks into eight major groups or orders and the batoids into four or five orders. The relationships of the nonbatoid shark orders to one another other and to the batoids (order Rajiformes) is approaching a tentative consensus following the work of Compagno (1977, 1988, 1999 and unpublished), Shirai (1996), and de Carvalho (1996). The following classification of shark-like fishes to order is used in this work and reflects a tentative cladogram based on a summary of previous work and analysis in progress (* starred orders are covered in this volume):

- Class Chondrichthyes (cartilaginous fishes)
  - Subclass Holocephali (chimaeras and fossil relatives)
    - Order Chimaeriformes (chimaeras or silver sharks)
  - Subclass Elasmobranchii (sharks)
    - Cohort Euselachii (modern sharks and fossil relatives)
      - Subcohort Neoselachii (modern sharks)
        - Superorder Squalomorphi (squalomorph sharks)
          - Order Hexanchiformes (cow and frilled sharks)
          - Order Squaliformes (dogfish sharks)
          - Order Squatiniformes (angel sharks)
          - Order Pristiophoriformes (sawsharks)
          - Order Rajiformes (batoids)
        - Superorder Galeomorphi (galeomorph sharks)
          - Order Heterodontiformes (bullhead sharks)*
          - Order Lamniformes (mackerel sharks)*
          - Order Orectolobiformes (carpet sharks)*
          - Order Carcharhiniformes (ground sharks)

Orders are the highest taxonomic groups dealt with here, and many of their synonyms are listed even though the present International Code of Zoological Nomenclature does not treat groups higher than the family-group level (superfamilies, families, subfamilies, tribes, etc.). The nomenclature for orders is modified from that of Compagno (1973, 1984, 1999), with synonyms listed from oldest to newest. The orders are suffixed with *-iformes* following common ichthyological practice at present. Families are suffixed with *-idae*, the universal ending for zoological families. Other levels between orders, families, genera and species are mostly not covered here. Subgenera are discussed under their appropriate genera but species are not grouped under subgenera and given parenthetical subgeneric names such as ***Somniosus (Rhinoscymnus) rostratus***, even where subgenera are considered valid, so as not to eliminate the utility of listing species alphabetically within genera. Subspecies are listed in the synonymies of their species but are not given separate coverage.

Valid families, genera and species are provided with citations for their author or authors, year of publication, reference and pagination (illustrations also included for species), while synonyms are similarly cited except for their references (which are listed in the bibliography). Other combinations of genera and species that have been used in the literature but are at variance with valid names are cited with author and date only. The bibliography covers a wide selection of references used in writing the catalogue, but is not intended to be all-inclusive.

The information pertaining to each family, genus and species is arranged in the form used in the first edition of this Catalogue (Compagno, 1984), with some modifications:

Family accounts include the valid modern form of the family name with author and year; the original citation of the family name with its author, year, reference and pagination; the valid type genus with author and date; the number of recognized genera in the family; the FAO family vernacular names in English, French and Spanish; family Synonyms with name, author, year, and pagination; Field Marks and Diagnostic Features of members of the family; an account of the natural history of the family under separate sections covering Distribution, Habitat and Biology; a section on Interest to Fisheries and Human Impact, a synopsis of the human issues affecting shark families; Local Names when available; a Literature section covering references to the entire family; a Remarks section mostly with systematic comments; and a Key to Genera, when families have more than one genus.

Generic accounts include the valid modern form of the genus name with author and year; the original citation of the genus or subgenus, with its author, year, reference and pagination, and, if a subgenus, the original genus name with author and year that the subgenus was originally placed in; the type species and means of designating it (for example, by original designation, monotypy, absolute tautonymy, or subsequent designation); the number of recognized species in the genus; the synonyms of genera, with their rank (genus, subgenus, or other genus-group ranking such as W.H. Leigh-Sharpe's 'pseudogenera'), author, year, pagination, and genus they were described in if originally ranked as subgenera or equivalents; FAO Names if they exist; sometimes Field Marks if genera are large and distinctive; Diagnostic Features of the genus; a Key to Species if the genus has more than one species (is not monotypic); and a Remarks section where necessary.

Species accounts include the valid modern names of the species, with author and date; the original citation of the species (or subspecies), with its author, year, reference pagination; the holotype, syntypes, lectotype or neotype of each species (paratypes are not listed in the present account), including the total length and sex of the specimen, its institutional deposition, and its catalogue number; the type locality including the location, coordinates and depth if available, where the holotype, syntypes, lectotype or neotype were caught; Synonyms of the species, including their names, authors and dates; a section listing other scientific names recently in use; the English, French, and Spanish FAO Names for the species; a lateral view illustration, and often other useful illustrations (lateral view drawings are given of each shark species, usually ventral views of heads, and often teeth and denticles of the shark in question); Field Marks; Diagnostic features (except in monotypic genera); Distribution, including a map; Habitat; Biology; Size; Interest to Fisheries and Human Impact; Local Names when available; a Remarks section when necessary; and Literature.

Synonyms include only true taxonomic synonyms of the valid family, genus and species given. For species, another category, **Other Combinations**, is provided for common misidentifications of a given species with another, valid species (for example, ***Carcharhinus brachyurus*** was often termed ***C. remotus***, but the latter is a junior synonym of ***C. acronotus***) as well as commonly used combinations that place a valid species in different genera (for example, ***Odontaspis taurus*** or ***Eugomphodus taurus*** for ***Carcharias taurus***).

FAO Family and Species Names. English, French and Spanish names for each family and species, primarily for use within FAO, were selected by the following criteria: (a) each name applies to a single family or species worldwide; (b) the name conforms with FAO spelling nomenclature; (c) the name conforms to prior usage when possible. FAO names are not intended to replace local species names, but are necessary to overcome the confusion caused by the use of a single name for more than one species or several names for one species. The FAO names used here conform with prior FAO usage and when possible and appropriate national and international checklists and reviews of species such as Whitley (1940), Fowler (1966-1970), Shiino (1972, 1976), Hureau and Monod (1973), Smith (1975), Robins et al. (1980, 1991a, b), and Lindberg, Heard and Rass (1980). The French names were selected jointly with Dr J.C. Quéro, Institut Scientifique et Technique de Pêches Maritimes, Ministère de la Marine Marchande, La Rochelle, France, and for recently discovered species with Dr B. Seret, Museum National d'Histoire Naturelle, Paris. When possible, the names selected correspond to official French species nomenclature established by the Direction des Pêches Maritimes. The selection of Spanish names presented considerable difficulties due to the lack of denominations for many species. Wherever possible, the "official" Spanish names adopted by F. Lozano in his book "Nomenclature ictiologica", Madrid, 1963, were used, along with names for additional species coined by Dr R. Bonfil, Fisheries Centre, University of British Columbia, Vancouver.

The broader use of 'shark' here for all living cartilaginous fishes is noted above. The term 'shark' is broadly and popularly used as a catchall term in English for all living members of the Class Chondrichthyes that are not batoids or chimaeras, although guitarfishes (Rhinobatidae) are also termed 'sand sharks', chimaeras are termed 'ghost sharks' or 'silver sharks', and even certain aquarium teleosts (some loaches, Cobitidae) are termed 'sharks'. The French 'requin' and Spanish 'tiburón' are comparable general terms to 'shark'. Several names not incorporating 'shark' or its French or Spanish equivalents are mostly used only for sharks and not for other fishes; these include the English 'dogfish', 'smoothhound', 'tope', 'porbeagle' and 'hammerhead'. However, 'freshwater dogfish' is a regional name for the bowfin, ***Amia calva***, in the USA. 'Wobbegong' is adapted from an Australian Aboriginal term for sharks of the genera ***Eucrossorhinus***, ***Orectolobus*** and ***Sutorectus***). French 'roussette', 'emissole', 'renard', 'milandre', 'marteau', and 'griset', and Spanish 'gato', 'cazón', 'tollo', 'pintarroja', 'tintorera', and 'cornuda', are similar terms for certain kinds of sharks.

Usage of local names for different kinds of sharks varies from country to country. 'Catshark' is used for members of the Scyliorhinidae and sometimes related families (such as Proscylliidae) in the United States, but also for various orectoloboids in Australia. 'Dogfish' is variably used for members of the families Squalidae ('spiny dogfishes'), Scyliorhinidae (especially ***Scyliorhinus***), and Triakidae ('smooth dogfishes', ***Mustelus* spp.**). 'Sand shark' may refer to Odontaspididae (especially ***Carcharias taurus***, the 'sand tiger shark' of the eastern USA, called 'ragged-tooth shark' in South Africa and 'grey nurse shark' in Australia), to Triakidae (especially to ***Mustelus* spp.**) off the western USA, or guitarfishes off South Africa. In the present Catalogue 'catshark' is restricted to members of the Scyliorhinidae and Proscylliidae ('false catsharks' are members of the Pseudotriakidae), 'dogfish' to the Squaliformes, and 'sand sharks' in the form of 'sand tiger shark' to the Odontaspididae. Orectoloboid 'catsharks' are termed 'carpet sharks', and 'sand sharks' and 'smooth dogfishes' of the triakid genus ***Mustelus*** are termed 'smoothhounds' (except for ***M. antarcticus***, the Australian 'gummy shark').

Keys, Field Marks and Diagnostic Features. These sections include identification data in different forms. Keys to orders, families, genera and species are standard dichotomous biological keys that are followed in steps of alternate choices to single out the taxa covered. Diagnostic Features are comprehensive lists of characters at the ordinal, familial, generic, and species level, with the character choice generally limited to external characters, particularly at the species level, because of space considerations and their primary purpose of identification rather than indication of relationships. Some exceptions are taken with higher taxonomic levels, to support a solid, sound higher classification. The Diagnostic Features sections are hierarchical, with characters at the ordinal level not duplicated at the family, genus and species levels. Monotypic orders with one family (such as Pristiophoriformes), monotypic families with one genus (Chlamydoselachidae) or monotypic genera with one species (***Carcharodon***) all have the Diagnostic Features section present only in the highest taxon covered. In a monotypic order, Diagnostic Features are omitted in the account of its single family; in a monotypic family, they are omitted from its single genus; and in a monotypic genus, they are omitted from its single species.

Field Marks generally include a few obvious characters of use in field identification, extracted from Diagnostic Features at various levels, but included in a separate section. Field Marks are listed at the ordinal, familial and species levels, and occasionally the generic level in cases of large genera with many species. The arrangement of Field Mark characters is semihierarchical and pragmatic and may include characters from a higher level such as an order in lower level taxonomic accounts such as those of species.

An example of the different application of Diagnostic Features and Field Marks is indicated with the sevengill shark, ***Heptranchias perlo***. Starting with the order Hexanchiformes, Diagnostic Features applicable to it are given at decreasing hierarchical levels through the family Hexanchidae and genus ***Heptranchias*** (a monotypic genus). However, the species account of ***H. perlo*** also has a short Field Marks section, "A narrow-headed, big-eyed, small seven-gilled shark with one dorsal fin, no dark spots, and a black blotch on the dorsal fin (inconspicuous in large individuals)", that can suffice to identify it without additional information, although this is available in the Diagnostic Features sections as needed. In some large families such as the Carcharhinidae the Field Marks for an easily recognized species such as ***Carcharhinus longimanus*** may not repeat familial and ordinal characters but merely indicates its family and unique characters.

Distribution and Maps. Geographic distributions for nearly all species of sharks are given by listing the countries off the coasts of which the sharks occur, and, in some instances with large countries (Australia) or those with coasts fronting more than one ocean (e.g. Mexico, South Africa), more detailed data are given when available. In compiling distributional data and preparing maps it was noted that the distributions of many wide-ranging coastal species are very spottily known as present, especially with species occurring in the Indian and western Pacific Oceans. In many cases gaps in distribution may not indicate absence of a given species but absence of knowledge. Continental slope shark faunas are poorly known for much of the world, and a number of deepwater species probably have wider ranges than are currently known. A recent example of this is the capture of the Australian and New Zealand sharks ***Proscymnodon plunketi*** and ***Parmaturus macmillani*** on submarine ridges south of Madagascar and east of South Africa by a commercial bottom trawler in 1999. The locality data in the literature and on specimen labels is often very general and imprecise; and even with bottom or pelagic trawl hauls with detailed oceanographic data and accurate coordinates, hauls may be of such long duration that locations are approximate. Longline locality data can be more accurate than trawls thanks to GPS or other navigation systems, but often is not accurate because detail data were not collected when specimens were landed. Hence distributional data and maps presented here are to be considered as rough approximations of distribution. Some of the data comes from a database (approximately 14 000 records) of shark distribution compiled by the writer and plotted with commercial digital mapping programmes and a spreadsheet-based programme for southern Africa developed by the writer. Much effort was made to screen out errors of shark distribution, based on misidentifications of species, at a cost of presenting distributional lists and maps that are spotty if more accurate. An extreme example is discussed in detail under ***Glyphis gangeticus*** (Carcharhinidae; see volume 3).

Elasmobranchs are primarily marine organisms, but a number of species readily enter brackish to almost freshwater estuaries, river mouths, lagoons and bays; a few species of the family Carcharhinidae and many batoids occur far up rivers and in freshwater lakes with connections to the sea. Records of elasmobranchs in fresh water were reviewed by Compagno and Cook (1995), who classified species as *euryhaline* (occurring in fresh, brackish and salt water, and found far from the sea), *marginal* (peripheral species penetrating fresh water in estuaries or the lower reaches of rivers, but not extending far up river), *brackish* (found in water of reduced salinity, but not in fresh or salt water), and *obligate* (found in fresh water only, and not in salt water).

In the case of certain carcharhinid sharks (the bull shark, ***Carcharhinus leucas*** and the river sharks, ***Glyphis* spp.**) that are known from verifiable records from entirely freshwater parts of rivers and freshwater lakes, the names of major river systems and lakes where they occur are noted. There are various freshwater records of other members of the family Carcharhinidae and several other families of nonbatoid sharks (including the zebra shark family, Stegostomatidae), but some of these records may be of marginal species from semi-brackish lower reaches of rivers and estuaries and may indicate that the species involved are tolerant of reduced salinities but are not truly euryhaline. Some of these carcharhinid freshwater records may be based on ***C. leucas*** or ***Glyphis*** species rather than the species indicated (such as ***C. melanopterus*** or ***C. hemiodon***). Batoids are more numerous than nonbatoid sharks in fresh water, including several sawfish (Pristidae), potamotrygonid stingrays, and several dasyatid stingrays. Many stingrays are obligate freshwater species.

For the compilation of maps of distribution in the present catalogue, a new approach has been undertaken to better represent the real distribution of each species. The main source of information for building the maps was that given in each species' account under **Habitat** and **Distribution**. It was possible to use this information using a modern GIS approach after standardizing all the terminology provided in the species accounts following the method briefly explained below.

For those species that show some type of relationship with the ocean bottom, the depth information given under **Habitat** has been translated into pre-chosen depth ranges using the tables shown below. These depth ranges were extracted from a single data set, i.e. GEBCO Digital Atlas (Natural Environment Research Council. 1994. Digital version of the IOC/IHO General Bathymetric Chart of the Oceans) and transferred to a GIS. Then, geographic distribution information on localities and oceanographic provinces were extracted from WVS (World Vector Shoreline, at scale 1:43.000.000) and ArcWorld (distributed by ESRI (Environmental Systems Research Institute), 380 New York St., Redlands, California, 92373-8100, USA) and overlaid with the previous information to produce the final output. With this methodology, the maps for bottom-dwelling or coastal species give a better idea of the spatial coverage of their distribution as inferred from our current knowledge. This can give an approximate idea of the relative size of different stocks among and between species.

Criteria used to define upper and lower limits of habitat when compiling maps of distribution.

Table 1
Lower limits (m) used for different marine habitats

Coast-line	Coastal area	Upper continental shelf	Deep shelf	Upper slope	Maximum limit of the slope
0	50	100	200	500	1 000

If specific depth ranges were given under **Habitat**, such values were used after rounding them according to Table 2 below, using the closest values found. In cases of values larger than 1 000 m, the 1 000 m isobath was used.

Table 2
Limits used to convert upper and lower limits of depth ranges (m)

For original depth data in the interval	Limit used
0-30	0
31-75	50
76-150	100
151-250	200
251-751	500
751 and below	1 000

If more than one bathymetric range of distribution was mentioned (e.g. different ranges for adults and juveniles), the widest range given was used. However, when different depth ranges existed for different regions or areas, each was chosen and plotted independently.

If no depth data was mentioned in the original account, textual descriptions have been translated using the criteria in Table 3 below.

Table 3
Upper and lower limits of depth ranges (m) used for textual descriptions of habitat

Fot text indicating	Upper limit	Lower limit
Shelf or continental shelf	0	200
Shallow waters, inshore waters, coastal	0	50
Continental shelf, neritic	0	200
Upper shelf	0	100
Deep shelf	100	200
Slope	200	1 000
Upper slope	200	500
Deep slope	500	1 000

Terms like benthic, pelagic, surface, bottom deeper water, deepish, great depths included under **Habitat** were not used. If more than one type of habitat was given, the one corresponding to the widest possible range of distribution was used.

For species with an oceanic habitat, the main source of information was their known geographic distribution irrespective of depth. Thus, the maps of oceanic species give only information on distribution.

All data were transferred to hand drawn maps which were directly digitized and georeferenced using WVS and ArcWorld for the exact plotting of localities and oceanic provinces.

Where necessary, maps show two different kinds of distribution for a given species. Dark red is used to show the **known** and certain distribution of a species from reliable records, whilst light red or orange is used to show the suspected or **uncertain** distribution of a species.

Maps presented in the Catalogue can be largely divided into two categories, Global (or world maps) and Regional maps. For better visualization, global maps include the species distribution and the land masses especially generalized and prepared from the WVS data set. The regional maps, in addition to the above, include the 200 m depth isobath as a reference of their depth distribution.

Note: Whenever the narrowness of the continental or insular shelves and the scale of the maps have caused parts of the distribution of a species to be undistinguishable, coloured arrows have been used on the map to point to such distribution areas.

Habitat. Habitat covers information on physical conditions where various sharks are found. The known depth range of the species (in metres), position in the water column, type of substrate occupied, and preferences relative to coasts are noted when available. In most cases data on salinity, oxygen content, and specific temperature of the water in which they occur was not available or was not in an easily usable form and has not been regularly compiled here.

Biology. Includes data on population structure and dynamics, reproduction, behaviour, sociobiology, age and growth, and feeding. Compilation of these data suggests that very few species of sharks are biologically well known, and even in the piked dogfish (***Squalus acanthias***), perhaps the best-known of living cartilaginous fishes, there are areas of its biology that are very poorly known (such as its behaviour and sociobiology). There is a bias in available natural history data towards reproductive biology, feeding, and fisheries-related subjects such as age and growth, and correspondingly little on ecology, behaviour and sociobiology.

Size. All size data are given as total lengths; this is the measurement most often used as an independent variable and standard measurement in the shark literature, although particularly in fisheries papers precaudal lengths, fork lengths, and other measurements have been used from choice or necessity. Unfortunately shark workers have not agreed on a standard method of measuring total length, so total lengths from different sources in the literature may not be strictly comparable. I prefer and advocate as a standard method a direct measurement, in which the shark is held belly down with its dorsal caudal-fin lobe depressed into line with its body axis and total length measured as a point to point distance (not over the curve of the body) from the snout tip to the tip of the dorsal caudal-fin lobe (see also Compagno, 1988). This method lends itself readily to quick use of a fishboard with a perpendicular front bar or plate to index the shark's snout against, a one metre or two metre ruler or folding rule slipped under the shark, or even a steel or cloth tape, and avoids the trouble of computation and possible errors and loss of data.

A comparable computational method adding the precaudal length and dorsal caudal-fin margin is advocated by Sadowsky (1968). Bigelow and Schroeder (1948) and Springer (1964) measured total length from the snout tip along the body axis to a vertical projection from the tip of the dorsal caudal-fin lobe with the caudal fin in a 'natural position'. Bass (1973) advocated a computational method which adds the precaudal length to a number computed by multiplying the length of the dorsal caudal-fin margin by a constant (1.0 or less, 0.97 and 0.80 were the numbers) that corrects for the different 'natural angles' of the caudal axis to the body axis in different species. The method advocated here and in Compagno (1984, 1988) dispenses with all computation and avoids arbitrary constants to correct for supposed 'natural positions' of the caudal axis as well as the difficulties in obtaining accurate vertical projections from the caudal tips held in 'natural positions'. Also, with the present method a comparable measurement can be obtained for all or most sharks, rays and chimaeras, although there are problems with species that have greatly elongated filamentous snouts or tails. In contrast methods using 'natural positions' arbitrarily generate incompatible total lengths for different groups of sharks, and also do not take into account changes in the angle of the caudal axis when sharks swim or as they grow (Compagno, 1988).

Total length data presented includes maximum size, size at maturity (in some cases, a size range at maturity, when abundant data were available) and maximum size for both sexes (as sexual dimorphism in size is nearly universal among sharks, with females usually attaining larger sizes than males, except for some scyliorhinid catsharks where the reverse occurs), and size at birth or hatching. Sometimes size at sexual maturity for either or both sexes is not known, in which cases reported minimum and maximum sizes of adult individuals are given. In some cases maximum size exceeds that recorded for either sex, in which case the sex of the outsized individual or individuals representing the maximum size measurements was not indicated. In some poorly known species only immature individuals are known, in which case the hypothetical maximum adult size is almost certainly larger than the known immature maximum (no cases are known of adult sharks that are considerably smaller than large immature individuals of the same sex, unlike some other vertebrates). The writer tends to discount old, unverifiable size records of some well-known species, but mentions them as such.

Some fisheries biologists and shark researchers use precaudal length (PCL) or fork length (FL) as standard lengths instead of total length. The first eliminates problems with sharks having damaged caudal fins but is difficult to determine on some sharks with weakly defined upper caudal-fin origins. The second is only applicable to species with notched caudal fins and defined upper and lower postcaudal-fin margins.

In some species length-weight equations are presented, usually of the form $W = a + TL^b$, where W is weight, a and b are constants, and TL is total length.

Interest to Fisheries and Human Impact. This section is expanded in scope from the 1984 catalogue, and in addition to fisheries information includes many other aspects of human interaction with sharks. In this section data on localities of fisheries, gear used, and uses of the particular species are noted when available. National fisheries data for sharks is often sketchy and combined for a number of species. Thus, catch statistics were available for relatively few species of sharks but are noted when available, with particular emphasis on data from those species reported to FAO. Additional data for sharks are increasingly available from national and regional fisheries bodies, but were used in a very limited way here due to time and literature constraints.

Initially data from the hard-copy FAO species yearbooks were used for compiling shark fisheries data on spreadsheets, as in Compagno (1990c), but this has been greatly facilitated by the advent of FAO FishStat, a data-handling and analytical software package which can be downloaded free from the FAO Fisheries website (http://www.fao.org/fi). FishStat handles a variety of annually revised FAO fisheries statistics databases and can export files into other programmes such as spreadsheets and databases.

Conservation and management issues and importance of sharks to human recreation including ecotouristic diving and visits to public aquaria are covered in this section. It also includes aspects of shark behaviour that were formerly placed in the biology section, that is, shark encounters with people. The 1984 Catalogue used the universal term 'shark attack' for encounters when sharks bite or otherwise injure people. I have tried to avoid this term in this Catalogue because of its extremely negative, subjective, and misleading connotations, along with a few other hyperbolic terms such as 'maneater'. I realize that the general public and especially the news and entertainment media will continue to use these emotive terms for a long time despite the limited realities. It is challenging to think of ways of discussing the subject without the dreadful, gory 'shark attack' image being brought forth, but it does help to build alternate and more realistic images of a minuscule objective phenomenon. This is discussed in more detail under Shark Encounters in the third volume of the Catalogue.

Local Names. A change from the 1984 Catalogue is that local or regional family and species names in various languages are generally listed when available under a separate local names heading. These were compiled from the same sources used for FAO names (see above), but what is presented here is not comprehensive and represents what was readily available to the writer. Many species have no vernacular names whatsoever or are lumped under catchall names, while some sharks such as the white and basking sharks have dozens of names. Obviously some sharks have more of an impact or are much more familiar than others, and these get more names (some of which seem like curses or jokes). Wherever possible local names are presented for important wide-ranging sharks, including fisheries species such as ***Galeorhinus galeus*** ('school shark' in Australia, 'tiburón vitaminico' or 'vitamin shark' in Uruguay and Argentina, 'soupfin' or 'oil shark' off the Pacific USA and Canada, and 'vaalhai' in South Africa) and ***Carcharias taurus***, the very popular shark for fisheries, public aquaria, ecotourism, and conservation (termed 'ragged-tooth shark' in South Africa, 'grey nurse shark' in Australia, 'requin sable' in West Africa, and 'sand tiger shark' or 'sand shark' off the east coast of the United States). The broadening interest in sharks and urgent need to acquire species-specific data for their management and conservation should encourage fisheries biologists and other researchers to compile local names for their own countries or regions, and add to our sketchy knowledge of local names worldwide.

Remarks. Important information, especially on systematics and nomenclature are given in the remarks section.

Literature. References cited here include specific works with important information for each species and family as well as comprehensive accounts, but are not intended as a comprehensive bibliography. Reference sections have been updated and given more extensive coverage than the 1984 Catalogue.

1.2 Technical Terms and Measurements

1.2.1 Picture Guide to External Terminology of Sharks

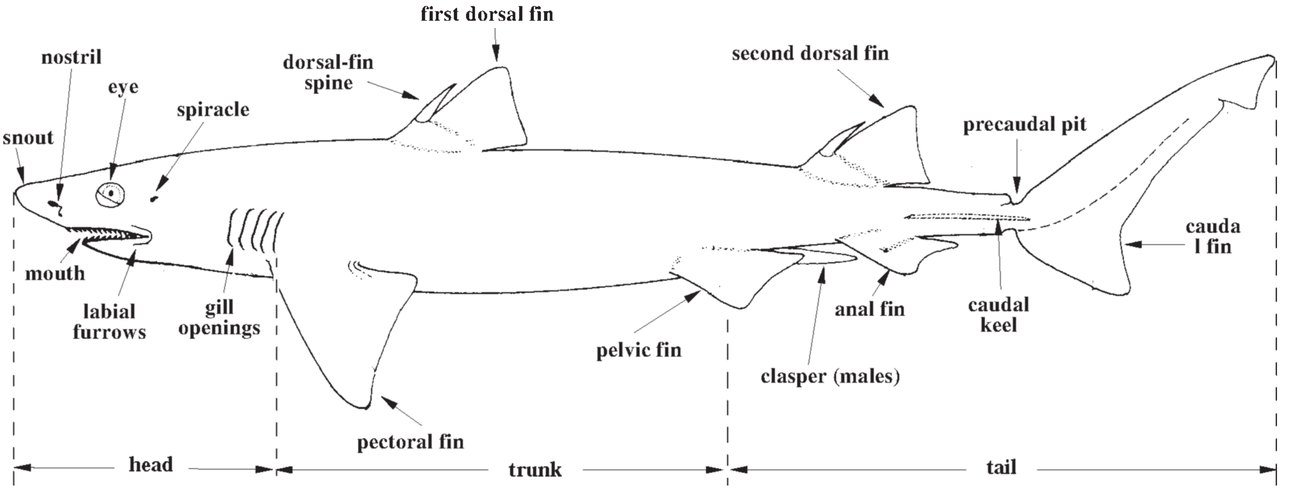


Fig. 2 Lateral view

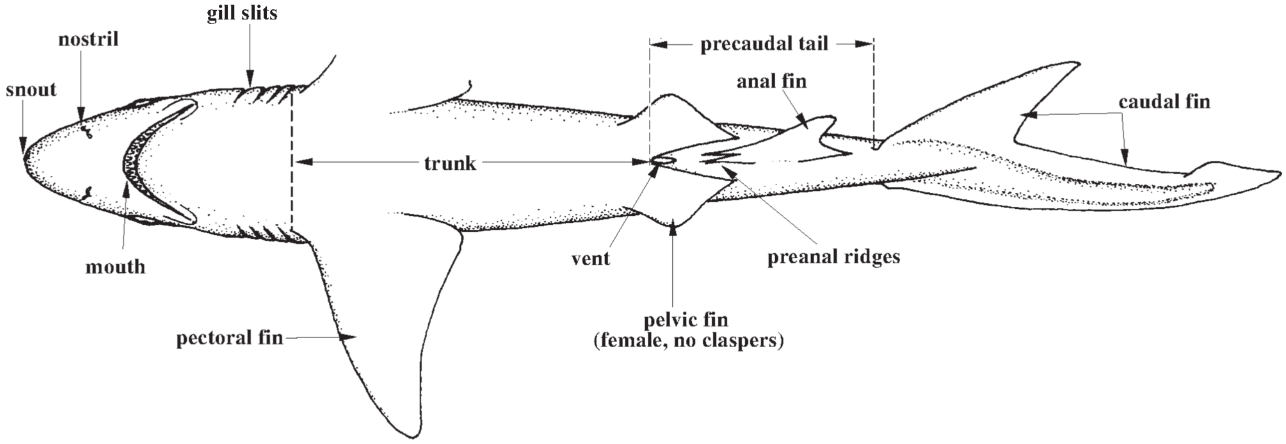


Fig. 3 Ventral view

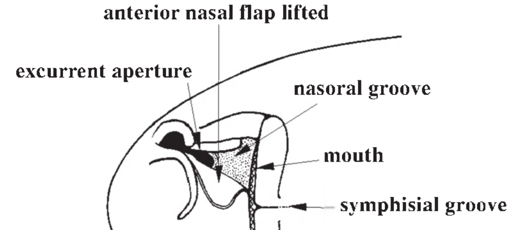


Fig. 4 Head of an orectoloboid shark (ventral view)

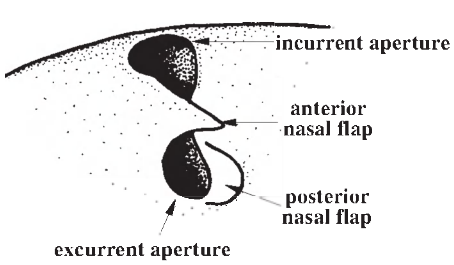


Fig. 5 Nostril

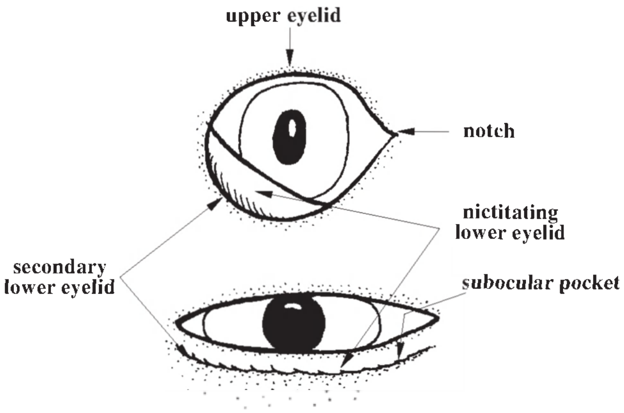


Fig. 6 Eyes

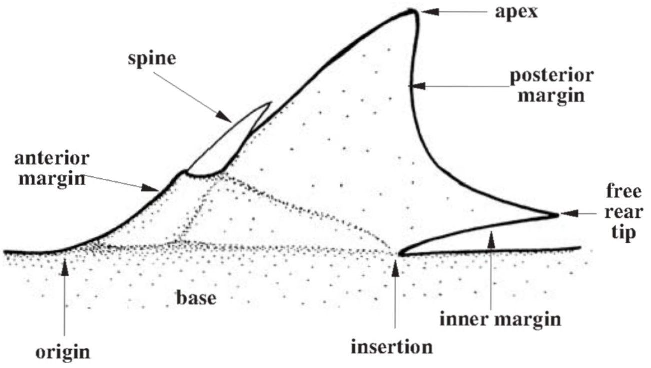


Fig. 8 Dorsal fin

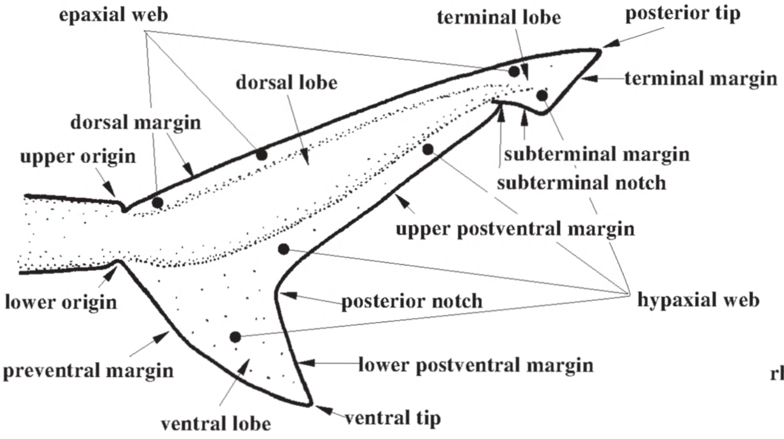


Fig. 9 Caudal fin

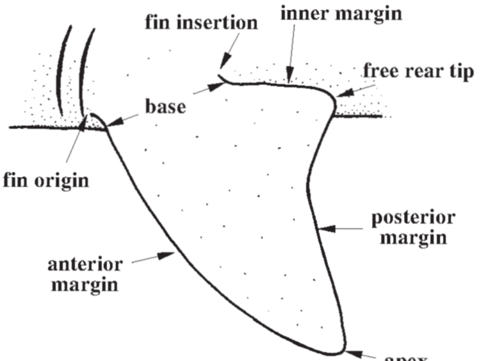


Fig. 10 Pectoral fin

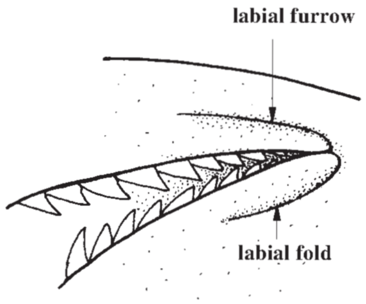


Fig. 7 Mouth corner

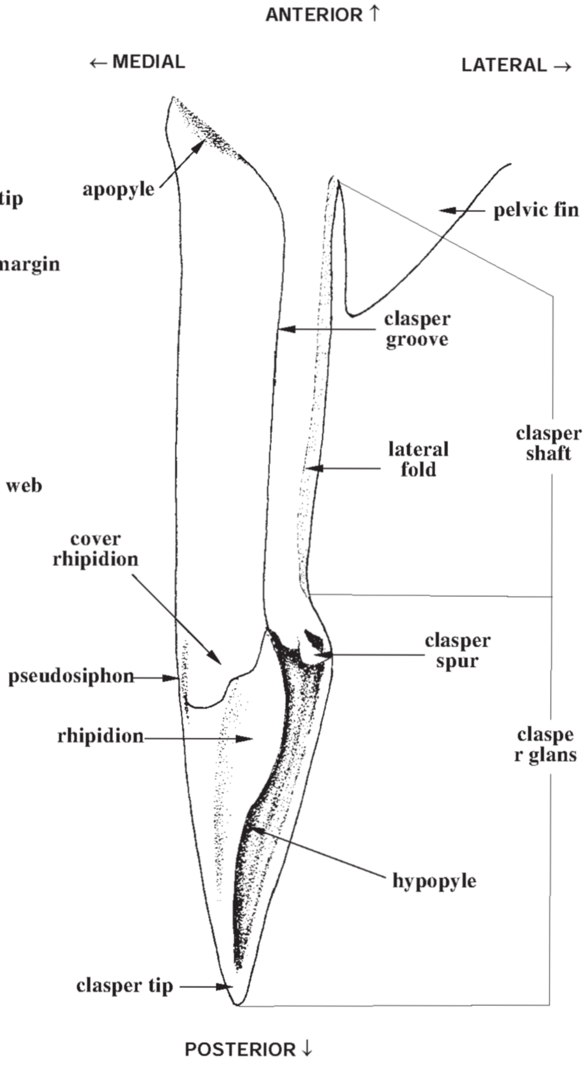
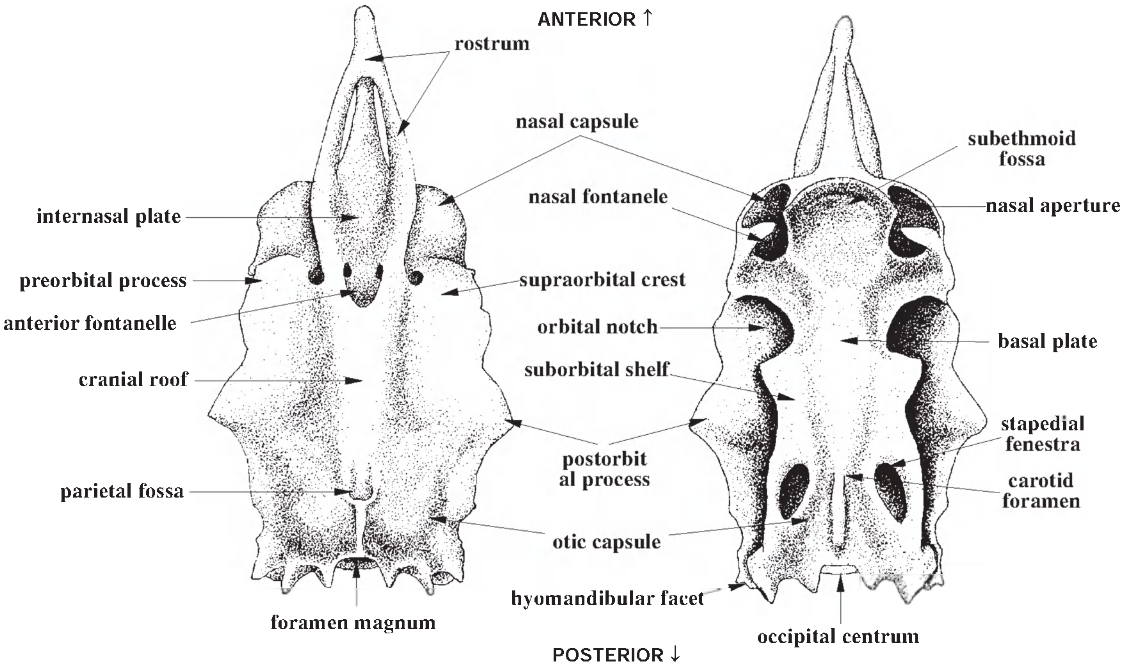
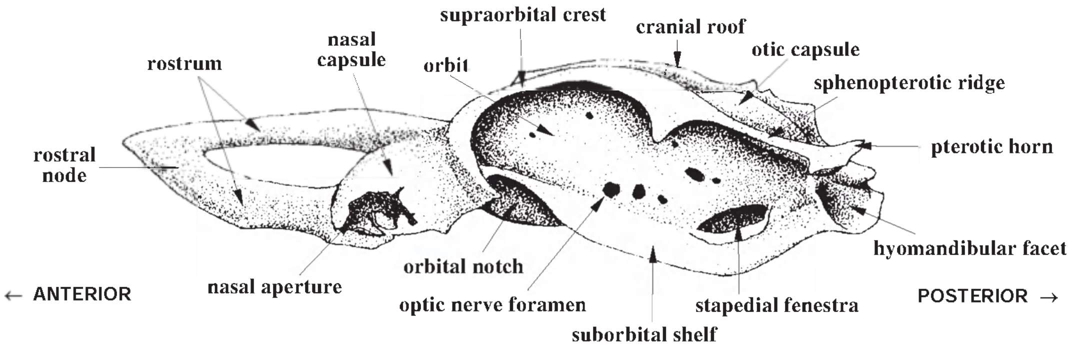


Fig. 11 Dorsal view of clasper (lamnid shark)

1.2.2 Picture Guide to Skeletal Terminology of Sharks

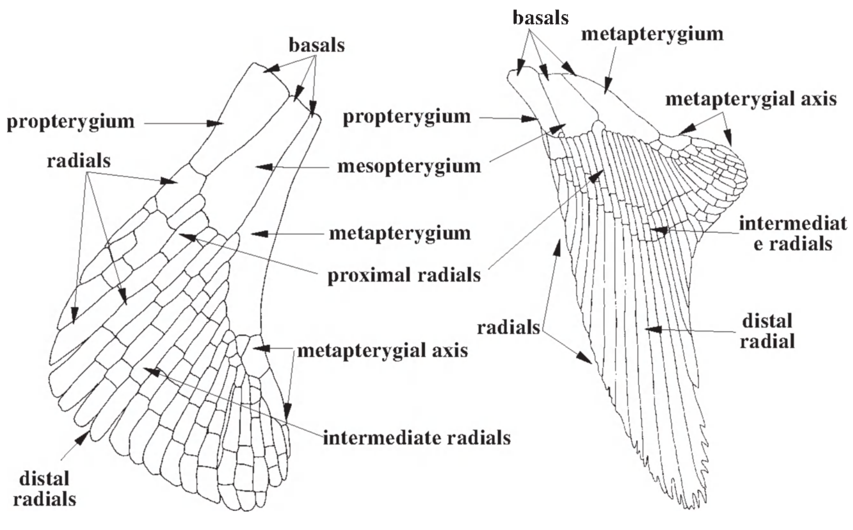


a) DORSAL VIEW b) VENTRAL VIEW



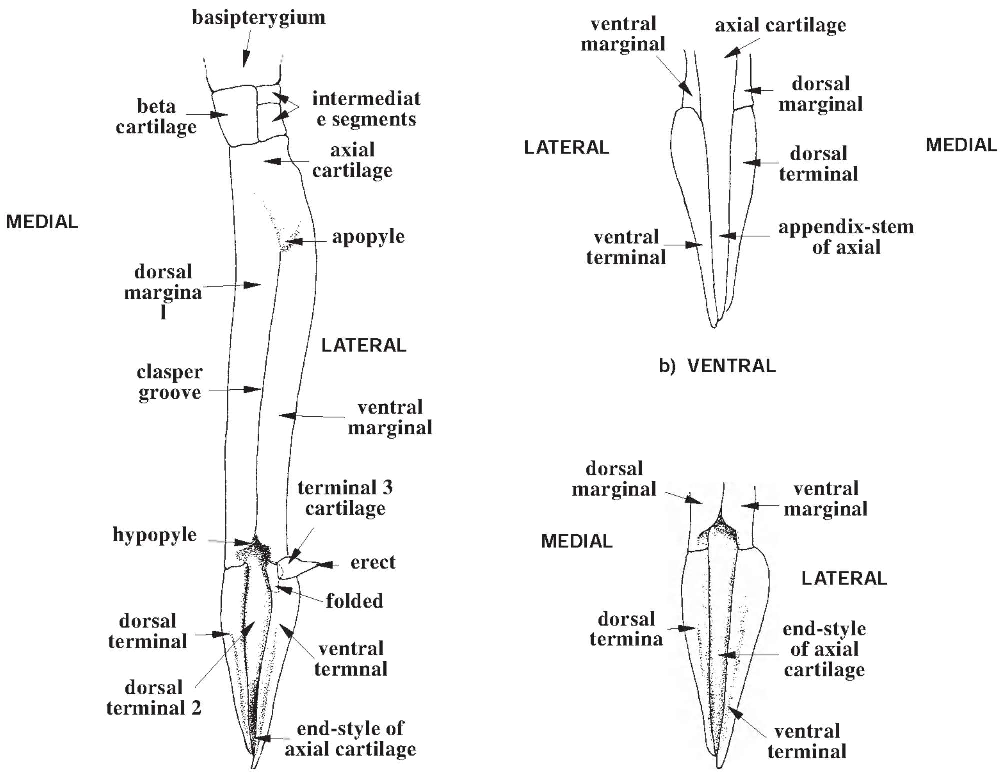
c) LATERAL VIEW

Fig. 12 Chondrocranium



a) APLESODIC b) PLESODIC

Fig. 13 Aplesodic and plesodic pectoral fins

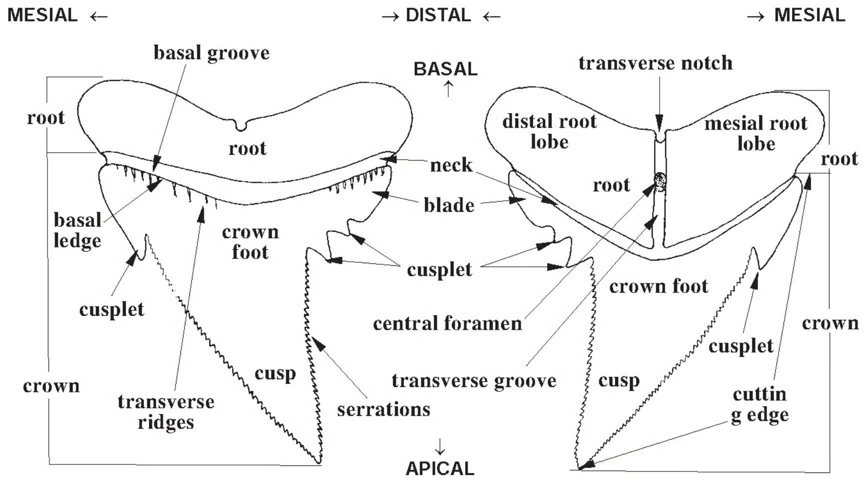


a) DORSAL

b) VENTRAL

c) DORSAL (TERMINAL 3 CARTILAGE AND DORSAL TERMINAL 2 REMOVED)

Fig. 14 Clasper skeleton of lamnid shark (right side)



a) LABIAL VIEW

b) LINGUAL VIEW

Fig. 15 Tooth terminology (left upper anterolateral tooth)

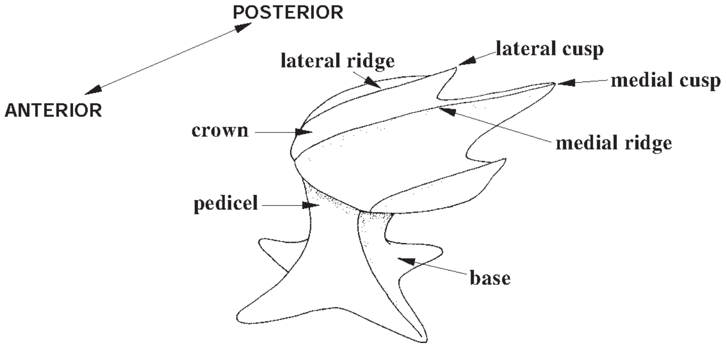


Fig. 16 Oblique anterolateral view of lateral trunk dermal denticle

1.2.3 Measurements Used for Sharks

TL = TOTAL LENGTH
FL = FORK LENGTH
PCL = PRECAUDAL-FIN LENGTH
PD2 = PRE-SECOND DORSAL-FIN LENGTH
PD1 = PRE-FIRST DORSAL-FIN LENGTH
HDL = HEAD LENGTH
PG1 = PREBRANCHIAL LENGTH
PSP = PRESPIRACULAR LENGTH
POB = PREORBITAL LENGTH
PP1 = PREPECTORAL-FIN LENGTH

PP2 = PREPELVIC-FIN LENGTH
SVL = SNOUT-VENT LENGTH
PAL = PREANAL-FIN LENGTH
IDS = INTERDORSAL SPACE
DCS = DORSAL CAUDAL-FIN SPACE
PPS = PECTORAL-FIN PELVIC-FIN SPACE
PAS = PELVIC-FIN ANAL-FIN SPACE
ACS = ANAL-FIN CAUDAL-FIN SPACE
PCA = PELVIC-FIN CAUDAL-FIN SPACE
VCL = VENT CAUDAL-FIN LENGTH

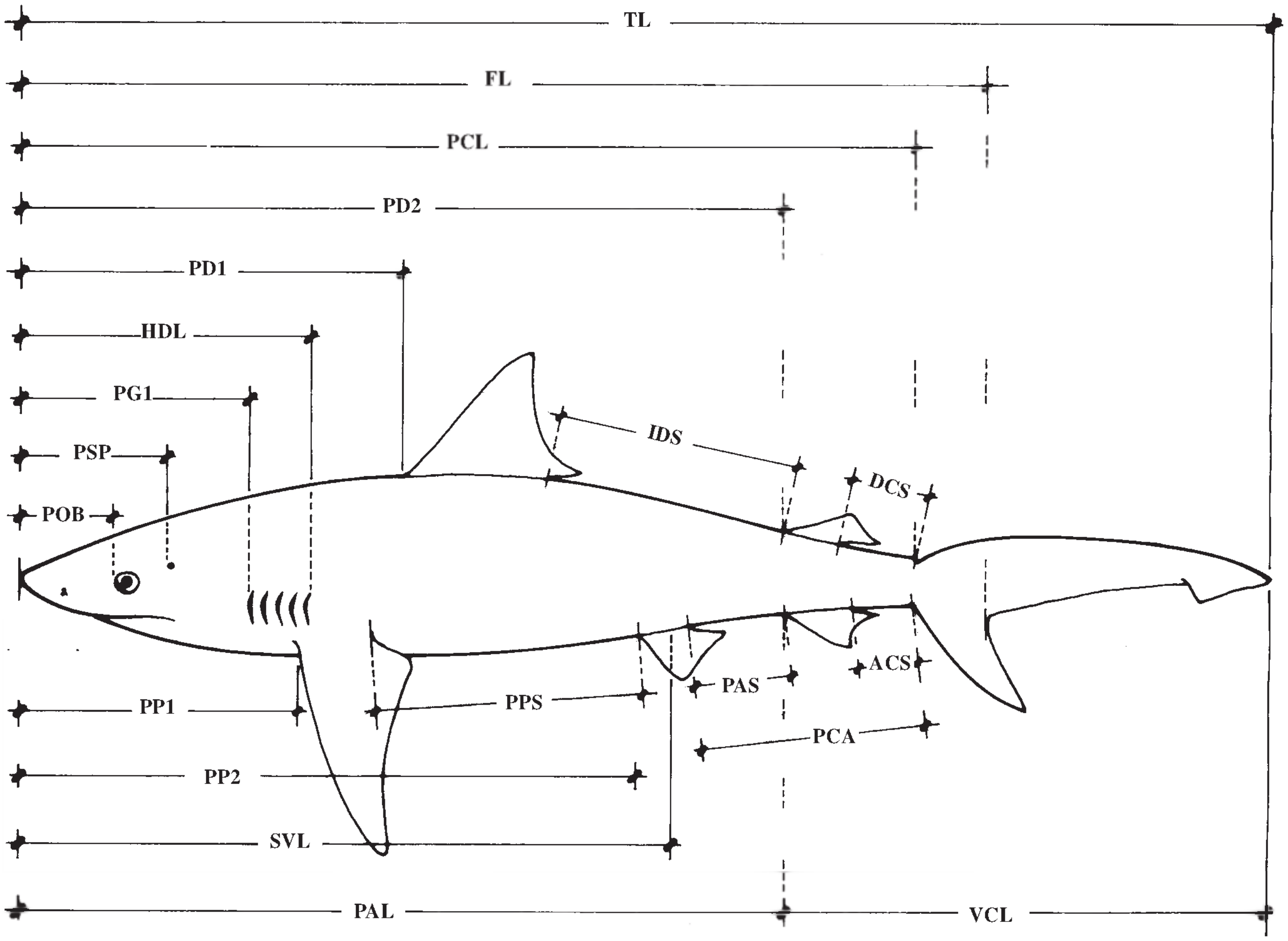


Fig. 17 Main longitudinal measures

PRN = PRENARIAL LENGTH
POR = PREORAL LENGTH
EYL = EYE LENGTH
EYH = EYE HEIGHT
ING = INTERGILL LENGTH
GS1 = FIRST GILL SLIT HEIGHT
GS2 = SECOND GILL SLIT HEIGHT
GS3 = THIRD GILL SLIT HEIGHT
GS4 = FOURTH GILL SLIT HEIGHT
GS5 = FIFTH GILL SLIT HEIGHT
GS6 = SIXTH GILL SLIT HEIGHT
GS7 = SEVENTH GILL SLIT HEIGHT
P1A = PECTORAL-FIN ANTERIOR MARGIN
P1R = PECTORAL-FIN RADIAL LENGTH
P1B = PECTORAL-FIN BASE
P1I = PECTORAL-FIN INNER MARGIN
P1P = PECTORAL-FIN POSTERIOR MARGIN
P1H = PECTORAL-FIN HEIGHT
P1L = PECTORAL-FIN LENGTH
SOD = SUBOCULAR POCKET DEPTH

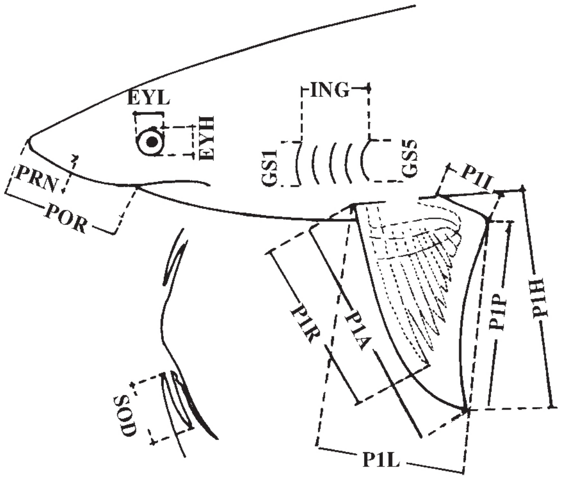


Fig. 18

CDM = DORSAL CAUDAL-FIN MARGIN
CPV = PREVENTRAL CAUDAL-FIN MARGIN
CPU = UPPER POSTVENTRAL CAUDAL-FIN MARGIN
CPL = LOWER POSTVENTRAL CAUDAL-FIN MARGIN
CFW = CAUDAL-FIN FORK WIDTH
CFL = CAUDAL-FIN FORK LENGTH
CST = SUBTERMINAL CAUDAL-FIN MARGIN
CSW = SUBTERMINAL CAUDAL-FIN WIDTH
CTR = TERMINAL CAUDAL-FIN MARGIN
CTL = TERMINAL CAUDAL-FIN LOBE

D1L = FIRST DORSAL-FIN LENGTH
D1A = FIRST DORSAL-FIN ANTERIOR MARGIN
D1B = FIRST DORSAL-FIN BASE
D1H = FIRST DORSAL-FIN HEIGHT
D1I = FIRST DORSAL-FIN INNER MARGIN
D1P = FIRST DORSAL-FIN POSTERIOR MARGIN

D2L = SECOND DORSAL-FIN LENGTH
D2A = SECOND DORSAL-FIN ANTERIOR MARGIN
D2B = SECOND DORSAL-FIN BASE
D2H = SECOND DORSAL-FIN HEIGHT
D2I = SECOND DORSAL-FIN INNER MARGIN
D2P = SECOND DORSAL-FIN POSTERIOR MARGIN

P2L = PELVIC-FIN LENGTH
P2A = PELVIC-FIN ANTERIOR MARGIN
P2B = PELVIC-FIN BASE
P2H = PELVIC-FIN HEIGHT
P2I = PELVIC-FIN INNER MARGIN [LENGTH]
P2P = PELVIC-FIN POSTERIOR MARGIN [LENGTH]

ANL = ANAL-FIN LENGTH
ANA = ANAL-FIN ANTERIOR MARGIN
ANB = ANAL-FIN BASE
ANH = ANAL-FIN HEIGHT
ANI = ANAL-FIN INNER MARGIN
ANP = ANAL-FIN POSTERIOR MARGIN

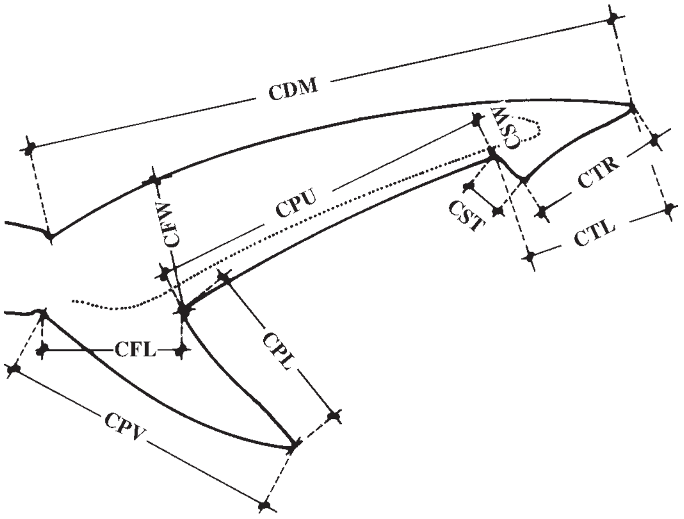


Fig. 19 Measurements of caudal fin

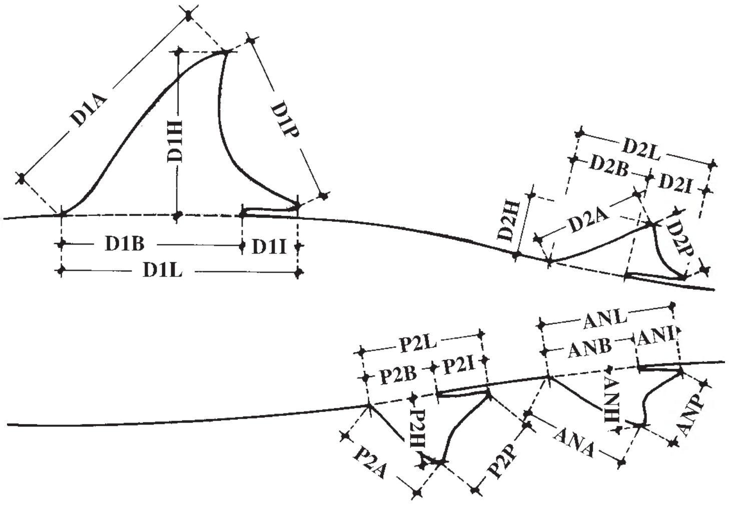


Fig. 20 Measurements of dorsal, pelvic and anal fins

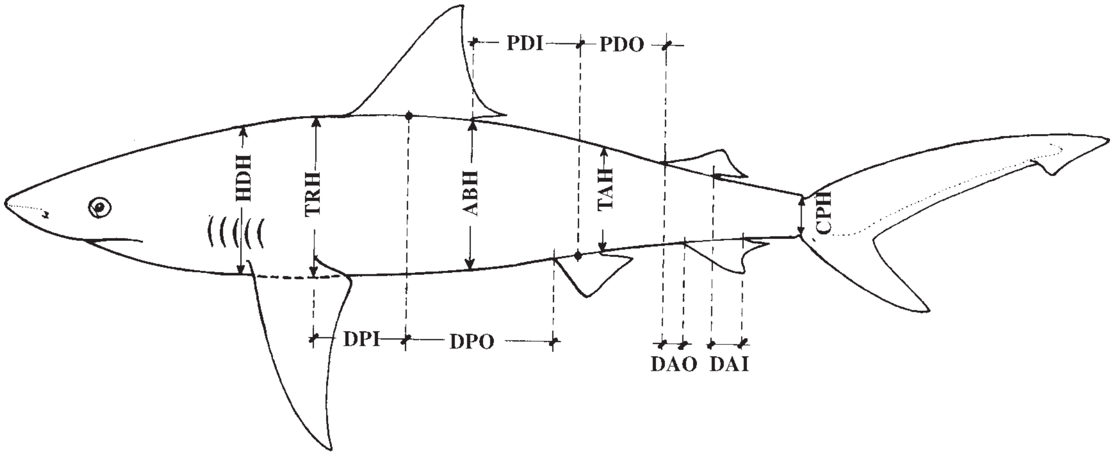


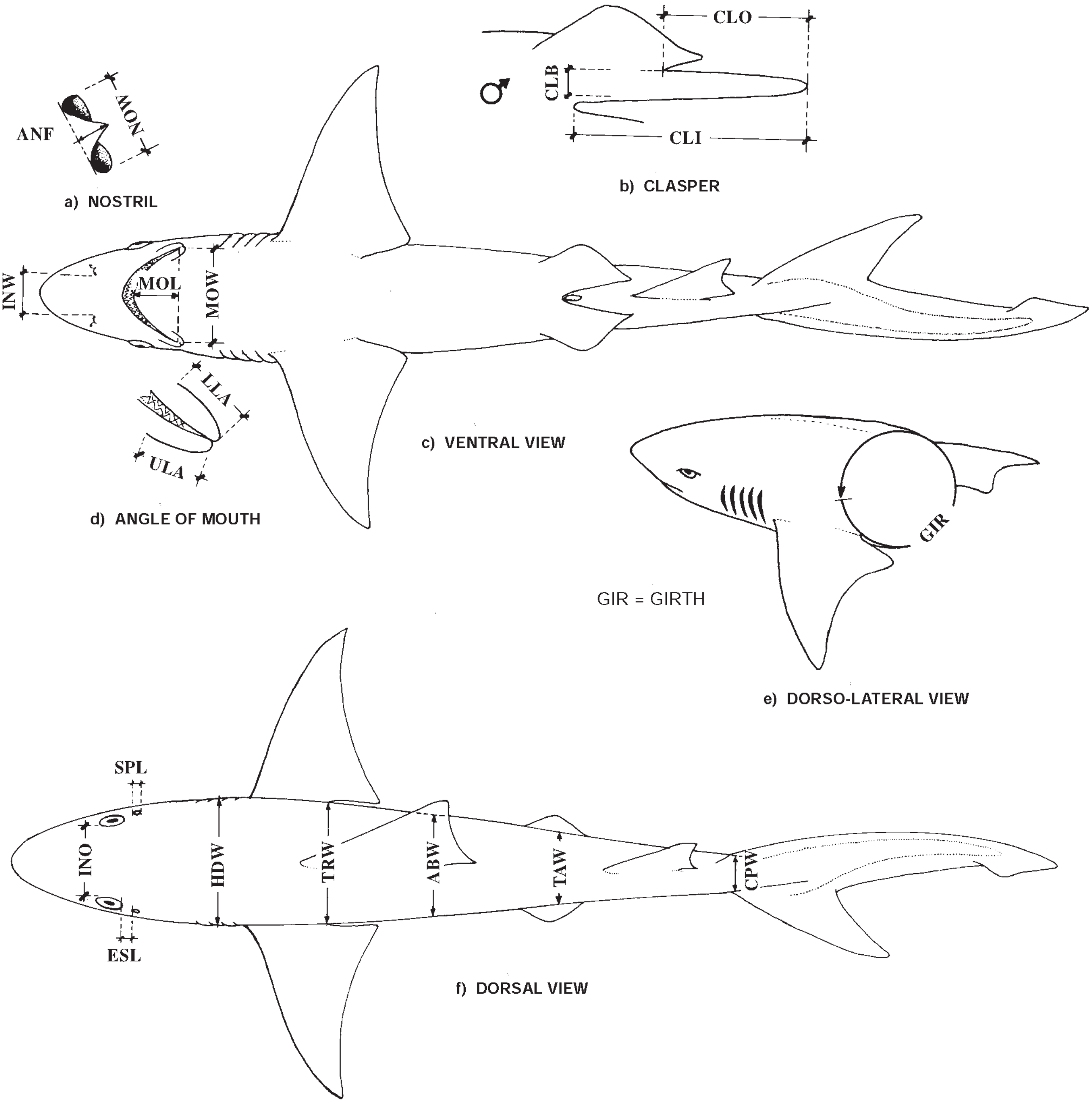
Fig. 21 Other common measurements

HDH = HEAD HEIGHT
TRH = TRUNK HEIGHT
ABH = ABDOMEN HEIGHT
TAH = TAIL HEIGHT
CPH = CAUDAL-FIN PEDUNCLE HEIGHT
DAI = SECOND DORSAL-FIN INSERTION ANAL-FIN INSERTION
DAO = SECOND DORSAL-FIN ORIGIN ANAL-FIN ORIGIN

DPI = FIRST DORSAL-FIN MIDPOINT PECTORAL-FIN INSERTION
DPO = FIRST DORSAL-FIN MIDPOINT PELVIC-FIN ORIGIN
PDI = PELVIC-FIN MIDPOINT FIRST DORSAL-FIN INSERTION
PDO = PELVIC-FIN MIDPOINT SECOND DORSAL-FIN ORIGIN

MOL = MOUTH LENGTH
MOW = MOUTH WIDTH
ULA = UPPER LABIAL-FURROW LENGTH
LLA = LOWER LABIAL-FURROW LENGTH
NOW = NOSTRIL WIDTH
INW = INTERNARIAL SPACE
ANF = ANTERIOR NASAL-FLAP LENGTH

CLO = CLASPER OUTER LENGTH
CLI = CLASPER INNER LENGTH
CLB = CLASPER BASE WIDTH



a) NOSTRIL

b) CLASPER

c) VENTRAL VIEW

d) ANGLE OF MOUTH

GIR = GIRTH

e) DORSO-LATERAL VIEW

f) DORSAL VIEW

Fig. 22

INO = INTERORBITAL SPACE
SPL = SPIRACLE LENGTH
ESL = EYE SPIRACLE SPACE
HDW = HEAD WIDTH
TRW = TRUNK WIDTH
ABW = ABDOMEN WIDTH
TAW = TAIL WIDTH
CPW = CAUDAL-FIN PEDUNCLE WIDTH

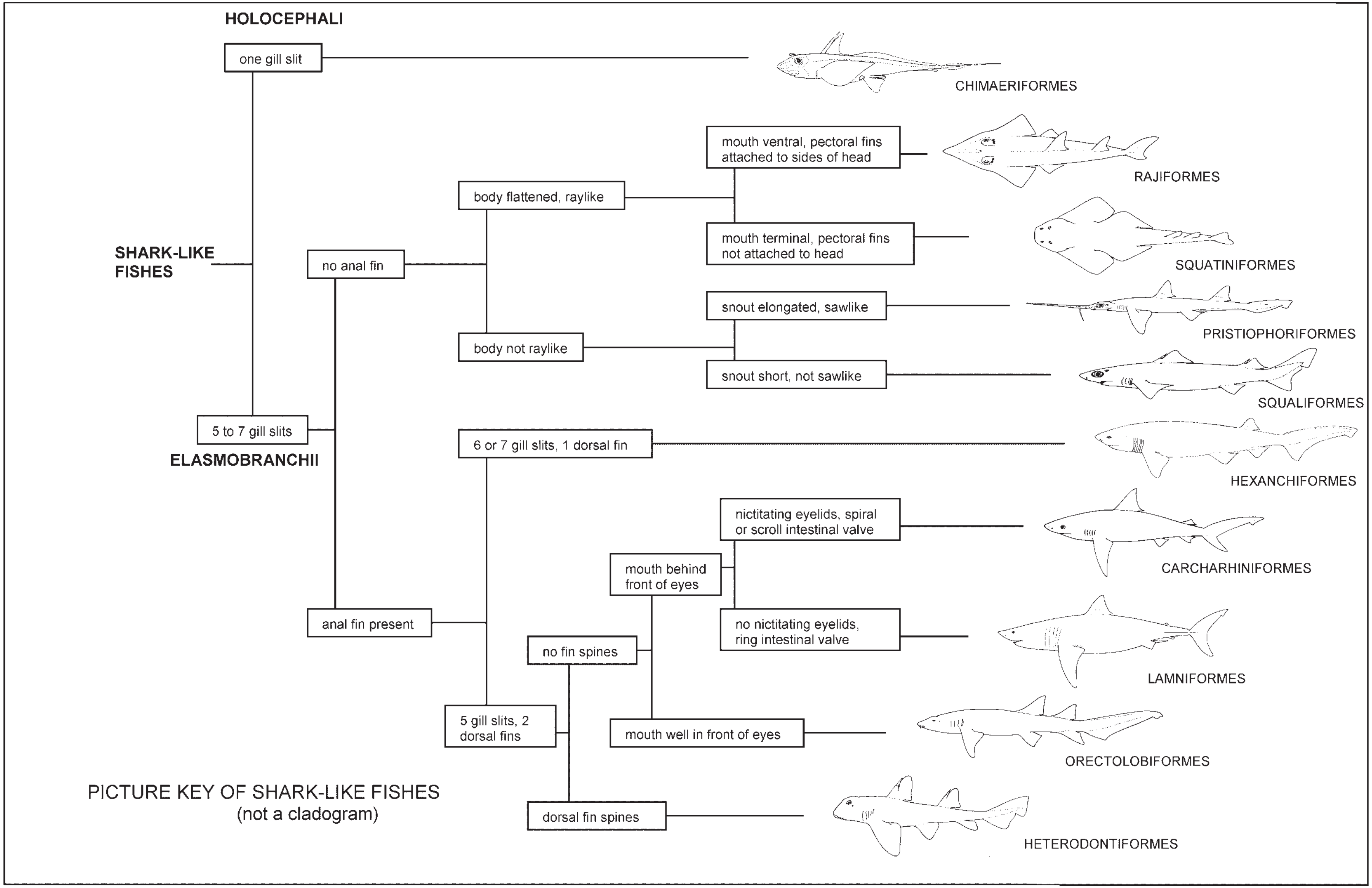


Fig. 23 Higher classification of sharks (Orders)

1.2.4 Glossary of Technical Terms

The following glossary of terms used for the anatomy and biology of shark-like fishes is modified from terms in Compagno (1984, 1988, 1999) and a short glossary in Compagno, Ebert and Smale (1989).

Abdominal ridges or keels: In some sharks, paired longitudinal dermal ridges that extend from the bases of the pectoral fins to the pelvic-fin bases.

Accessory dorsal marginal: In the clasper skeleton, a flat cartilage on the posterior end of the dorsal marginal cartilage that supports the cover rhipidion.

Adductor mandibulae muscles: Paired head muscles originating on the lateral faces of the quadrate process of the palatoquadrates and inserting on the lateral surface of the Meckel's cartilages; the primary jaw-closing muscles of sharks.

Adelphophagy: Foetus-eating, a mode of live-bearing reproduction employing uterine cannibalism; early foetuses deplete their yolk-sacks early and subsist by first eating their smaller siblings and then eating nutritive eggs produced by the mother. At present only known for certain in the sand tiger shark (***Carcharias taurus***), but suspected in a few other lamnoids.

Alternate teeth: Small oral teeth with asymmetrical crowns that form two interdigitated rows on the symphysis, with the cusps of each row hooked mesially towards the opposite row. Additional paired rows of alternates may be present distal to the symphysial rows.

Amphitemperate: Referring to a species that occurs in temperate water in the northern and southern hemispheres, but is absent from the tropics.

Anal fin: A single fin on the ventral surface of the tail between the pelvic fins and caudal fin of some sharks, absent in batoids, dogfish, sawsharks, angel sharks, and some chimaeras.

Annular rings or **annuli:** In a vertebral centrum in cross section, rings of calcified cartilage separated by uncalcified cartilage that occupy the intermedialia only, or concentric rings that cross both the intermedialia and basalia.

Anterior: Forward, in the longitudinal direction of the snout tip. Also, **cranial**.

Anterior fontanelle: On the elasmobranch neurocranium, an aperture on the anterodorsomedial surface, usually at the rear of the ethmoid region and forming a passage into the internal cranial cavity. It is closed by a tough membrane, varies tremendously in shape, and may be pinched off by the medially expanded orbits in a few sharks.

Anterior margin: In precaudal fins, the margin from the fin origin to its apex.

Anterior nasal flap: A flap on the front edges of the nostrils, that serves to partially divide the nostril into incurrent and excurrent apertures or openings.

Anterior teeth: Enlarged, tall, narrow-rooted oral teeth near the symphysis, often with lingually curved cusps.

Anterodorsal palpebral depressor muscle: In the orectoloboid family Parascylliidae, paired head muscles that originate at the insertions of the preorbitalis muscles on the anterolateroventral face of the Meckel's cartilage, and insert on the skin of the upper eyelid anterior to the eye. These are possibly for depressing the upper eyelids and closing the eyes, and are not found in any other sharks.

Antorbital cartilages: On the neurocranium of sawsharks and batoids, separate cartilages attached to the sides of the nasal capsules that support the sides or front of the head.

Apex: In precaudal fins, the distal tip, which can be acutely pointed to broadly rounded.

Apical: In oral teeth, towards the tip of the crown or cusp. Can also be used as indicating direction towards the apex or tip of a fin, fin-spine, etc.

Aplacental viviparity: Live-bearing in which the young do not have a yolk-sac placenta. Found in all groups of live-bearing sharks.

Aplesodic fin: A pectoral, pelvic, dorsal, or anal fin in which the fin radial cartilages do not extend into the distal fin web and between the supporting ceratotrichia of the fin web. Modern sharks always have aplesodic caudal fins, in which the haemal arches of the caudal vertebrae do not support the ventral caudal lobe.

Apopyle: The anterior opening of the clasper, on the anteromesial surface of the clasper and close to the vent. The apopyle receives sperm from the cloaca and fluid from the siphons, which enter the clasper groove and are discharged through the hypopyle. Apopyle is also used for clasper skeletons for the anterior opening of the tubular shafts formed by enlarged marginal and axial cartilages.

Axial cartilage: In the clasper skeleton, the elongated ventral rod or plate-shaped cartilage that forms the main support of the clasper. Also termed **appendix-stem**.

Barbels: Long conical paired dermal lobes on the snouts of sharks, that may serve to locate prey. Sawsharks have barbels on the underside of the snout in front of the nostrils as in sturgeon, but most barbelled sharks have them associated with the nostrils, either as an extension of the anterior nasal flaps or as separate structures medial to the nasal apertures.

Basal: In oral teeth, a proximal direction towards the crown foot and roots.

Basal cartilages or **basals:** In precaudal fins the large cartilages of the fin bases, immediately distal to the pectoral and pelvic fin girdles or the vertebral column (dorsal and anal fins), on which the radials articulate distally. The paired pectoral fins of living sharks primitively have a tribasal pectoral fin, with a propterygium, mesopterygium, and metapterygium as basals, although these may be fused; in batoids, additional neopterygial basals may be added between the mesopterygium and metapterygium and the propterygium is variably expanded anterior with a propterygial basal and axis. The pelvic fins have a basipterygium that supports the pelvic radials and, in males, the claspers. The caudal fin has no basals, but these are functionally replaced by expanded neural and haemal arches of the vertebral column.

Basal communicating canals: See **subnasal fenestrae.**

Basal groove: In oral teeth, a deep groove proximal to the basal ledge on the labial surface of the crown neck and apical root margin.

Basal ledge: In oral teeth, a shelf-like projection on the labial surface of the crown foot.

Basal plate: The floor of the cranial cavity of the neurocranium, a ventral, medial plate extending from the ethmoid region between the orbits and otic capsules and below the cranial cavity to the occipital condyles, occipital centrum and foramen magnum.

Basals or **basalia:** In a vertebral centrum, the diagonal spaces below the attachment surfaces of the basidorsal cartilages, above the basiventral cartilages, and between the two halves of the double cone. Basalia may be filled with uncalcified cartilage, may have diagonal calcifications penetrating the uncalcified cartilage, or may have calcified annuli or solid calcified cartilage that are continuous with calcification of the intermedialia. See diagonal calcifications and intermedialia.

Base: In precaudal fins, the proximal part of the fin between the origin and insertion, extending distally, and supported by the cartilaginous fin skeleton. In the caudal fin, that thickened longitudinal part of the fin enclosing the vertebral column and between the epaxial and hypaxial lobes or webs of the fin. In oral teeth, the proximal root and crown foot, in apposition to the distal cusp. In denticles, the proximal anchoring structures, often with four or more lobes, holding the denticles in the skin.

Basidorsal cartilages: A pair of wedge-shaped arched, thin cartilages articulating with the dorsolateral surfaces of a vertebral centrum and forming a continuous neural arch with the interdorsal cartilages to protect the spinal cord.

Basipterygium: The large elongate longitudinal cartilage at the fin base of the pelvic fin, attached to the posterolateral ends of the pelvic girdle or puboischiadic bar. The basipterygium has pelvic radials attached along its distal edge and has the clasper skeleton attached posteriorly in males.

Basiventral cartilages: A pair of rounded or wedge-shaped cartilages on the ventrolateral surfaces of a vertebral centrum that form the bases for attachment of ribs in monospondylous precaudal vertebrae. In diplospondylous precaudal and caudal vertebrae the basiventrals form haemal arches along with the interventral cartilages for protecting the caudal artery and vein.

Batoid: A ray or flat or winged shark, a neoselachian of the superorder Squalomorphii, order Rajiformes: a sawfish, sharkray, wedgefish, guitarfish, thornray, panray, electric ray, skate, stingray, butterfly ray, eagle ray, cownose ray, devil ray or manta. Rays are closely allied to the sawsharks (Pristiophoriformes) and angel sharks (Squatiniformes), but differ from them in having the pectoral fins fused to the sides of the head over the gill openings, which are ventral rather than laterally or ventrolaterally placed.

Beta cartilage: In the clasper skeleton, a single, dorsolateral flattened, wedge-shaped or cylindrical cartilage connecting the pelvic basipterygium and axial cartilage and reinforcing the intermediate segments, possibly derived from a pelvic radial.

Blade: In oral teeth, an arcuate, convex-edged section of the cutting edge of the crown foot, without cusplets.

Body ridges: Elongated longitudinal dermal ridges on the sides of the trunk and precaudal tail in certain carpet sharks (Orectolobiformes), in the whale, zebra and some bamboo sharks.

Body: Can refer to an entire shark, sometimes restricted to the trunk and precaudal tail.

Branchial arches: The paired visceral arches behind the hyoid arch and just in front of the scapulocoracoid that support the gills. In elasmobranchs the five to seven branchial arches primitively consist of a pair of dorsomedial and wedge-shaped cartilages, the **pharyngobranchials,** closely situated against the roof of the pharynx, a pair of dorsolateral and more cylindrical **epibranchials** that are connected dorsomedially to the pharyngobranchials, a pair of ventrolateral cylindrical **ceratobranchials** that are connected ventrolaterally to the epibranchials, a pair of ventromedial **hypobranchials** that are connected ventrolaterally to the ceratobranchials, and unpaired ventromedial **basibranchials** that are connected ventrolaterally to the hypobranchials. The hypobranchials and basibranchials along with the expanded ventral ends of the ceratobranchials form the **basibranchial skeleton** of the floor of the branchial pharynx. The branchial skeleton is variably modified in elasmobranchs, with basibranchials and sometimes hypobranchials often lost, the last two pharyngobranchials and the last epibranchial often fused together, and the last basibranchial often expanded into a long, broad **copula** with which the anterior hypobranchials and posterior ceratobranchials articulate.

Calcified cartilage: Shark skeletons are formed of hyaline cartilage or gristle, but this is often reinforced with layers of calcified cartilage, cartilage impregnated with a mineral, hydroxyapatite, similar to that of bone but organized differently, in a hard, tile-like pavement of tiny **tesserae**, or more compactly as in the calcified structures of vertebral centra.

Calcified double cones: In vertebrae, the primary calcifications of the notochordal sheath, in lateral view resembling two hollow, horizontal cones with their apices merged, or an hourglass.

Cannibal viviparity: See **uterine cannibalism**.

Carcharhinoid: A ground shark, a member of the order Carcharhiniformes, and including the catsharks, false catsharks, finbacked catsharks, barbeled houndsharks, houndsharks, weasel sharks, requiem sharks and hammerheads.

Carina: On the crowns of oral teeth, a low blunt mesodistal ridge replacing the cusp and cutting edge, in sharks that eat hard-shelled invertebrate prey.

Carotid foramen: A single foramen or one of a pair of foramina that penetrate the basal plate usually near its midlength and allow passage of the internal carotid arteries into the cranial cavity. In some advanced elasmobranchs the carotid foramina shift through the stapedial foramina and onto the medial wall of the orbit.

Cartilaginous fishes: Members of the class Chondrichthyes.

Caudal crest: A prominent saw-like row of enlarged pointed denticles along the dorsal caudal margin and sometimes along the ventral caudal margin of the caudal fin. Found in certain sharks including hexanchoids and some carcharhinoids.

Caudal fin: The fin on the end of the tail in shark-like fishes, lost in some batoids.

Caudal keels: A dermal keel on each side of the caudal peduncle that may extend onto the base of the caudal fin, and may, in a few sharks, extend forward as a body keel to the side of the trunk.

Caudal peduncle: That part of the precaudal tail extending from the insertions of the dorsal and anal fins to the front of the caudal fin.

Central foramen: In oral teeth, a nutrient foramen on the midline of the lingual surface of the root, in the transverse groove.

Centrum (plural, Centra): A spool-shaped, partially or usually fully calcified structure that forms as a segmental constriction in the notochordal sheath of neoselachians, and which as an articulated string forms the principal structural units of the vertebral column. Centra are primarily formed by the calcified double cones in the notochordal sheath, which may be their only calcification, but additional secondary calcification may occur in the centrum between the outer surfaces of the calcified double cones, including calcified intermedialia, radii, annuli, and diagonal calcifications.

Ceratotrichia: Slender soft or stiff filaments of an elastic protein, superficially resembling keratin or horn, from the Greek *keratos*, horn, and *trichos*, hair. Ceratotrichia run in parallel and radial to the fin base and support the fin webs. The prime ingredient of shark-fin soup.

Chimaera: A member of the order Chimaeriformes, subclass Holocephali, see also **Chimaeroid**, **Holocephali**.

Chimaeroid: A chimaera, ratfish, silver shark, ghost shark, spookfish or elephant fish, a member of the order Chimaeriformes.

Chondrichthyan: Referring to the class Chondrichthyes.

Chondrichthyes: The class Chondrichthyes, from Greek *chondros*, cartilage, and *ichthos*, fish, a major taxonomic group of aquatic, gill-breathing, jawed, finned vertebrates with primarily cartilaginous skeletons, 1 to 7 external gill openings, oral teeth in transverse rows on their jaws, and mostly small, tooth-like scales or dermal denticles. Chondrichthyes include the living elasmobranchs and holocephalans and their numerous fossil relatives, and also can be termed shark-like fishes or simply sharks.

Chondrocranium: See **neurocranium**.

Circumnarial fold: A raised semicircular, lateral flap of skin around the incurrent aperture of a nostril, in heterodontoids, orectoloboids, and a few batoids, defined by a circumnarial groove.

Circumnarial groove: A shallow groove defining the lateral bases of the circumnarial folds.

Clasper claws: In parascylliid orectoloboids, a longitudinal row of large anterolaterally directed claw-like denticles on the dorsolateral surface of the clasper glans, supported by the terminal ventral.

Clasper dactyl: In parascylliid orectoloboids, a large finger-like process on the medial face of the clasper, supported by the dorsal terminal and having a **mesospur**, an analogue to the lateral spur or spine of the terminal 3 cartilage of other orectoloboids and other sharks.

Clasper gaff or **hook:** In the external clasper glans, a posterior hook-like structure, like a clasper spur but formed from the dorsal terminal cartilage, found in squaloids of the family Squalidae.

Clasper glans: The distal and dorsal part of the external clasper from the hypopyle to its tip, and including various movable terminal structures; also, the same area of the clasper skeleton.

Clasper groove: The longitudinal groove through the clasper, surrounded by the axial and marginal cartilages, and connecting the apopyle and hypopyle.

Clasper hooks: In the clasper glans of some carcharhinoid sharks, small claw-like dermal denticles arranged in a row along the ventral surface of the free edge of the exorhipidion.

Clasper sacs: Dermal sacs with longitudinally ribbed walls on the ventral and medial surfaces of the claspers of hexanchoids.

Clasper shaft: That part of the clasper skeleton from its origin on the pelvic fin basipterygium to the hypopyle; also, that part of the external clasper from its base to the hypopyle.

Clasper spine: In the external clasper, a projection of the terminal 3 cartilage on the lateral surface of the clasper glans, which forms a short to long, acutely pointed, spine that is covered with shiny hard tissue, possibly enameloid, dentine or both. In some squaloids other terminal cartilages may have spines.

Clasper spur: In the external clasper, a projection of the terminal 3 cartilage on the lateral surface of the clasper glans, which may be pointed but is not covered with shiny hard tissue.

Clasper tip: The posterior end of a clasper.

Claspers: The paired copulatory organs present on the pelvic fins of male cartilaginous fishes, for internal fertilization of eggs, also termed **mixopterygia**.

Classification: The ordering of organisms into groups on the basis of their relationships, which may be by similarity or common ancestry.

Cloaca: The common chamber at the rear of the body cavity of elasmobranchs through which body wastes and reproductive products including sperm, eggs, and young pass, to be expelled to the outside through a common opening or **vent**.

Cover rhipidion: On the external clasper glans, an elongated, longitudinal blade or flap on its dorsomedial external edge, often supported by an accessory dorsal marginal cartilage.

Cranial cavity: The central cavity of the neurocranium, containing the brain, pituitary gland, and roots of the cranial nerves. It extends posteriorly between the orbits and otic capsules to the foramen magnum.

Cranial roof: The anterior roof of the cranial cavity of the neurocranium, a dorsomedial, arched or flattened plate extending from the anterior fontanelle and between the orbits to the parietal fossa of the otic capsule. Sometimes perforated by a frontal or parietal foramen or fenestra, which may be continuous with the anterior fontanelle and can occupy most of the cranial roof.

Craniomandibular muscles: Paired head muscles in heterodontoid sharks that originate from long tendons on the medial walls of the orbits that extend below and transverse to the levator palatoquadrati and spiracular constrictor muscles and behind the spiracles to insert on the posterodorsolateral face of the Meckel's cartilages. They are found in no other sharks and may serve to retract or elevate the jaws.

Crown: The distal part of the oral tooth, almost entirely covered with shiny enameloid except for the neck. In denticles, a flat dorsal plate-like or thorn-like structure, elevated above the denticle base on a stalk or pedicle or confluent with the base.

Crown foot: The expanded, proximal, basal part of the crown, often bearing cusplets or blades.

Cusp: A usually pointed large distal projection of the crown. A **primary cusp** is situated on the midline of the crown foot. **Multicuspid** refers to oral teeth or denticles with more than one cusp. In lateral trunk denticles, the posterior ends of the crown may have **medial** and **lateral cusps**, sharp or blunt projections associated with the medial and lateral ridges.

Cusplet: As with a cusp, but a small projection in association with a cusp, and usually mesial and distal but not medial on the crown foot.

Cutting edge: In oral teeth, the compressed sharp longitudinal ridge on the mesodistal edges of the crown.

Dentine: The primary material of shark oral teeth, a hard tissue with numerous vascular and nonvascular canals.

Dermal denticle or **placoid scale:** A small tooth-like scale found in cartilaginous fishes, covered with enameloid, with a core and base of dentine and usually small and often close-set to one another and covering the body. A few nonbatoid sharks, many batoids, and chimaeroids generally have them enlarged and sparse or reduced in numbers.

Dermal lobes: In wobbegongs, family Orectolobidae, narrow or broad-based, simple or branched projections of skin along the horizontal head rim and on the chin.

Diagonal calcifications: In a vertebral centrum in cross-section, plate-like (**diagonal calcified lamellae**) or knob-like (**diagonal calcified lobes**) structures of calcified cartilage that partially fills the uncalcified basalia. These have a radial orientation from the centre of the centrum.

Diphycercal: A caudal fin with the vertebral axis running horizontally into the fin base, which is not elevated.

Diplospondylous vertebrae: Vertebrae of the tail with two centra and two basidorsal and basiventral elements per segment, and mostly with a haemal arch formed by the basiventral and interventral elements. These include diplospondylous precaudal vertebrae between the monospondylous vertebrae and the base of the caudal fin, and diplospondylous caudal vertebrae in the caudal fin.

Distal: In any direction, at the far end of a structure. In oral teeth, used in a special sense for structures on the teeth towards the posterolateral mouth corners or rictuses. See **apical** and **basal**.

Dorsal: Upwards, in the vertical direction of the back. See **ventral**.

Dorsal fin: A fin located on the trunk or precaudal tail or both, and between the head and caudal fin. Most sharks have two dorsal fins, some batoids one or none.

Dorsal fin spine: A small to large enameloid-covered, dentine-cored spine located on the anterior margins of one or both of the dorsal fins, found on bullhead sharks (Heterodontiformes), many dogfish sharks, fossil (but not living) batoids, chimaeroids, but lost entirely or buried in the fin bases of other shark-like fishes.

Dorsal lobe: In the caudal fin, the entire fin including its base, epaxial and hypaxial webs but excepting the ventral lobe.

Dorsal margin: In the caudal fin, the margin from the upper origin to its posterior tip. Usually continuous, but in angel sharks (Squatiniformes) with their hypocercal, superficially inverted caudal fins, it is subdivided. See **squatinoid caudal fin**.

Dorsal marginal: In the clasper skeleton, a flat semicylindrical cartilage that is partially fused to the medial edge of the axial cartilage, and forms the medial wall of the clasper groove.

Dorsal terminal: On the skeleton of the clasper glans, an often triangular, elongated, curved, plate-like cartilage that articulates or is attached to the medial or dorsomedial edge of the end-style and anteriorly to the dorsal marginal.

Dorsal terminal 2: A flat elongated cartilage with its mesial edge attached to the floor of the glans, and supporting the rhipidion.

Ectethmoid chambers: On the neurocranium, cavities in the nasal capsule that drain the nasal sinuses through the orbitonasal canals into the orbital sinuses.

Ectethmoid processes: On the neurocranium of hexanchoid and some squaloid sharks, posteroventrolateral angular or lobular projections of the nasal capsules and the preorbital walls.

Egg case: A stiff-walled elongate-oval, rounded rectangular, conical, or dart-shaped capsule that surrounds the eggs of oviparous sharks, and is deposited by the female shark on the substrate. It is analogous to the shell of a bird's egg and is made of protein, which is a type of collagen that superficially resembles horn or keratin. Egg cases often have pairs of tendrils or horn-like structures on their ends, or flat flanges on their sides or spiral flanges around their lengths, which anchor the cases to the bottom. As the egg travels from the ovaries into the oviducts and through the nidamental glands, the egg case is secreted around it and the egg is fertilized. Live-bearing sharks may retain egg cases, and these vary from being rigid and similar to those of oviparous sharks to soft, bag-like, degenerate and membranous. Soft egg cases may disintegrate during the birth cycle.

Elasmobranch: Referring to the subclass Elasmobranchii.

Elasmobranchii: The subclass Elasmobranchii, (from Greek *elasmos*, plate, and *branchos*, gills, in allusion to their plate-like gill septa), the shark-like fishes other than the Holocephali or chimaeras, and including the living nonbatoid sharks, batoids, and a host of fossil species. They differ from holocephalans in having 5 to 7 pairs of gill openings open to the exterior and not covered by a soft gill cover, oral teeth separate and not formed as tooth plates, a fixed first dorsal fin with or without a fin spine, and a short spined or spineless second dorsal.

Embryo: An earlier development stage of the young of a live-bearing shark, ranging from nearly microscopic to moderate-sized but not like a miniature adult. See **foetus**.

Enameloid: The shiny hard external coating of the crowns of shark oral teeth, superficially similar to enamel in land vertebrates.

End-style: In the clasper skeleton, the posterior end of the axial cartilage, between the dorsal and ventral terminal cartilages.

Endemic: A species or higher taxonomic group of organisms that is only found in a given area. It can include national endemics found in a river system or along part or all of the coast of a given country, but also regional endemics, found off or in adjacent countries with similar habitat, but not elsewhere.

Epaxial lobe or **web:** In the caudal fin, that part of the caudal fin between the base and dorsal margin, supported by ceratotrichia.

Epaxial web: The entire fin web above the vertebral column and caudal base.

Epiphysial foramen or **notch:** On the neurocranium, a foramen or notch in the cranial roof at the dorsomedial edge of the anterior fontanelle, that houses the pineal body.

Ethmoid region: That anteriormost sector of the neurocranium including the nasal capsules, internasal plate between them, and the rostrum.

Ethmonuchal muscles: In the orectoloboid family Parascylliidae, paired head muscles that originate on the dorsal myomeres of the nape, and insert via long tendons on the nasal capsules. These are possibly for elevating the snout. Not found in any other sharks, though analogous muscles exist in batoids.

Euselachian: Referring to the Euselachii.

Euselachii: The cohort Euselachii (Greek *Eu*, true, good or original, and *selachos*, shark or cartilaginous fish), the spined or 'phalacanthous' sharks, including the modern sharks or Neoselachii, and fossil shark groups including the hybodonts, the ctenacanths, and the xenacanths, all primitively with anal fins and having two dorsal fins with fin spines.

Excurrent apertures: The posterior and ventrally facing openings of the nostrils, which direct water out of the nasal cavities and which are often partially covered by the anterior nasal flaps. These are usually medial on the nostrils and posteromedial to the incurrent apertures, but may be posterior to the incurrent apertures only.

Exorhipidion: In claspers, a longitudinally elongated, external blade or flap with its base attached to the dorsolateral edge of the clasper glans, and with its free edge directed medially. It is supported by the **ventral terminal 2 cartilage**.

Eye notch: A sharp anterior or posterior indentation in the eyelid, where present cleanly dividing the upper and lower eyelids.

Filter screens: In the whale shark (Rhincodontidae) and devil rays (Mobulidae), transverse bars with lateral dermal lobes on the internal gill openings that form devices for screening out plankton.

Fin skeletons: In unpaired precaudal fins, the basal plates and radials; in the caudal fin, the vertebral column including expanded neural and haemal arches; and in the paired fins, the fin girdles, basals, and radials.

Fin web: The usually thin, compressed part of the fin, distal to the base, that is supported by ceratotrichia alone (in aplesodic fins) or by ceratotrichia surrounding expanded fin radials or by radials only (plesodic fin).

First dorsal constrictor muscles: Paired head muscles that are confluent and functionally part of the levator palatoquadrati muscles in most nonbatoid sharks, except in orectoloboids where they are discrete muscles with separate origins and insertions similar to but more lateral than the levators.

First dorsal fin: The anteriormost dorsal fin of two, ranging in position from over the pectoral fin bases to far posterior on the precaudal tail.

Foetus: A later development stage of the unborn young of a live-bearing shark, that essentially resembles a small adult. **Term foetuses** are ready to be born, and generally have oral teeth and denticles erupting, have a colour pattern (often more striking than adults), and, in ovoviviparous sharks, have their yolk-sacs reabsorbed.

Foramen magnum: On the neurocranium, the 'great hole' or posteromedial aperture through the occiput into the cranial cavity, above the occipital centrum and medial and usually dorsal to the occipital condyles. The spinal cord passes from the brain through the foramen magnum into the neural canal of the vertebral column.

Free rear tips: The pectoral, pelvic, dorsal, and anal fins all have a movable rear corner or flap, the free rear tip, that is separated from the trunk or tail by a notch and an inner margin. In some sharks the rear tips of some fins are very elongated.

Frontal and **parietal fenestrae:** On the neurocranium, medial apertures in the cranial roof between the anterior fontanelle and the parietal fossa, the frontal fenestra being closer to the anterior fontanelle and the parietal fenestra to the parietal fossa. Sometimes the two merge and become a **frontoparietal fenestra**, while in many batoids and in some orectoloboid sharks there is a merging of the anterior fontanelle with the frontoparietal fenestra so that it extends nearly to the parietal fossa. All of these fenestrae are closed by tough membranes.

Functional series: A series of oral teeth that are in functional position on the jaw.

Galeomorph: Referring to the Galeomorphii.

Galeomorphii: The neoselachian superorder Galeomorphii, including the heterodontoid, lamnoid, orectoloboid, and carcharhinoid sharks.

Gill openings or **slits:** In elasmobranchs, the paired rows of five to seven transverse openings on the sides or underside of the head for the discharge of water through the gills. Chimaeras have their four gill openings hidden by a soft gill cover and discharge water through a single external gill opening.

Gill-raker denticles: In the basking shark (Cetorhinidae), elongated denticles with hair-like cusps arranged in rows on the internal gill openings, which filter out planktonic organisms.

Gill-raker papillae: Sparse to dense dermal papillae on the gill arches of some sharks that serve as filters to collect small food organisms.

Girdle: A bar of cartilage buried in the body wall that supports the basals of the paired fins: the pectoral girdle (scapulocoracoid) and pelvic girdle (puboischiadic bar).

Haemal arch: The arch ventral to the notochord or vertebral centra on tail vertebrae that is formed by the basiventrals and interventrals and which houses the caudal artery and caudal vein in a **haemal canal**.

Haemal spines: On the haemal arches of the diplospondylous precaudal and caudal vertebrae, elongated ventral surfaces forming vertical plates, particularly well-developed on the caudal fin.

Head: That part of a cartilaginous fish from its snout tip to the last or (in chimaeras) only gill slits.

Heterocercal: A caudal fin with the vertebral axis slanted dorsally into the fin base, which is also dorsally elevated.

Heterodontoid: A bullhead shark, horn shark, or Port Jackson shark, a member of the order Heterodontiformes, family Heterodontidae.

Heterodonty: In oral teeth, structural differences between teeth in various positions on the jaws, between teeth in the same position during different life stages, or between teeth in the same positions in the two sexes.

Hexanchoid: A cowshark or frilled shark, members of the order Hexanchiformes, and including the sixgill sharks, sevengill sharks, and frilled sharks.

Holocephalan: Referring to the Holocephali.

Holocephali: The subclass Holocephali (from Greek *holos*, entire, and *kephalos*, head), the living chimaeras and their numerous fossil relatives, a major subdivision of the class Chondrichthyes. The name is in reference to the fusion of the upper jaws or palatoquadrates to the skull in all living species and in many but not all fossils. The living holocephalans include three families in the order Chimaeriformes. The living species differ from elasmobranchs in having four pairs of gill openings covered by a soft gill cover and with a single pair of external gill openings, oral teeth fused and reduced to three pairs of ever-growing tooth plates, an erectile first dorsal fin with a spine and a long, low spineless second dorsal.

Holotype: Either the only specimen used and mentioned in an original description of a species, with or without a designation of such, or one of two or more specimens used and mentioned in an original description of a species and designated as such. This becomes the 'name-bearer' of the species, and is used to validate the species or scientific name by anchoring it to a single specimen.

Homodonty: In oral teeth, structural similarity between teeth in various positions on the jaws, between teeth in the same position during different life stages, or between teeth in the same positions in the two sexes.

Hyoid arch: The visceral arch that supports the tongue and, in elasmobranchs, the rear of the upper jaws. The hyoid arch is between the mandibular arch and the first branchial arch, and has the spiracular pocket between it and the mandibular arch. The hyoid arch in elasmobranchs includes a medial **basihyoid** in the floor of the mouth and inside the tongue, a pair of elongated **ceratohyals** articulating with the basihyoid and the hyomandibulae, and a pair of **hyomandibulae** articulating with the ceratohyals and the hyomandibular facets of the neurocranium. Chimaeroids have a nonsuspensory hyoid arch similar to the gill arches, with a pair of **epihyals** and **pharyngohyals** equivalent to the hyomandibulae. Batoids have the ceratohyals reduced and separated from the hyomandibulars or absent, and functionally replaced by paired dorsal and ventral **pseudohyoids**.

Hyomandibular facet: On the neurocranium of elasmobranchs, a joint surface, socket or cotyle that is usually on the ventrolateral surfaces of each otic capsule but may be extended posteriorly or arched dorsally. The heads of the hyomandibulae articulate with these facets. Chimaeras lack hyomandibular facets and differentiated hyomandibulae.

Hyomandibular nerve foramina: Foramina for the roots of the hyomandibular nerves, behind the orbital fissures. These foramina are confluent with the orbital fissure in many sharks.

Hypaxial web: The entire fin web below the vertebral column (vertebral axis) and the caudal base.

Hypercalcified structures: Parts of the skeleton that have developed extremely dense calcified cartilage, primarily during growth and maturation, which sometimes swell to knobs that distort and engulf existing cartilaginous structures. The rostrum of the salmon shark (***Lamna ditropis***) is a particularly impressive hypercalcified structure.

Hypocercal: A caudal fin with the vertebral axis slanted ventrally into the fin base, which is also ventrally depressed. Found only in angel sharks (Squatiniformes) among living sharks.

Hypopyle: On the external clasper and clasper skeleton, the posterior opening of the clasper groove onto the clasper glans.

Incurrent apertures: The anterior and ventrally facing openings of the nostrils, which direct water into the nasal cavities. These are usually lateral on the nostrils and anterolateral to the excurrent apertures, but may be anterior to the excurrent apertures only.

Independent dentition: Teeth along a mesodistal series in which the roots do not overlap and are separated by a space. See **overlapping dentition**.

Inner margin: In precaudal fins including the pectoral, pelvic, dorsal and anal fins, the margin from the fin insertion to the rear tip.

Insertion: The posterior or rear end of the fin base in precaudal fins. The caudal fin lacks insertions except with many batoids and some chimaeroids that have a caudal filament that extends posterior to the fin. See **origin**.

Interdorsal cartilages: A pair of wedge-shaped arched thin cartilages fitting between the basidorsal cartilages of each vertebra to complete the neural arch.

Interdorsal ridge: A ridge of skin on the midback of sharks, in a line between the first and second dorsal fins; particularly important in identifying grey sharks (genus ***Carcharhinus***, family Carcharhinidae).

Intermedialia: In a vertebral centrum, dorsal, ventral and lateral spaces between the attachment surfaces of the basidorsal and basiventral cartilages and between the two halves of the double cone. These can be filled with uncalcified cartilage, with solid or hollow wedges of calcified cartilage, or with plate-like, branched calcified radii within uncalcified cartilage. See **basalia**.

Intermediate segments: In the clasper skeleton, one or more short cylindrical cartilages connecting the pelvic basipterygium to the axial cartilage of the clasper. Also termed **stem-joints**.

Intermediate teeth: Small oral teeth between the laterals and anteriors of the upper jaw, found in most lamnoids.

Internasal plate or septum: On the neurocranium, a plate or partition between the two nasal capsules. It ranges from a vertical plate to a broad horizontal plate.

Interventral cartilages: A pair of rounded or wedge-shaped cartilages fitting between the basiventral cartilages of each vertebra, that in diplospondylous precaudal and caudal vertebrae form the haemal arches with the basiventral cartilages.

Intestinal valve: A dermal flap inside the intestine, protruding into its cavity or lumen, and of various forms in different cartilaginous fishes. Often formed like a corkscrew or augur. See **spiral, ring** and **scroll valves**.

Jaws: See **mandibular arch**.

Labial cartilages: Paired cartilages that are internal and support the labial folds at the lateral angles of the mouth. Living neoselachians typically have two pairs of upper labial cartilages, the **anterodorsal** and **posterodorsal** labial cartilages, and one pair of **ventral labial cartilages**, but these are variably reduced and sometimes absent in many sharks. Chimaeras have more elaborate labial cartilages than living elasmobranchs.

Labial flange: On tooth crowns of many squaloids and some orectoloboids, a narrow, vertically elongated labial basal ledge.

Labial folds: Lobes of skin at the lateral angles of the mouth, usually with labial cartilages inside them, separated from the sides of the jaws by pockets of skin (labial grooves or furrows).

Labial furrows or **labial grooves:** Grooves around the mouth angles on the outer surface of the jaws of many cartilaginous fishes, isolating the labial folds. Primitively there is a distinct **upper labial furrow** above the mouth corner and a **lower labial furrow** below it.

Labial: In oral teeth, the outer face of the tooth that is directed outside the mouth and towards the lips. See **lingual**.

Lamnoid: A mackerel shark, a member of the order Lamniformes, and including the sand tiger sharks, goblin sharks, crocodile sharks, megamouth shark, thresher sharks, basking shark, and the makos, porbeagle, salmon shark and white shark.

Lateral clasper fold: In mackerel sharks (family Lamnidae), a unique longitudinal flap of skin along the lateral edge of the external clasper shaft.

Lateral commissures: On the neurocranium, tube-like or ring-like enclosed passages for the lateral head veins, which drain the orbital sinuses, through the postorbital walls of the orbits and below the sphenopterotic ridges and above the hyomandibular facets in neoselachians. The lateral commissures are reduced or absent in many living neoselachians.

Lateral or **laterad:** Outwards, in the transverse direction towards the periphery of the body. See **medial**.

Lateral orolabial grooves: Shallow longitudinal grooves on the lower jaw that connect the edge of the lip on each side with the medial ends of the lower labial furrows. Found in more advanced orectoloboids.

Lateral teeth: Large broad-rooted, compressed, high crowned oral teeth on the sides of the jaws between the anteriors and posteriors.

Lateral trunk denticle: A dermal denticle from the dorsolateral surface of the back below the first dorsal fin base.

Lectotype: One of two or more specimens that were syntypes in an original description, designated as a lectotype by a subsequent writer. It then becomes equivalent to a holotype, and anchors the name of the species to a specimen unless invalidated by a ruling of the International Commission on Zoological Nomenclature or a previous designation of a lectotype.

Levator palatoquadrati muscles: Paired head muscles that primitively originate on the underside of the postorbital processes and sphenopterotic ridges, extend vertically, and insert on the posteromedial surfaces of the quadrate processes of the palatoquadrates. In advanced carcharhinoids the origins of the levator palatoquadrati muscles are expanded far forwards and diagonally into the orbits. Primitively these muscles lift or retract the jaws upwards, but in advanced carcharhinoids may help rotate the jaws forwards and downwards in opposition to the levator hyomandibularis muscles, which retract the jaws.

Lingual: In oral teeth, the inner face of the tooth that is directed inside the mouth and towards the tongue. See **labial**.

Live-bearing: A mode of reproduction in which female sharks give birth to young sharks, which are miniatures of the adults. See **viviparity**.

Longitudinal ridges: In lateral trunk denticles, parallel ridges that extend anteroposteriorly on the distal surface of the crown. These may be in the form of a single **medial ridge** (sometimes paired), and paired **lateral ridges**, and may terminate in medial and lateral cusps.

Lower eyelid: The ventral half of the eyelid, separated by a deep pocket (conjunctival fornix) from the eyeball. In some derived batoids the pocket also fuses with the eyeball.

Lower origin: In the caudal fin, the anteroventral beginning of the hypaxial or lower web of the caudal fin, at the posterior end of the anal-caudal or pelvic-caudal space (see measurement illustrations).

Lower postventral margin: In the caudal fin, the lower part of the postventral margin of the hypaxial web, from the ventral tip to the posterior notch.

Mandibular arch: The paired primary jaw cartilages of sharks, including the dorsal palatoquadrates and the ventral Meckel's cartilages.

Mandibulocutaneous muscles: Paired head muscles in squaloid and hexanchoid sharks, that originate on the inside of the skin of the head behind the eyes and near the spiracles, and insert on the dorsoposterolateral face of the quadrate processes of the palatoquadrates.

Meckel's cartilages: The paired lower jaw cartilages, articulating mesially with each other at the midline or symphysis of the lower jaw, and articulating laterally with the distal ends of the palatoquadrates. The Meckel's cartilages are fused together at the symphysis in some shark-like fishes or are articulated to a symphysial cartilage in others.

Medial teeth: Small oral teeth, generally symmetrical and with narrow roots, in one row at the symphysis and often in additional paired rows on either side of the symphysial one.

Medial: Inwards, in the transverse direction towards the middle of the body. See **lateral**.

Mesial: In oral teeth, mesial structures are towards the midlines of the jaws, the symphyses. See **distal**.

Mesopterygium: In the pectoral fin skeleton of living neoselachians, the middle basal cartilage, between the propterygium and metapterygium. The mesopterygium is sometimes fused to the propterygium or metapterygium, or to both.

Mesorhipidion: A knife-like or blade-like structure on the lateral clasper glans of some carcharhinoid sharks, formed from the terminal 3 cartilage, and over and partially lateral to the ventral terminal and mesial to the pseudopera.

Metapterygial axis: In the pectoral fin skeleton of living neoselachians, the posterior extension of the mesopterygium as a flattened, elongated segmented series of cartilages that supports the distal bases and free rear tips of the pectoral fins; the axis has radials along its distal edge continuous with the radials on the metapterygial basal.

Metapterygial basal: In the pectoral fin skeleton of living neoselachians, the anteriormost, expanded cartilage of the metapterygium.

Metapterygial proximal segment: In the hexanchoid pectoral fin skeleton, a short jointed segment on the proximal end of the metapterygial basal, not found in other sharks.

Metapterygium: In the pectoral fin skeleton of living neoselachians, the rearmost basal cartilage, adjacent to the posterior edge of the mesopterygium and with several radials attached to its distal edge. It includes the **metapterygial basal** and the **metapterygial axis**.

Molariform: In oral teeth, referring to a tooth with a broad flat crown with low cusps or none, for crushing hard-shelled invertebrate prey.

Monospondylous precaudal vertebrae: Vertebrae with one centrum and one pair of basidorsals, basiventrals, and ribs per body segment (myotome), and generally extending from the occiput to the end of the body cavity and to over the pelvic girdle. However there is much variation in the position of the monospondylous-diplospondylous transition, which can range well in front or behind the pelvic girdle.

Monospondylous-diplospondylous transition: The position on the vertebral column where monospondylous centra end and diplospondylous centra begin. In lateral view the transition often appears as an abrupt decrease in length of the diplospondylous centrum compared to the last monospondylous centrum, but this can be obscure in various sharks with very numerous, very short centra. Often a centrum of intermediate length appears between a long monospondylous centrum and a short diplospondylous centrum. In a few sharks there is a **stutter zone** of alternating long and short centra that marks the transition. Also, the basidorsals and basiventrals have foramina for the spinal nerves on every other vertebra, rather than on each vertebra as in monospondylous vertebrae. The transition from long to short centra is generally coordinated with the transition of vertebrae with free ribs and no haemal arches to those without ribs and with haemal arches. However, in some sharks the two transitions can be anterior or posterior to each other.

Multiple oviparity: A mode of egg-laying or oviparity in which female sharks retain several pairs of cased eggs in the oviducts, in which embryos grow to advanced developmental stages. When deposited on the bottom (in captivity) the eggs may take less than a month to hatch. Found only in the scyliorhinid genus ***Halaelurus***, with some uncertainty as to whether the eggs are normally retained in the oviducts until hatching. Eggs laid by these sharks may be abnormal, unusual, or an alternate to ovoviviparity. The whale shark (***Rhincodon typus***) may have multiple retention of egg cases; near-term foetuses have been found in their uteri and egg-cases with developing foetuses have been collected on the bottom.

Nasal aperture: On the neurocranium, an aperture in the anteroventral surface or floor of each nasal capsule, through which the nostril directs water into and out of the nasal organ.

Nasal capsules: On the neurocranium, a pair of spherical, oval or trumpet-shaped, thin-walled structures behind the rostrum (when present) and in front of the orbits, cranial roof and basal plate. They serve as containers for the nasal organs or organs of smell, and have passages into the cranial cavity to connect the nasal organs with the brain.

Nasal curtain: Anterior nasal flaps that are expanded medially and posteriorly and have fused with each other. Nasal curtains are found in some carcharhinoid sharks and in many batoids.

Nasal flap: One of a set of dermal flaps associated with the nostrils, and serving to direct water into and out of them, including the anterior, posterior, and mesonarial flaps.

Nasal fontanelle: On the neurocranium, an aperture in the posteroventral surface or floor of each nasal capsule, behind the nasal apertures and closed by a dermal membrane.

Nasoral grooves: Many bottom-dwelling, relatively inactive sharks have nasoral grooves, shallow or deep grooves on the ventral surface of the snout between the excurrent apertures and the mouth. The nasoral grooves are covered by expanded anterior nasal flaps that reach the mouth, and form water channels that allow the respiratory current to pull water by partial pressure into and out of the nostrils and into the mouth. This allows the shark to actively irrigate its nasal cavities while sitting still or when slowly moving. Nasoral grooves occur in heterodontoids, orectoloboids, chimaeroids, some carcharhinoids, and most batoids. Also termed **oronasal grooves**.

Neck: A narrow band of finely porous dull tissue (possibly orthodentine) encircling the proximal end of the crown of a tooth, and apparently covered with dental membrane.

Neoselachian: Referring to the Neoselachii.

Neoselachii: From Greek *neos*, new, and *selachos*, shark. The modern sharks, the subcohort Neoselachii, consisting of the living elasmobranchs and their immediate fossil relatives. See **Euselachii**.

Neotype: A specimen, not part of the original type series for a species, which is designated by a subsequent author, particularly if the holotype or other types have been destroyed, were never designated in the original description, or are presently useless.

Neural arch: In shark vertebrae, a dorsal arch formed by basidorsal and interdorsal cartilages above the centrum and forming a **neural canal** containing the spinal cord.

Neural spines: On the neural arches of shark vertebrae, elevated dorsal plate-like surfaces, particularly well-developed in many squalomorph sharks.

Neurocranium: In sharks, a box-shaped complex cartilaginous structure at the anterior end of the vertebral column, containing the brain, housing and supporting the nasal organs, eyes, ears, and other sense organs, and supporting the visceral arches or splanchnocranium. Also termed **chondrocranium**, **chondroneurocranium**, or **endocranium**.

Nictitating lower eyelid: In the ground sharks (order Carcharhiniformes), a movable lower eyelid that has special posterior eyelid muscles that lift it and, in some species, completely close the eye opening (or palpebral aperture). Often incorrectly termed **nictitating membrane**, a different, nonhomologous structure in terrestrial vertebrates.

Nictitating upper eyelid: In parascylliid orectoloboids, the upper eyelid has anterior eyelid muscles that pull it down and close the eye opening, analogous to the nictitating lower eyelids of carcharhinoids.

Nomenclature: In biology, the application of distinctive names to groups of organisms.

Nostrils: The external openings of the cavities of the nasal organs, or organs of smell.

Notochord: In embryonic sharks (and other chordates) the notochord is a fluid-filled tube below the spinal cord that has a connective-tissue notochordal sheath surrounding it. The notochord forms the primitive developmental base of the chondrichthyan vertebral column. Chimaeroids retain the notochord and its sheath without constriction (although some have ring-like centra in the sheath), but in neoselachians it is constricted by the development of double-cone calcifications of the centra within the sheath into biconical chambers between each centrum. The addition of centra to the notochordal sheath strengthens the vertebral column. Some deepwater squaloid, hexanchoid, and lamnoid sharks have the sheath constriction and calcified double cones variably reduced, sometimes to connective tissue septa only. Some of these taxa with a 'notochordal' vertebral column have been considered primitive but are apparently derived from ancestors with well-calcified, constricted vertebral centra.

Occipital centrum: On the occiput of the neurocranium, the posterior half of a calcified double cone of the vertebral column, imbedded in the basal plate and articulating with the anteriormost centrum of the vertebral column. Also termed **occipital hemicentrum**.

Occiput: The posteriormost sector of the neurocranium, behind and partially between the otic capsules, with its dorsal surface from the parietal fossa rearwards to the foramen magnum, and its posterior surface including the occipital condyles, the occipital centrum, the paired vagus nerve foramina, the paired glossopharyngial nerve foramina, and the rear surface of the hyomandibular facets.

Ocelli or **eyespots:** Large eye-like pigment spots located on the dorsal surface of the pectoral fins or bodies of some sharks including rays, angel sharks, and some bamboo sharks, possibly serving to frighten potential enemies.

Oophagy: From Greek *oön*, egg, and *phagos*, to eat. Egg-eating, a mode of live-bearing reproduction employing uterine cannibalism; early foetuses deplete their yolk-sacks early and subsist by eating nutritive eggs produced by the mother. Known in several lamnoid sharks, the carcharhinoid family Pseudotriakidae, and in the orectoloboid family Ginglymostomatidae (***Nebrius ferrugineus***).

Optic nerve foramen: A large foramen usually in the middle of the orbital wall, passing the optic nerve from the brain to the eye.

Optic pedicel: On the neurocranium, a slender cartilage that projects from the medial orbital wall and articulates with the eyeball; it serves as a pivot point for the eyeball and a spacer between the eyeball and the orbital wall.

Orbital fissures: The main foramina or fenestrae that pass the trigeminal and facial nerves from the brain to the orbits, located on the posteroventral ends of the medial walls of the orbits.

Orbital notches: On the neurocranium, the paired anterior notches in the suborbital shelves that articulate with the orbital processes of the palatoquadrates. In many squalomorph sharks these are enlarged, deepened, socket-like, and posteriorly situated in the orbits, with telescoping of the suborbital shelves, and are lost in batoids.

Orbits: Large, paired cavities on the sides of the neurocranium, behind the nasal capsules, mostly in front of the otic capsules, and separated medially by the cranial cavity. They are bounded anteriorly by the preorbital walls and processes, dorsally by the supraorbital crests, ventrally by the suborbital shelves (reduced or lost in various squalomorphs), and posteriorly by the postorbital processes and walls. The orbits contain the eyeballs and their muscles, venous sinuses, several arteries that connect to the cranial cavity, and most of the cranial nerves.

Orectoloboid: A carpet shark, a member of the order Orectolobiformes, including barbelthroat carpet sharks, blind sharks, wobbegong sharks, bamboo sharks, epaulette sharks, nurse sharks, zebra sharks, and whale sharks.

Origin: The anterior or front end of the fin base in all fins. The caudal fin has **upper** and **lower** origins but no insertion. See **insertion**.

Orthodentine: A primary hard tissue comprising the crown of oral teeth in sharks, with numerous fine mostly parallel nonvascular tubules.

Orthodont: An oral tooth with its crown filled with orthodentine, and with a prominent central pulp cavity.

Osteodentine: A primary hard tissue comprising the roots and sometimes the inside of the crown in the oral tooth, with bone-like large reticulating, thick-walled tubules.

Osteodont: An oral tooth with its crown filled with osteodentine, continuous with the root, and without a pulp cavity.

Otic capsules: On the neurocranium, a pair of complex thick-walled capsules containing the inner ears, and located between the orbits and the occiput, and partially separated medially by the cranial cavity.

Overlapping dentition: Teeth along a mesodistal series in which the roots overlap and are not separated by a space. Two types of overlap patterns occur, **alternate overlap**, in which teeth in a series alternate from more labial to more lingual, and **imbricate overlap**, in which the distal end of each tooth lingually or labially overlaps the mesial end of the succeeding tooth, repeating to the distal ends of the dental band. **Alternate-imbricate dentitions** combine both alternate and imbricate overlap. See **independent dentition**.

Oviparity: A mode of reproduction in which female sharks deposit eggs enclosed in oblong or conical egg-cases on the bottom, which hatch in less than a month to more than a year, producing young sharks which are miniatures of the adults.

Ovoviviparity: Generally equivalent to **yolk-sac viviparity**, live-bearing in which the young are nourished primarily by the yolk in the yolk-sac, which is gradually depleted and the yolk-sac reabsorbed until the young are ready to be born. Sometimes used to cover all forms of **aplacental viviparity**, including **cannibal viviparity**.

Paired fins: The pectoral and pelvic fins.

Palatoquadrates: The paired upper jaw cartilages, articulating mesially with each other at the midline or symphysis of the upper jaw, and articulating laterally with the distal ends of the Meckel's cartilages. The palatoquadrates are fused to the neurocranium in all living holocephalans. The palatoquadrates of neoselachians are divided into cylindrical anteromedial sectors or **palatine processes**, which articulate or are otherwise attached to each other at the symphysis; variably modified conical to flattened articular structures or **orbital processes** on the middle of the palatoquadrates for attachment to the neurocranium at the orbital notches; and often elevated posterodistal **quadrate processes** that articulate with the distal ends of the Meckel's cartilages and are loosely or firmly attached to the distal ends of the hyomandibulae. In a few living neoselachians, and many fossil elasmobranchs, the quadrate processes have **postorbital articulations** with the rear surfaces of the postorbital processes of the neurocranium.

Palpebral aperture: The eye opening, defined by the upper and lower eyelids.

Papillae: Elongated finger-like processes of skin, located around the spiracles of torpedo rays, and in the mouths and on the gill arches of other sharks.

Papillose gill rakers: See **gill raker papillae**.

Paralectotype: One of two or more specimens that were syntypes in an original description, but which became a paralectotype or paralectotypes when a subsequent author designated one of the syntypes as a lectotype. Paralectotypes are equivalent to paratypes.

Paratype: Each specimen of a type series other than the holotype. Specimens other than the holotype automatically become paratypes unless the author designates them as referred specimens that are not part of the type series.

Parietal fossa: On the neurocranium, a shallow or deep depression between the otic capsules and at the rear of the cranial roof, that houses foramina for paired ducts leading to the inner ears and for the spaces around them.

Pectoral fins: A symmetrical pair of fins on each side of the trunk just behind the head and in front of the abdomen. These are present in all cartilaginous fishes and correspond to the forelimbs of a land vertebrate (a tetrapod or four-footed vertebrate).

Pectoral or **shoulder girdle:** See **scapulocoracoid**.

Pedicel: In lateral trunk denticles, a narrow stalk separating the crown from the base.

Pelvic fin: A symmetrical pair of fins on the sides of the body between the abdomen and precaudal tail which correspond to the hindlimbs of land vertebrate (a tetrapod or four-footed vertebrate). Also, **ventral fins**.

Pelvic girdle: See **puboischiadic bar**.

Photophores: Conspicuously pigmented small spots on the bodies of most lantern sharks (family Etmopteridae) and some kitefin sharks (family Dalatiidae). These are tiny round organs that are covered with a conspicuous dark pigment (melanin) and produce light by a low-temperature chemical reaction.

Placenta: See **yolk-sac placenta**.

Placental viviparity: Live-bearing in which the young develop a yolk-sac placenta, which is apparently confined to the carcharhinoid sharks.

Placoid scale: See **dermal denticle**.

Plesodic fin: A pectoral, pelvic, dorsal, or anal fin in which the radial cartilages of the fin skeleton extend far into the distal fin web, often near its edges, and between the supporting ceratotrichia of the fin web. Some fossil sharks also have plesodic caudal fins, in which the expanded haemal arches of the caudal vertebrae extend far into the fin web. In more advanced batoids the radials of the plesodic paired fins become highly branched and segmented, very narrow and slender, and essentially replace the ceratotrichia as supports for the fin webs.

Pores, pigmented: In a few sharks and skates, the pores for the lateral line and ampullae of Lorenzini are conspicuously black-pigmented, and look like little black specks.

Posterior: Rearwards, in the longitudinal direction of the caudal-fin tip or tail filament. Also **caudal**.

Posterior margin: In precaudal fins, the margin from the fin apex to either the free rear tip (in sharks with distinct inner margins) or the fin insertion (for those without inner margins).

Posterior nasal flaps: Low flaps or ridges arising on the posterior edges of the excurrent apertures of the nostrils.

Posterior notch: In the caudal fin, the notch in the postventral margin dividing it into upper and lower parts.

Posterior teeth: Small or sometimes enlarged irregular oral teeth near and at the distal ends of the dental bands, with low crowns and sometimes missing cusps.

Posterior tip: The posteriormost corner or end of the terminal lobe of the caudal fin.

Postocular eyelid muscles: A complex of paired head muscles unique to carcharhinoid sharks that originate around the spiracles and insert on the posterior ends of the upper eyelids and nictitating lower eyelids. Primitively they depress the upper eyelid and elevate the nictitating lower eyelid to close the eye, but in more derived carcharhinoids the eye is closed only by elevation of the nictitating lower eyelid.

Postorbital processes: On the neurocranium, posterolateral projections of the supraorbital crests, below which the postorbital walls originate.

Postorbital walls: On the neurocranium, the posterior boundaries of the orbits, variously reduced vertical plates of cartilage that close the orbits between the postorbital processes and the suborbital shelves, more or less reduced in living neoselachians.

Postventral margin: In the caudal fin, the margin from the ventral tip to the subterminal notch of the caudal fin. See **lower** and **upper** postventral margins.

Preanal ridges: A pair of low, short to long, narrow ridges on the midline of the caudal peduncle extending anteriorly from the anal fin base.

Precaudal fins: All fins in front of the caudal fin.

Precaudal pit: A depression at the upper and sometimes lower origin of the caudal fin where it joins the caudal peduncle.

Precaudal tail: That part of the tail from its base at the vent to the origins of the caudal fin.

Precaudal vertebrae: Vertebrae from the occiput to the dorsal origin of the caudal fin.

Predorsal ridge: A low narrow ridge of skin on the midline of the back anterior to the first dorsal fin base.

Preorbital canals: On the neurocranium, anterior passages for the superficial opthalmic nerves out of the orbits and onto the nasal capsules and rostrum, situated at the anteromesial edges of the supraorbital crests at the rear bases of the preorbital processes; sometimes greatly expanded posteriorly.

Preorbital processes: On the neurocranium, anterolateral projections of the supraorbital crests, below which the preorbital walls originate.

Preorbital walls: On the neurocranium, the anterior boundaries of the orbits, curved vertical plates of cartilage that vary from complete to absent in neoselachians.

Preorbitalis muscles: Paired head muscles that primitively originate on the rear of the nasal capsules or on the preorbital walls, run diagonally rearwards, and insert on the adductor mandibulae at the mouth angles. Orectoloboids and heterodontoids have the preorbitalis vertical, with cross-biased fibres in the latter, and the insertions are along the ventral edge of Meckel’s cartilage. In derived orectoloboids the origins of the preorbitalis are expanded onto the cranial roof and the muscles greatly expanded.

Primitively the preorbitalis may primarily serve to protrude the jaws, but they may primarily serve to increase the power of the bite in orectoloboids and heterodontoids. Also termed **levator labii superioris muscles**.

Preventral margin: In the caudal fin, the margin from the lower origin to the ventral tip of the caudal fin.

Pristiophoroid: A saw shark, order Pristiophoriformes, family Pristiophoridae.

Propterygium: In the pectoral fin skeleton of living neoselachians, the anteriormost basal cartilage, adjacent to the anterior edge of the mesopterygium and with one or more radials attached to its distal end. In batoids with expanded anterior pectoral fin lobes it becomes expanded and segmented into a **propterygial basal** and **propterygial axis**, similar to the metapterygial basal and axis.

Proximal: In any direction, at the near end of a structure.

Pseudopera: On the external clasper glans, a dorsally opening blind pocket along the lateral edge of the clasper, and about opposite the anterior edge of the glans.

Pseudosiphon: On the external clasper glans, a dorsally opening blind pocket along the medial edge of the clasper, and about opposite the cover rhipidion.

Pterotic horn or **process:** On the neurocranium, elongated posterior projections of the sphenopterotic ridges of the otic capsules.

Puboischiadic bar: A transverse flattened or cylindrical plate in the posterior body wall opposite the anterior ends of the pelvic fins, in front of the vent and at the posterior end of the body cavity, that supports a few anterior pelvic radials and a basal cartilage, the basipterygium. The **pelvic girdle.**

Radial cartilages or **radials:** The small, segmented, more distal cartilages of the precaudal fins, attached proximally to the distal edges of the basal cartilages. In the pectoral fin skeleton of living neoselachians, the radials mostly have three segments but range from no segments to 30 or more. The radial segments adjacent to the pectoral basals are the **proximal radials,** the radial segments furthest from the basals are the **distal radials**, and any segments between them are **intermediate radials**.

Radii: In a vertebral centrum in cross-section, branching plates of calcified cartilage in the intermedialia. These have a radial orientation from the centre of the centrum.

Ray: See **batoid**.

Replacement series: A series of oral teeth that are lingual to the functional series, and not in a functional position on the jaw.

Rhipidion: In nonbatoid sharks, a longitudinal, elongated flap attached to the floor of the glans along its base and with its free edge directed laterally. In skates (Rajoidei) rhipidion is used for a soft mass of erectile tissue in the glans, not necessarily homologous to the rhipidion of nonbatoid sharks.

Rhomboidal: In the form of a rhombus or diamond.

Ribs: On the shark vertebral column, short to elongated paired and typically pointed cartilages attached to the basiventral cartilages and extending into the horizontal septum of the segmented trunk musculature or myomeres. Chondrichthyan ribs are therefore dorsal ribs rather than ventral ribs as in bony fishes (which support the body cavity).

Ring valve: A type of spiral intestinal valve in which the valve turns are very numerous and short and resemble a stack of washers.

Root lobe: Sharks often have the roots of their oral teeth divided into separate lobes at their midlengths, which are termed **mesial** and **distal root lobes**.

Root: The proximal part of the oral tooth, made of porous osteodentine and anchoring the tooth in the dental membrane of the jaw.

Rostral keel: In the neurocranium of squaloids, a large vertical plate on the underside of the rostrum and internasal septum, sometimes reduced, and with the cavities of the subnasal fenestrae on either side of the keel.

Rostral node: On the neurocranium, the anterior end of the rostrum of cartilaginous fishes, and the plate formed by the fused anterior ends of the tripodal rostra in many galeomorph sharks.

Rostromandibular muscle: In the orectoloboid family Parascylliidae, paired head muscles that originate on the sides of the adductor mandibulae muscles and insert via long tendons on the medial rostral cartilage. These are possibly for depressing the snout. Not found in any other sharks, though analogous muscles exist in batoids.

Rostronuchal muscles: In the orectoloboid family Parascylliidae, paired head muscles that originate on the dorsal myomeres of the nape, and insert via long tendons on the medial rostral cartilage. These are possibly for elevating the snout. Not found in any other sharks, though analogous muscles exist in batoids.

Rostrum: On the neurocranium, the cartilaginous anteriormost structure which supports the prenasal snout including lateral line canals and masses of ampullae, and is located in front of the nasal capsules and anterior fontanelle. The rostrum is very variable, and in squalomorph sharks is primitively trough or basin-shaped, while it may be primitively rod-shaped or tripodal in galeomorph sharks. It is absent in a few nonbatoid sharks and in many batoids. See **rostrum, tripodal**.

Rostrum, tripodal: The rostrum of the neurocranium in lamnoid and carcharhinoids is primitively tripodal, with a pair of dorsolateral **lateral rostral cartilages** that arise from the posterolaterodorsal surfaces of the nasal capsules or from the preorbital wall, and a **medial rostral cartilage** that arises from the anteromedial surface of the internasal septum. The medial and lateral rostral cartilages extend anteriorly and articulate or fuse at the rostral node. Living orectoloboids have only the medial rostral cartilage although a tripodal rostrum may be present in some fossil orectoloboids, while heterodontoid sharks lack a rostrum as adults but apparently lose it as embryos.

Row: In oral teeth, a single replicating line of teeth, approximately transverse to the longitudinal jaw axis, which includes functional teeth and their replacements, derived from one tooth-producing area on the jaw.

Saw or **saw-snout:** The elongated snout in sawfish and sawsharks, with side and (in sawsharks) ventral teeth formed from enlarged denticles, used to kill, ensnare or dig for prey. Also termed rostral saw.

Scapulocoracoid: The primitively U-shaped cartilage in the body wall just behind the gills and at the anterior end of the pectoral bases, that supports the pectoral fins and articulates with the pectoral basals. The scapulocoracoid consists of a ventral **coracoid bar** connecting its paired **lateral faces** with articular condyles or ridges for the pectoral basals, and a pair of dorsal **scapular processes** dorsal to the lateral faces. The scapular processes sometimes have separate **suprascapulae** above them, but they are sometimes fused with the scapular processes. The coracoid bar has a medial joint or even a separate medial cartilage (sternal cartilage) in a few living sharks, as with many fossil cartilaginous fishes. The **pectoral** or **shoulder girdle**.

Scroll valve: A type of spiral intestinal valve in requiem and hammerhead sharks in which the valve has uncoiled and resembles a rolled-up bib or scroll.

Second dorsal fin: The posteriormost dorsal fin of two in cartilaginous fishes, ranging in position from over the pelvic-fin bases to far posterior on the precaudal tail.

Secondary caudal keels: Low horizontal dermal keels on the ventral base of the caudal fin in mackerel sharks (Lamnidae) and sometimes somniosids.

Secondary lower eyelid: The eyelid below or lateral to the nictitating lower eyelid, separated from it by a subocular groove or pocket, and, in many carcharhinoids with internal nictitating lower eyelids, functionally replacing them as lower eyelids. Some orectoloboids have shallow subocular grooves separating their non-nictitating lower eyelids from weakly developed secondary lower eyelids. They may, however, be able to close their eye openings by retracting the eyeballs.

Semiplesodic fin: In some sharks, a pectoral or dorsal fin with the fin radial cartilages extending partway into the fin web but not to its distal edges, essentially intermediate between plesodic and aplesodic fins.

Series: In oral teeth, a line of teeth along the jaws which is parallel to the jaw axis and includes teeth from all rows present.

Serrations: In oral teeth, minute teeth formed by the cutting edge of the crown that enhance the slicing abilities of the teeth.

Shark: Generally used for cylindrical or flattened cartilaginous fishes with 5 to 7 external gill openings on the sides of their heads, pectoral fins that are not attached to the head above the gill openings, and a large, stout tail with a large caudal fin; that is, all living elasmobranchs except the rays or batoids. Living sharks in this sense are all members of the Neoselachii, the modern sharks and rays. Shark is also used loosely for fossil chondrichthyans that are not neoselachians but have a shark-like form, and even for 'spiny sharks' (acanthodians) and for certain teleosts. Rays are essentially flattened sharks with the pectoral fins attached to their heads and are cladistically nested within the squalomorph sharks, while living chimaeras are the immediate sister group of living neoselachians and are called ghost sharks or silver sharks. Hence shark is used here in an alternate and broader sense to include the rays and chimaeras.

Shoulder: In oral teeth, an arcuate or straight, convex-edged section of the crown foot, without cusplets and similar to a blade but without a cutting edge.

Single oviparity: A mode of egg-laying or oviparity in which female sharks produce encased eggs in pairs, which are not retained in the oviducts and are deposited on the bottom. Embryos in the egg-cases are at an early developmental stage, and take a few months to over a year to hatch. Found in almost all oviparous cartilaginous fishes.

Siphons: A pair of dermal sacs in the ventral abdominal wall of male sharks, connecting posteriorly with the apopyles of the claspers, and extending anteriorly a variable distance from about opposite the pelvic origins to opposite the pectoral bases.

Skull or **cranium:** The skull or head skeleton of sharks includes the **neurocranium** and the **splanchnocranium** or visceral arches. The visceral arches articulate with and are associated with the neurocranium, but, except for the upper jaws of many holocephalans, are not fused to it. Also termed **syncranium**.

Snout: That part of a cartilaginous fish in front of its eyes and mouth, and including the nostrils.

Sphenopterotic ridge: On the neurocranium, a horizontal ridge along the dorsolateral edge of each otic capsule that either ends at the occiput or terminates in an expanded pterotic process.

Spiracle: A small to large opening between the eye and first gill opening of most sharks and rays, representing the modified gill opening between the jaws and hyoid (tongue) arch. This is secondarily lost in chimaeras and some sharks.

Spiral or **conicospiral valve:** An intestinal valve shaped like a corkscrew or augur, with the valve angled anteriorly and medially in the intestine.

Splanchnocranium: That part of the shark skull including the visceral arches. These include the jaws or mandibular arch, the tongue or hyoid arch, and the five to seven gill or branchial arches. Also, **viscerocranium**.

Squalene: A long-chain oily hydrocarbon present in the liver oil of deepwater cartilaginous fishes. It is highly valued for industrial and medicinal use.

Squaloid: A dogfish shark, a member of the order Squaliformes, including bramble sharks, spiny dogfish, gulper sharks, lantern sharks, viper sharks, rough sharks, sleeper sharks, kitefin sharks, and cookiecutter sharks.

Squalomorph: Referring to the Squalomorphii.

Squalomorphii: The neoselachian superorder Squalomorphii, including the hexanchoid, squaloid, squatinoid, pristiophoroid, and batoid sharks.

Squatinoid: An angel shark, order Squatiniformes, family Squatinidae.

Squatinoid caudal fin: Angel sharks (Squatiniformes) are unique among living sharks in having hypocercal caudal fins that resemble inverted caudal fins of ordinary sharks. The dorsal margin is subdivided into a **predorsal** margin from the upper origin to its **dorsal tip** (analogous to the preventral margin and ventral tips in ordinary sharks), a **postdorsal** margin (like the postventral margin) from the dorsal tip to its supraterminal notch (similar to the subterminal notch), and a short **supraterminal margin** and large **ventral terminal margin** (similar to the subterminal and terminal margins) between the supraterminal notch and the ventral tip of the caudal. The ventral margin has a preventral margin forming a ventral lobe with the ventral tip and the ventral terminal margin.

Stapedial foramen or fenestra: On the neurocranium, a foramen through the posteroventromedial surface of each suborbital shelf into the orbit, for the stapedial or orbital arteries. It may be greatly expanded into a stapedial fenestra in sharks with greatly coiled stapedial arteries or lost in sharks with the suborbital shelves greatly reduced or absent.

Stapediocarotid foramen: On the neurocranium of certain sharks, fusion of the stapedial and carotid foramina on either side produces a single pair of stapediocarotid foramina.

Subcaudal keel: In a few dogfish sharks (family Centrophoridae), a single longitudinal dermal keel on the underside of the caudal peduncle.

Subethmoid fossa: On the neurocranium, a deep cavity on the ventral surfaces of the nasal capsules and the internasal plate, into which fit the palatine processes of the upper jaws.

Subnasal fenestrae: On the neurocranium of squaloids, a pair of apertures in the internasal plate between the nasal capsules that connect the cerebral cavity with two ventral fluid-filled cavities between the nasal capsules and the rostral keel. The fenestrae themselves are covered by tough membranes as with the anterior fontanelle. Subnasal fenestrae are present in most squaloids but reduced in a few derived species, and are not found in other sharks. Their function is obscure but may be sensory. Also termed **basal communicating canals**.

Suborbital shelf: On the neurocranium, a horizontal plate arising on the ventral junction of the orbital wall and basal plate on each side which extends from the nasal capsule to the otic capsule; it forms the floor of the orbit. A well-developed suborbital shelf is apparently primitive for shark-like fishes but is variably telescoped, reduced or lost in many squalomorph sharks and a few galeomorphs.

Subterminal margin: In the caudal fin, the margin from the subterminal notch to the ventral beginning of the terminal margin.

Subterminal mouth or **ventral mouth:** Mouth located on the underside of the head, behind the snout. Also termed an **inferior mouth**, in reference to its ventral position but not its function. A **superior mouth** (not found in living cartilaginous fishes) is on the dorsal surface of the head.

Subterminal notch: On the caudal fin of most nonbatoid sharks and at least one batoid, the notch in the lower distal end of the caudal fin, between the postventral and subterminal margins, and defining the anterior end of the terminal lobe.

Superficial ophthalmic nerve foramina: Foramina for the roots of the superficial ophthalmic nerves in the medial wall of the orbits, separate from the orbital fissure. These foramina are confluent with the orbital fissure in many sharks.

Supraorbital crest: On the neurocranium, an arched horizontal plate of cartilage forming the dorsal edge of the orbit on each side; it arises from the medial orbital wall and the cranial roof and extends horizontally from the preorbital process to the postorbital process. It is apparently primitive for shark-like fishes but is variably reduced or absent in some living elasmobranchs.

Supraorbital or **brow ridge:** A dermal ridge above each eye, particularly well-developed in heterodontoids and some orectoloboids.

Symphyseal or **symphysial groove:** A longitudinal groove on the ventral surface of the lower jaw of some orectoloboid sharks, extending posteriorly from the lower symphysis.

Symphysial teeth: Larger oral teeth in one row on either side of the symphysis, distal to medials or alternates where present. Symphysials are broader than medials and usually have asymmetrical roots.

Symphysis: The midline of the upper and lower jaws, where the paired jaw cartilages articulate with each other.

Syntype: Two or more specimens used and mentioned in an original description of a species, where there was no designation of a holotype or a holotype and paratype(s) by the describer of the species.

Systematics: Scientific study of the kinds and diversity of organisms, including relationships between them.

Tail: That part of a cartilaginous fish from the cloacal opening or vent (anus in chimaeroids, which lack a cloaca) to the tip of the caudal fin or caudal filament, and including the anal fin, usually the second dorsal fin when present, and caudal fin.

Taxon, plural **taxa:** A taxonomic group at any level in a classification. Thus the taxon Chondrichthyes is a class with two taxa as subclasses, Elasmobranchii and Holocephali, and the taxon ***Galeorhinus***, a genus, has one taxon as a species, ***G. galeus***.

Taxonomy: Often used as a synonym of systematics or classification, but narrowed by some researchers to the theoretical study of the principles of classification.

Term foetus: See **foetus**.

Terminal 3 cartilage: A wedge-shaped or elongated cartilage articulating with the posterior edge of the ventral marginal cartilage and over the ventral terminal cartilages. It supports a variety of structures, including clasper spines and spurs, the shields of many skates (Rajoidei), and the mesorhipidion of some carcharhinoid sharks.

Terminal lobe: In the caudal fin of most nonbatoid sharks and at least one batoid, the free rear wedge-shaped lobe at the tip of the caudal fin, extending from the subterminal notch to the posterior tip.

Terminal margin: In the caudal fin, the margin from the ventral end of the subterminal margin to the posterior tip.

Terminal mouth: Mouth located at the very front of the animal. Most cartilaginous fishes have subterminal mouths, but some species (viper sharks, wobbegongs, angel sharks, frilled sharks, whale sharks, megamouth sharks, and *Manta*) have it terminal or nearly so.

Thorn: In many batoids, most angel sharks and the bramble shark (***Echinorhinus brucus)***, enlarged, flat conical denticles with a sharp, erect crown and a flattened base (which may grow as the shark grows).

Tongue arch: See **hyoid arch**.

Transverse groove: In oral teeth, a deep groove transverse on the lingual root surface, transecting it into mesial and distal root lobes.

Transverse notch: In oral teeth, a distinct notch in the proximal labial edge of the root at about its midlength.

Transverse ridges: Small narrow ridges on the labial and lingual surfaces of the crown, apicobasally oriented and sometimes extending to the cusp edges.

Tribasal pectoral fin: A pectoral fin skeleton with three basal cartilages, the propterygium, mesopterygium, and metapterygium, primitively found in most euselachians including living neoselachians.

Trilobate lower lip: In advanced orectoloboids, shallow orolabial grooves divide the lower lips into a medial section and a pair of lateral sections.

Tropeic folds: Longitudinal paired ridges on the ventral midline of the abdomen in frilled sharks (Chlamydoselachidae).

Truncate: Blunt, abbreviated.

Trunk: That part of a cartilaginous fish between its head and tail, from the last gill openings to the vent, including the abdomen, back, pectoral and pelvic fins, and often the first dorsal fin.

Umbilical cord: A modified yolk stalk in placental viviparous sharks, carrying nutrients from the placenta to the foetus.

Unpaired fins: The dorsal, anal, and caudal fins.

Upper eyelid: The dorsal half of the eyelid, separated by a deep pocket (conjunctival fornix) from the eyeball. The upper eyelid fuses with the eyeball and the pocket is lost in all batoids.

Upper origin: In the caudal fin, the anterodorsal beginning of the epaxial or upper web of the caudal fin, at the posterior end of the dorso-caudal space (see measurement illustrations).

Upper postventral margin: In the caudal fin, the upper part of the postventral margin of the hypaxial web, from the posterior notch to the subterminal notch.

Uterine cannibalism or **cannibal viviparity:** A mode of reproduction in which foetuses deplete their yolk-sacks early and subsist by eating nutritive eggs produced by the mother (see **oophagy**) or first eat smaller siblings and then nutritive eggs (see **adelphophagy**).

Vent: The opening of the cloaca on the ventral surface of the body between the inner margins and at the level of the pelvic fin insertions.

Ventral: Downward, in the vertical direction of the abdomen. See **dorsal**.

Ventral fin: See **pelvic fin**.

Ventral lobe: In the caudal fin, the expanded distal end of the preventral and lower postventral margins, defined by the posterior notch of the caudal fin.

Ventral margin: In the caudal fin, the entire ventral margin from lower origin to posterior tip, either a continuous margin or variably subdivided into preventral, postventral, subterminal and terminal margins.

Ventral marginal: In the clasper skeleton, a flat semicylindrical cartilage that is partially fused to the lateral edge of the axial cartilage, and forms the lateral wall of the clasper groove.

Ventral terminal: On the skeleton of the clasper glans, an often triangular, elongated, curved, plate-like cartilage that articulates or is attached to the lateral or ventrolateral edge of the end-style and to the posterior end of the ventral marginal cartilage.

Ventral tip: In the caudal fin, the ventral apex of the caudal fin where the preventral and postventral margins merge.

Vertebra, plural **vertebrae:** A single unit of the vertebral column, including a vertebral centrum and associated cartilages that form neural arches and ribs or haemal arches.

Vertebral axis: That part of the vertebral column inside the base of the caudal fin.

Vertebral column: The entire set or string of vertebrae or ‘backbone’ of a shark, from the rear of the chondrocranium to the end of the caudal base. Living elasmobranchs range from having as few as 60 vertebrae (some squaloids of the family Dalatiidae) to as many as 477 vertebrae (thresher sharks).

Visceral arches: See **splanchnocranium**.

Viviparity: Used in two ways in recent literature, as being equivalent to **placental viviparity** only, that is for carcharhinoid sharks with a yolk-sac placenta; or for all forms of live-bearing or **aplacental viviparity**.

Web, fin: See **fin web**.

Yolk sac or **yolk sack:** Almost all sharks start embryonic development somewhat like a chicken, as a large spherical yolky egg inside an elongated shell, the egg case. A small disk of dividing cells represents the pre-embryo or blastula atop the huge yolk mass. The blastula expands around the sides and ventral surface of the yolk mass, and differentiates into an increasingly shark-like embryo, the yolk sac or bag-like structure containing the yolk, and a narrow tubular yolk stalk, between the abdomen of the embryo and the yolk sac.

Yolk stalk: The connecting passage between embryo or foetus and yolk sac, which allows yolk to pass from the sac into the embryonic gut.

Yolk-sac placenta: An organ in the uterus of some ground sharks (order Carcharhiniformes), formed from the embryonic yolk-sac of the embryo and maternal uterine lining, through which maternal nutriment is passed to the embryo. It is analogous to the placenta of live-bearing mammals. There are several forms of yolk-sac placentas in carcharhinoid sharks, including entire, discoidal, globular, and columnar placentas (see Compagno, 1988).

Yolk-sac viviparity: Live-bearing in which the young are nourished primarily by the yolk in the yolk sacs, which is gradually depleted and the yolk sacs reabsorbed until the young are ready to be born.

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2. SYSTEMATIC CATALOGUE

2.1 Order HETERODONTIFORMES - Bullhead sharks

Order: [Group] Heterodonti Garman, 1885, *Bull. Mus. Comp. Zool. Harvard*, 12(1): 30, emended to Order Heterodontiformes.

Number of Recognized Families: 1.

Synonyms: [Part] 1 Squali, Abtheilung [Division] 2: Müller and Henle, 1838: 27; Müller and Henle, 1839: 27; also [Part] 1 Squali, Abtheilung [Division] 2, Unterabtheilung [Subdivision] 3: Müller and Henle, 1839: 66. Ordo Plagiostomi, Subordo Squalini, Sectio Proktopterides, Tribus Dinotopterini: Bleeker, 1859: xi. Order Squali, Suborder Squali: Gill, 1862b: 396. Order Squali, Suborder Galei: Gill, 1872: 23. Order Plagiostomi diplospondyli, Suborder Plagiostomi Asterospondyli, Group 3 Acrodonten: Hasse, 1879: 50. Order Selachii, Suborder Asterospondyli: Woodward, 1889: 157. Order Prosarthri: Gill, 1893: 129. Order Asterospondyli, Suborder Proarthri: Jordan and Evermann, 1896: 19. Order Euselachii, Suborder Pleurotremata, Division Squaloidei: Regan, 1906a: 723. Order Selachii, Group 2, Division A, Suborder Heterodonti: Goodrich, 1909 (in part): 143. Order Plagiostoma, Suborder Antacea, "Group" Centracoidei: Garman, 1913: 11, 13. Order Pleurotremata, Suborder Squaloidei: Engelhardt, 1913: 100. Order Centraciones, Suborder Prosarthri: Jordan, 1923: 95. Order Heterodontea, Suborder Heterodontida, Superfamily Heterodontoidea: White, 1936: 4; White, 1937: 37, tab. 1; Whitley, 1940: 69. Order Euselachii, Suborder Heterodontiformes: Bertin 1939a: 9. Order Heterodontiformes: Berg, 1940: 134, 135; Berg and Svetovidov, 1955: 61; Arambourg and Bertin, 1958: 2028; Patterson, 1967: 667; Lindberg, 1971: 8, 256; Rass and Lindberg, 1971: 303; Compagno, 1973: 28; Applegate, 1974: 743; Nelson, 1976: 32; Chu and Meng, 1979: 114, tab. 2; Compagno, 1984: 154; Nelson, 1984: 50; Gubanov, Kondyurin and Myagkov, 1986: 3, 42; Cappetta, 1987: 26, 69; Compagno, 1988: 382; Nelson, 1994: 45; Shirai, 1996: 32; Eschmeyer, 1998. Order Heterodontiformes, Suborder Heterodontoidei: Berg, 1940: 134, 135; Berg and Svetovidov, 1955: 61. Order Asterospondyli: Fowler, 1941: 4, 13; Smith, 1949: 37, 39. Order Selachii, Suborder Heterodontoidea: Romer, 1945: 576; Bigelow and Schroeder, 1948: 95; Romer, 1966: 349. Order Heterodontoidea: Schultz and Stern, 1948: 224. Order Pleurotremata, Suborder Heterodontiformes: Budker and Whitehead, 1971: 5, tab. 2. Order Heterodontida, Suborder Heterodontina, Superfamily Heterodonticae: Fowler, 1966: 321, 330, 331. Order Pleurotremata, Suborder Squaloidea: Norman, 1966: 24. Order Hexanchida, Suborder Heterodontoidei: Glikman, 1967: 214. Order Selachii: Blot, 1969: 702-776. Order Heterodontiformes, Suborder Heterodontoidea: Chu and Meng, 1979: 114, tab. 2. Order Galeomorpha, Suborder Heterodontoidea: Carroll, 1988: 598.

FAO Names: En - Bullhead sharks.

Field Marks: The only living sharks with two spined dorsal fins and an anal fin; also a pig-like snout, small anterior mouth, enlarged molariform teeth in the back of the mouth, supraorbital ridges, rough skin, paddle-like paired fins, and enlarged first gill slits.

Diagnostic Features: Head elevated with crests above eyes, not depressed or expanded laterally. Snout very short, slightly depressed and bluntly rounded, and without lateral teeth or rostral barbels. Eyes dorsolateral on head, without nictitating lower eyelids, secondary lower eyelids, or subocular pouches; upper eyelids not fused to eyeball. Spiracles very small, just behind or about opposite eyes but well below eye level. Five pairs of gill openings present on sides of head, with posteriormost two or three behind pectoral-fin origins. Nostrils diagonal on front of snout, without barbels but with prominent circumnarial grooves around incurrent apertures; nostrils with deep nasoral grooves connecting excurrent apertures to mouth, anterior nasal flaps moderately long and reaching mouth. Mouth small, almost terminal on head, broadly arched and short, ending in front of posterior corners of eyes. Labial furrows large and present on both jaws. Teeth strongly differentiated along the jaws, with small anterolateral teeth and enlarged molariform posterior teeth; no gap or small intermediate teeth between anterior and lateral teeth in the upper jaw; anterolateral teeth with orthodont histological structure but posterior teeth osteodont. Trunk cylindrical, not flattened and ray-like. Caudal peduncle without lateral dermal ridges or keels. Dermal denticles covering entire body, not enlarged as thorns or spines. Pectoral fins moderately large, not expanded and ray-like, without triangular anterior lobes that cover the gill openings. Pectoral girdle (scapulocoracoid) high, U-shaped, without a medial joint, and with superscapulae directed dorsally and not contacting vertebral column. Pectoral-fin skeleton primitively tribasal (dibasal with propterygium fused to mesopterygium in some species), with propterygium in contact with radials and metapterygium without a proximal segment; pectoral fins semiplesodic, with radials extending into the basal fin webs; radial count 15 to 19 with mostly 2 to 8 segments. Pelvic fins small, with vent continuous with their inner margins. Claspers with short siphons in the abdomen at the pelvic-fin bases but without clasper sacs; clasper glans with a large pseudosiphon, a cover rhipidion, a rhipidion and clasper spine; dorsal and ventral marginals of clasper skeleton well-developed but with only the dorsal marginal partially rolled into a tube for clasper canal. Two spine-bearing dorsal fins present, with origin of first well in front of pelvic-fin bases and over pectoral fins; dorsal-fin skeleton with segmented radials articulating with enlarged intermediate cartilages and a single basal plate that also carries the large fin spine. Anal fin present. Caudal fin with a long dorsal lobe and a short ventral lobe; vertebral axis elevated into the dorsal caudal lobe (heterocercal caudal fin). Vertebral calcification strong, secondary calcification in form of several radii that extend under the basals but without intermedial wedges, annuli, or diagonal calcifications. Total vertebral count 103 to 123, precaudal vertebrae 60 to 81. Neurocranium without a rostrum; nasal capsules trumpet-shaped and without subnasal fenestrae (basal communicating canals) or antorbital cartilages; orbits with incomplete preorbital walls, strong supraorbital crests, strong suborbital shelves, separate foramina for hyomandibular nerves but no separate foramina for superficial ophthalmic nerves, and incomplete postorbital walls without lateral commissures for lateral head vein; occipital condyles low but broad, with a prominent occipital hemicentrum between them. Jaws elongated, upper jaws (palatoquadrates) with low, ridge-like orbital processes that articulate with nasal capsules and orbits in horizontal grooves contacting ethmoid region, basal plate and suborbital shelves; orbital processes not penetrating supraorbital crests. Hyobranchial skeleton with moderately broad, elongated basihyoid; posterior two pharyngobranchials and last epibranchial fused as a yoke-shaped element. Head muscles include broad enlarged vertical preorbitalis with cross-biased fibres; narrow levator palatoquadrati and separate first dorsal constrictor under postorbital process and not extending behind orbits; adductor mandibulae muscles not segmented and not notched anteriorly for mouth gape; a discrete craniomandibular muscle between the lower jaw and orbital walls; no mandibulocutaneous muscle between upper jaw and skin; and no postocular eyelid muscles. Intestinal valve of conicospiral type, with seven turns. Reproduction oviparous (egg laying), with unique screw-shaped egg cases.

Distribution, Habitat, Biology, Interest to Fisheries and Human Impact, and Local Names: See family Heterodontidae below.

Remarks: The Heterodontiformes are a small but highly distinctive group of sharks that have generally been recognized as a discrete taxon at the genus, family, and higher levels. They have a long fossil record extending to almost the beginning of the Mesozoic era and agree with hybodont sharks and other extinct euselachians in having stout dorsal-fin spines and an anal fin.

Bullhead sharks were first discovered in Australia in the late eighteenth century in the form of the Port Jackson shark (***Squalus portus jacksoni*** Meyer, 1793 and several synonyms). This species was initially classified in the Linnaean shark genus ***Squalus*** but soon was accorded two genus-group names, ***Heterodontus*** Blainville, 1816 and its junior synonym ***Cestracion*** Oken, 1817, which initially were proposed as subgenera of ***Squalus*** but were recognized as genera by most subsequent authors. Bonaparte (1838) proposed the new subfamily Cestraciontini (family Squalidae) and Müller and Henle (1839) proposed a new family Cestraciontes for ***Cestracion***, while Gray (1851) proposed the new tribe Heterodontina for ***Heterodontus*** which was raised in rank to the family Heterodontoidae by Gill (1862b).

Many nineteenth and early twentieth century writers used the genus ***Cestracion*** in favour of ***Heterodontus*** and recognized the family Cestracionidae (or variants), including Müller (1845, family Cestraciontes), Bleeker (1859, family Cestracionoidei), Dumeril (1865, family Cestraciontes), Owen (1866), Günther (1870), Woodward (1889, 1898), Zittel et al. (1902), Regan (1906a), Goodrich (1909), Garman (1913, family Centraciontidae), Engelhardt (1913), and Zittel, Broili and Schlosser (1923). Swainson (1839) placed ***Cestracion*** in the family Squalidae, subfamily Centrininae along with various squaloids and other sharks. Van der Hoeven (1858) placed ***Cestracion*** in the family Selachii along with all other sharks while Hasse (1879) placed it in his Group 3, Acrodonten without familial assignment. The use of ***Heterodontus*** as a senior synonym of ***Cestracion*** began in the second half of the nineteenth century and became universal for most of the twentieth century. The family Heterodontidae was recognized by Gill (1872, 1893), Jordan and Gilbert (1883), Jordan and Evermann (1896), Bridge (1910), Jordan (1923), White (1936, 1937), Bertin (1939a), Berg (1940), Whitley (1940), Fowler (1941, 1966), Romer (1945, 1966), Bigelow and Schroeder (1948), Schultz and Stern (1948), Smith (1949), Berg and Svedovidov (1955), Matsubara (1955), Arambourg and Bertin (1958), Norman (1966), Glickman (1967), Patterson (1967), Blot (1969), Bailey et al. (1970), Rass and Lindberg (1971), Budker and Whitehead (1971), Pinchuk (1972), Compagno (1973, 1981b, 1984), Nelson (1976, 1984, 1994), Chu and Meng (1979), McEachran and Compagno (1982), Gubanov, Kondyurin and Myagkov (1986), Cappetta (1987), Carroll (1988), Eschmeyer (1990, 1998), and Shirai (1992, 1996).

The Heterodontidae (or Cestraciontidae) were often grouped with various fossil shark groups by earlier authors, particularly the hybodonts, and with various families of living sharks including lamnoids, carcharhinoids, and squaloids. The concept of a separate ordinal-group for Heterodontidae dates from Garman (1885) as a "group" Heterodonti, while Gill (1893) included it in a separate order Prosarthri (suborder Proarthri of Jordan and Evermann, 1896 and of Jordan, 1923, who also recognized an order Centraciones). Goodrich (1909) included Heterodontidae in the suborder Heterodonti, and Garman (1913) included it in the "group" Centracoidei. White (1936, 1937) recognized the order Heterodontea, which was listed by Bertin (1939a) as the suborder Heterodontiformes, by Berg (1940) as the order Heterodontiformes, and by Bigelow and Schroeder (1948) as the suborder Heterodontoidea. Most subsequent writers tend to accord it a separate order Heterodontiformes, including the writer (Compagno 1973, 1977, 1984, 1988, 1999, and present work).

The anatomy of heterodontoids was described by Gegenbaur (1865, 1872), Haswell (1885), Daniel (1914, 1915, 1928), Holmgren (1941), Kesteven (1942), Compagno (1973, 1977), Shirai (1992, 1996), and de Carvalho (1996), while general morphology and systematics were summarized by Dumeril (1865), Miklouho-Maclay and Macleay (1879, 1886), Günther (1870), Regan (1908b), Garman (1913), Smith (1942), Taylor (1972), and Compagno (1984). It is likely that the heterodontoids are related to the lamnoids, carcharhinoids and orectoloboids, with the most likely hypothesis being that the heterodontoids are a sister group to the three 'galeoid' orders rather than to the orectoloboids alone (see discussions in Compagno, 1973, 1977, 1988; Shirai, 1996; and de Carvalho 1996).

2.1.1 Family HETERODONTIDAE

Family: Tribe Heterodontina Gray, 1851, *List Fish British Mus., Pt. 1, Chondropterygii, British Mus. (Nat. Hist.)*: 65 (Family Squalidae).

Type Genus: ***Heterodontus*** Blainville, 1816. Raised to the rank of Family Heterodontoidae by Gill, 1862b, *Ann. Lyceum Nat. Hist. New York*, 7(32): 403.

Number of Recognized Genera: 1.

Synonyms: Subfamily Cestraciontini Bonaparte, 1838: 211 (Family Squalidae). Family Cestraciontes Müller and Henle, 1839: 76. Type genus: ***Cestracion*** Cuvier = Oken, 1817. Family Centraciontidae Garman, 1913: 13, 180. Type genus: ***Centracion*** Gray, 1831, possible error for ***Cestracion*** Cuvier, = Oken, 1817. Family Heterondontidae Bass, D'Aubrey and Kistnasamy, 1975d: 17. Apparent error for Heterodontidae, repeated twice on the same page but correctly spelled elsewhere (title page and table of contents, p. 2).

FAO Names: En - Bullhead sharks, Horn sharks; **Fr** - Requins dormeurs; **Sp** - Dormilones.

Field Marks: See order Heterodontiformes above.

Diagnostic Features: See order Heterodontiformes above.

Distribution: Bullhead sharks occur in warm-temperate and tropical continental waters of the western Indian Ocean, western and eastern Pacific, but are absent from the Atlantic and from oceanic insular waters.

Habitat: These are warm-temperate and tropical bottom sharks of water above 21°C, mostly confined to the continental and insular shelves and uppermost slopes. They occur from the intertidal to 275 m depth, but most are found in water shallower than 100 m.

Biology: As far as is known, these are sluggish, rare to uncommon night-active sharks, slowly swimming and crawling on rocky, kelp-covered and sandy bottom. Some species at least favour rocky crevices and caves, where they spend the day resting. At least one species is migratory in coastal waters when adult, and returns to its breeding sites each year after long migrations.

These sharks are oviparous, producing eggs in unique, large, spiral-flanged egg cases. At least two species lay eggs in specific 'nesting' sites. Eggs may take over five months to hatch, and young hatch at a large size, over 14 cm.

Bullhead sharks primarily feed on benthic invertebrates. Sea urchins (echinoids) are a favourite food, but crabs, shrimp and other crustaceans, abalone, top shells (Trochidae; Gastropoda) and other marine gastropods, oysters, polychaetes, sipunculid worms and more rarely small fish are also eaten.

Interest to Fisheries and Human Impact: These sharks are of minimal interest to fisheries, being caught as a bycatch of bottom trawl and line fisheries and utilized for human consumption and for fishmeal or discarded. They are commonly caught by divers and sportsfishers and at least one species is prized by divers for its fin spines, which are made into jewellery.

Several species of bullhead sharks have been kept in aquaria, where they have proved to be extremely hardy and can live for over a decade. Mating, egg-laying, hatching of eggs, and growth to maturity can occur in captivity.

Some bullhead sharks are encountered by divers, who have commonly harassed them. Although regarded as harmless, these sharks can and do snap when provoked and occasionally pursue and bite their tormentors. One species is the subject of ecotouristic diving in California at present.

At least two species of bullhead sharks may be declining as a result of fishing pressure. Most bullhead sharks are caught as low-level bycatch of fisheries for abundant commercial species (such as shrimp). Their presence in tropical coastal waters with heavy fishing pressure and habitat destruction (such as dynamite and poison-fishing of coral reefs), makes for possible conservation problems in some areas where they occur, such as the Indo-West Pacific and the tropical eastern Pacific.

Local Names: Bullhead sharks, Port Jackson bull-head sharks, Port Jackson sharks, Horn sharks (English); Requin de Port Jackson (French); Husha k'o, Bulkophaaie (South Africa), Nekozame-ka (Japan); Akula rogataia, Rogatye akuly, Bych'i akuli (Russia); Tubarões dorminhocos (Mozambique).

Remarks: Most authors have recognized a single genus, ***Heterodontus*** or its synonym ***Cestracion***, but ***Gyropleurodus*** has been used as a separate genus by some authors for eastern Pacific species (***Heterodontus francisci*** and ***H. quoyi***) or species with carinate teeth, following Gill (1863). Whitley (1931, 1940) separated the distinctive crested bullhead shark (***H. galeatus***), in its own genus ***Molochophrys***, while Fowler (1934) coined a subgenus, ***Wuia***, for the zebra bullhead shark (***Heterodontus zebra***). The systematic arrangement of the family Heterodontidae with a single genus ***Heterodontus*** follows Taylor (1972) and Compagno (1984). There is possible scope for subgeneric allocations within the family, but this should follow an analysis of the phyletics of these sharks.

Literature: Dumeril (1865); Günther (1870); Garman (1913); Fowler (1941, 1966); Smith (1942); Taylor (1972); Compagno (1984); Michael (1993); Last and Stevens (1994).

Heterodontus Blainville, 1816

Genus: Subgenus ***Heterodontus*** Blainville, 1816 (Genus ***Squalus*** Linnaeus, 1758), *Bull. Sci. Soc. Philomat. Paris*, (8): 121.

Type Species: "***Philippi***" = ***Squalus philippi*** Bloch and Schneider, 1801, by monotypy, a junior synonym of ***Squalus portus jacksoni*** Meyer, 1793.

Number of Recognized Species: 9.

Synonyms: Genus ***Cestracion*** Oken, 1817: 1183. Latinization of "Les Cestracions. Cuv." Cuvier, 1816: 129. Type species: ***Squalus philippi*** Bloch and Schneider, 1801, by monotypy? Genus ***Centracion*** Gray, 1831: 5. Type species: ***Centracion zebra*** Gray, 1831, by monotypy? Error or emendation of ***Cestracion*** Oken, 1817? Genus ***Cestralion*** Müller and Henle, 1838: 85. Probable error for ***Cestracion*** Oken, 1817. Genus ***Heterodontes*** Gill, 1862b: 403. Obvious error for ***Heterodontus*** Blainville, 1816, as name is spelled correctly on same page. Genus ***Gyropleurodus*** Gill, 1863: 331. Type species: ***Cestracion francisci*** Girard, 1854, by monotypy (or original designation). Genus ***Tropidodus*** Gill, 1863: 489. Type species: ***Cestracion pantherinus*** Valenciennes, 1846, by original designation. Genus ***Molochophrys*** Whitley, 1931: 310. Type species: ***Cestracion galeatus*** Günther, 1870, by original designation. Subgenus ***Wuia*** Fowler, 1934: 233 (Genus ***Heterodontus*** Blainville, 1816). Type species: ***Centracion zebra*** Gray, 1831, by original designation. Genus ***Tropidopus*** Beebe and Tee-Van, 1941: 118. Apparent error for ***Tropidodus*** Gill, 1863. Genus ***Cestraction*** Fowler, 1941: 17. Apparent error for ***Cestracion*** Oken, 1817. Genus ***Cetracion*** Fowler, 1941: 17. Error for ***Cestracion*** Oken, 1817 or ***Centracion*** Gray, 1831.

Diagnostic Features: See family Heterodontidae above.

Key to Species:

1a. Supraorbital ridges very high (Fig. 24) . . . . ***Heterodontus galeatus***
1b. Supraorbital ridges moderate to low (Fig. 25) . . . . **→ 2**

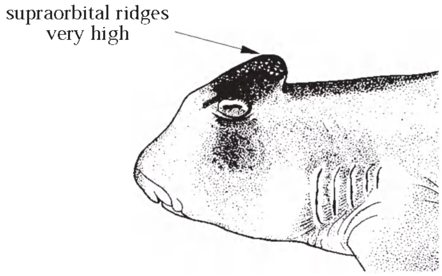


Fig. 24 *Heterodontus galeatus*

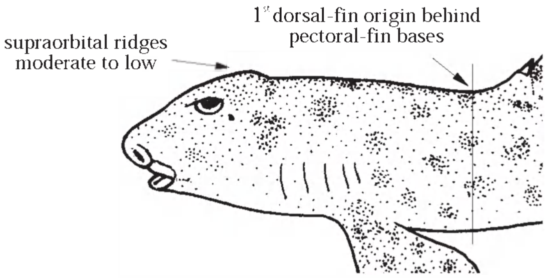


Fig. 25 *Heterodontus quoyi*

2a. First dorsal-fin origin behind pectoral-fin bases (Fig. 25) . . . . ***Heterodontus quoyi***
2b. First dorsal-fin origin over pectoral-fin bases (Fig. 26) . . . . **→ 3**

3a. Body and fins spotted (Fig. 26) . . . . **→ 4**
3b. Body and fins striped or banded (Fig. 27) . . . . **→ 6**

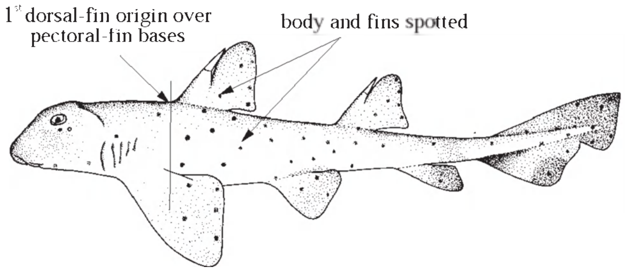


Fig. 26 *Heterodontus francisci*

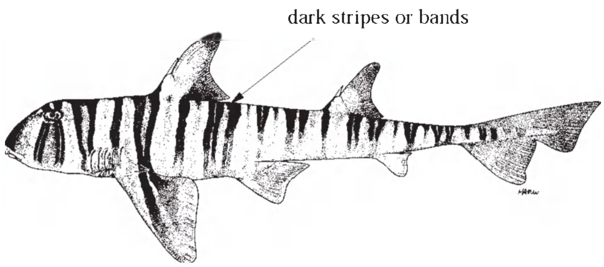


Fig. 27 *Heterodontus zebra*

4a. Body and fins with white spots in adults and subadults (Fig. 28); hatchlings with thin curved parallel lines on body . . . . **Heterodontus ramalheira**

4b. Body and fins with dark spots and (particularly in young), darker saddles (Fig. 29) . . . . → **5**

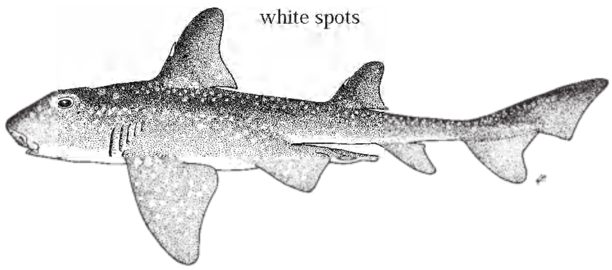


Fig. 28 ***Heterodontus ramalheira***

5a. Back and sides with small dark spots less than a third of eye diameter (Fig. 26); no light-coloured bar on interorbital surface of head . . . . **Heterodontus francisci**

5b. Back and sides with larger dark spots a half eye diameter or more (Fig. 29); a light-coloured bar on interorbital surface of head . . . . **Heterodontus mexicanus**

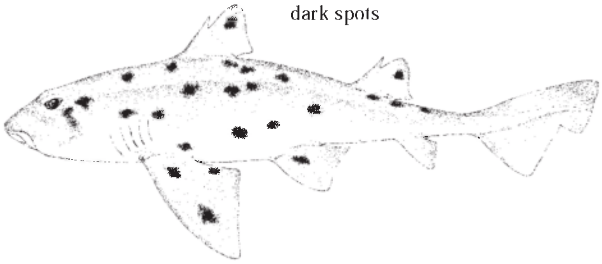


Fig. 29 ***Heterodontus mexicanus***

6a. Body with a harness pattern of dark stripes (Fig. 30) . . . **Heterodontus portusjacksoni**

6b. Body with vertical dark bands or saddles, not arranged in a harness pattern (Fig. 27) . . . . → **7**

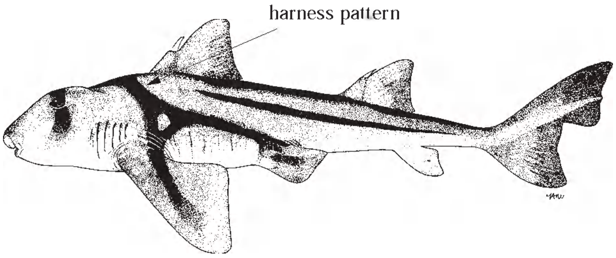


Fig. 30 ***Heterodontus portusjacksoni***

7a. Background colour of dorsal surface white or cream with a zebra pattern of 22 to 36 narrow dark markings from snout to origin of caudal fin; anal-caudal space over twice anal-fin base (Fig. 27). . . . . **Heterodontus zebra**

7b. Background colour of dorsal surface tan to brown with 5 to 14 broad or narrow, diffuse-edged markings from snout to origin of caudal fin; anal-caudal space less than twice anal-fin base (Fig. 31). . . . . → **8**

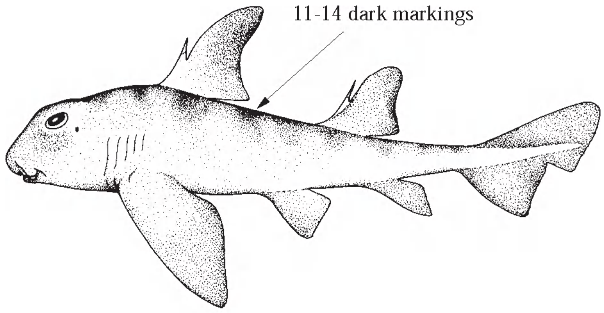


Fig. 31 ***Heterodontus japonicus***

8a. Dorsal, pectoral and caudal fins without abruptly black tips or white apical spots; about 11 to 14 dark markings from snout to origin of caudal fin, including broad dark saddles and narrow bands between them . . . . **Heterodontus japonicus**

8b. Dorsal and pectoral fins, and ventral caudal-fin lobe, with abruptly black tips, dorsal fins with white apical spots; 4 or 5 broad dark saddles from snout tip to origin of caudal fin, without narrow dark bands between them (Fig. 32) . . . . **Heterodontus sp. A (Oman)**

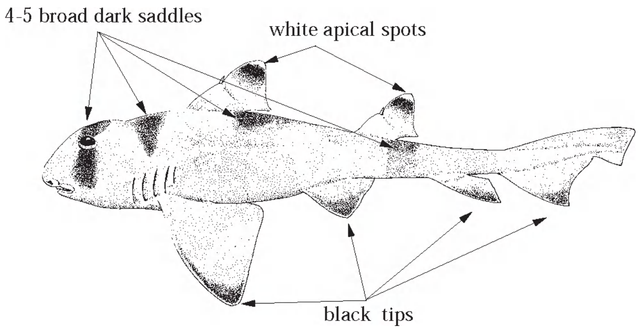


Fig. 32 ***Heterodontus* sp. A**

Heterodontus francisci (Girard, 1854)

Fig. 33

Cestracion francisci Girard, 1854, *Proc. Acad. Nat. Sci. Philadelphia*, 7(6): 196. Holotype: U.S. National Museum of Natural History, apparently lost according to Taylor (1972, Rev. shark fam. Heterodontidae: 47). Type locality, Monterey Bay, California. Not listed in catalogue of USNM shark types by Howe and Springer (1993, *Smiths. Contr. Zool.*, [540]: 1-19). Syntypes possibly USNM 933 (2) according to Eschmeyer (1998, *Cat. Fish.*: CD-ROM).

Synonyms: ***Heterodontus californicus*** Herald, 1961: 49. Apparent error for ***H. francisci***, which was cited correctly by Herald on p. 32.

Other Combinations: ***Gyropleurodus francisci*** (Girard, 1854).

FAO Names: En - Horn shark; **Fr** - Requin dormeur cornu; **Sp** - Dormilón cornudo.

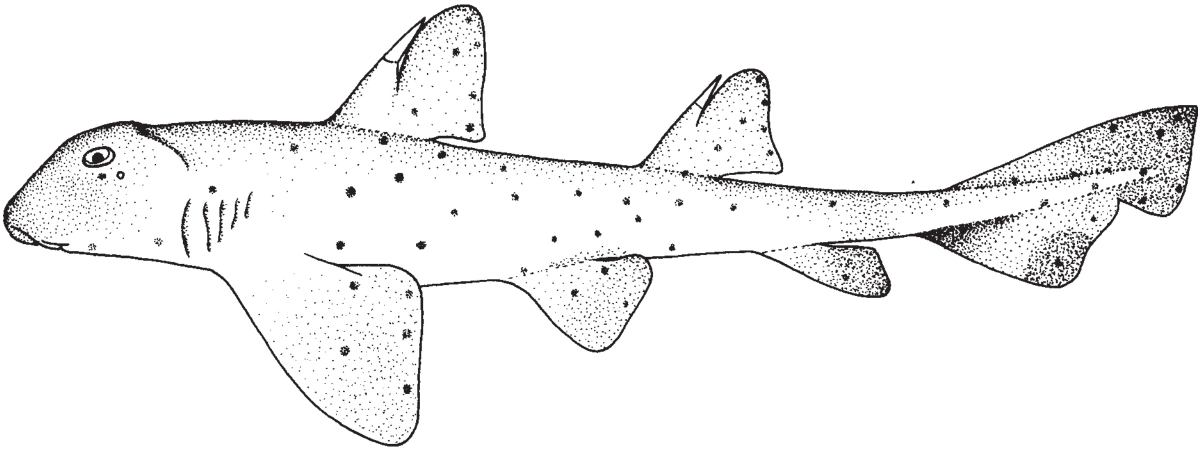
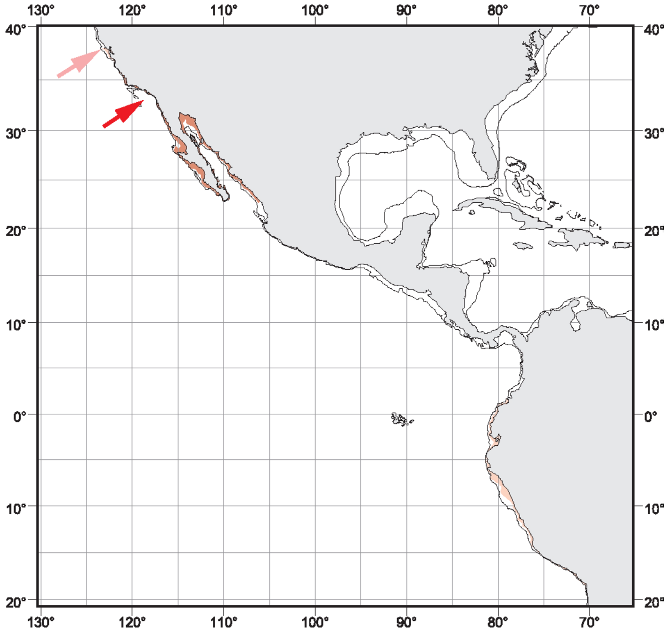


Fig. 33 *Heterodontus francisci*

Field Marks: Dorsal fins with spines, anal fin present, colour pattern of small dark spots less than one-third eye diameter on light background, no light bar on interorbital space between supraorbital ridges, first dorsal-fin origin over pectoral-fin bases.

Diagnostic Features: Supraorbital ridges moderately low, abruptly truncated posteriorly; interorbital space deeply concave, depth between ridges less than one-fourth eye length. Anterior holding teeth with a cusp and a pair of cusplets in adults, posterior molariform teeth strongly carinate and not greatly expanded and rounded. Pre-first dorsal-fin length 22 to 27%, and anal-caudal space 4 to 8%, of total length. Lateral trunk denticles small and smooth, area behind first dorsal fin with about 200 denticles per cm^2 in adults. Propterygium separate, not fused to mesopterygium. First dorsal-fin spine directed obliquely posterodorsally in juveniles and adults; first dorsal-fin origin anterior to pectoral-fin insertions, over or slightly behind midbases of pectoral fins and well posterior to fifth gill openings; first dorsal-fin insertion well anterior to pelvic-fin origin and well behind pectoral-fin insertion; first dorsal-fin free rear tip opposite or somewhat anterior to pelvic-fin origins; first dorsal fin moderately high and semifalcate in adults, height 9 to 14% of total length, slightly larger than pelvic fins. Second dorsal-fin origin over or slightly in front of pelvic-fin rear tips, second dorsal fin somewhat falcate and nearly as large as first dorsal fin. Anal fin subangular and weakly falcate, with apex reaching lower caudal-fin origin when laid back; anal-caudal space about equal to anal-fin base. Total vertebral count 103 to 123, precaudal count 65 to 76, monospondylous precaudal count 30 to 38, diplospondylous precaudal count 32 to 46, pre-first dorsal-fin spine count 12 to 16, count from diplospondylous transition to second dorsal-fin spine 7 to 16. Egg cases with flat thin spiral flanges diagonal to case axis and no tendrils on case apices; flanges with five turns. A large species, mature between 59 and 122 cm. **Colour**: background colour of dorsal surface dark to light grey or brown with dark brown or black spots on body and fins, spots generally less than one-third eye diameter; body without a dark harness pattern; head without a light bar on interorbital surface; small dark spots present below eye on a dusky patch; fins without abrupt dark tips and white dorsal-fin apices; hatchlings without whorls on fins and body, colour pattern as in adults although brighter.



Distribution: Warm-temperate and subtropical waters of the eastern Pacific: USA (Central and southern California), Mexico (Baja California, Gulf of California), and probably Ecuador and Peru. Off the USA it is most common off southern California but ranges to Monterey Bay and may occasionally penetrate as far north as San Francisco Bay (where it is not resident) during northern influxes of warm water.

Habitat: A common benthic and epibenthic shark, found on the eastern Pacific continental shelf most abundantly at depths from 2 to 11 m but ranging from the intertidal down to at least 150 m. Found on rocky bottoms including reefs, kelp beds, sandy draws between rocks, and on sand flats. On rocks it often occurs in deep crevices and small caves, and ventures far into large underwater caverns. Juveniles shelter on sandy bottom, often near algae, rocks, detritus, or in feeding holes excavated by bat rays (***Myliobatis californica***).

Biology: The horn shark is sluggish, nocturnal, and mostly solitary, though small aggregations have been seen by divers. It is seldom seen moving during the daytime but commonly has its head in a crevice. Shortly after dusk this shark becomes active and apparently feeds mostly at night, but ceases activity after dawn. Adults tend to return to the same resting place every day, but range at night over a small home range of roughly 0.1 hectare. According to Michael (1993) these sharks migrate into deeper water in winter, but it is uncertain if this occurs in the tropical part of their range. Experimentation with captive horn sharks indicates that their diel activity pattern is controlled by light intensity. The broad, muscular paired fins of the horn shark are used as limbs for clambering on the bottom, and are highly mobile and flexible. Swimming is slow and sporadic.

Courtship and copulation have been observed in captivity. The male horn shark chases the female until the latter is ready, then both drop to the bottom. The male grabs the female's pectoral fin with his teeth and inserts a single clasper in her cloaca; copulation lasts 30 to 40 min. One to two weeks later eggs are laid by captive females, one of which laid two eggs per day at 11 to 14 day intervals for four months. In nature these sharks mate in December or January and females drop eggs in February to April. Females normally deposit eggs under rocks or in crevices between them, but in captivity they drop eggs on the bottom where the contents of egg cases may be subsequently sucked out and eaten by these sharks. Eggs can be readily hatched in aquaria and take 7 to 9 months to hatch; the young begin to feed a month after hatching.

The horn shark feeds on benthic invertebrates,including sea urchins (echinoids), crabs, shrimp, isopods, sipunculid worms, anemones, bivalves, gastropods (possibly abalone), cephalopods (octopuses), but less commonly on small fish including pipefish (Syngnathidae) and blacksmith (***Chromis punctipinnis***, Pomacentridae). According to Michael (1993), the active diurnal blacksmith is eaten at night by the horn shark while it is resting on the bottom. Predators are little known: a Pacific angelshark (***Squatina californica***) has been filmed as swallowing small horn sharks and spitting them out alive, possibly because of their strong spines.

Size: Maximum 122 cm but most adults are below 97 cm. Egg cases 10 to 12 cm long and 3 to 4 cm wide at broad end (not over flanges); length at hatching 15 to 16 cm; males maturing at about 58 to 59 cm and adult at 59 to 84 cm; females mature above 58 cm.

Interest to Fisheries and Human Impact: Interest to fisheries minimal, probably utilized or formerly utilized for fishmeal as a bycatch of the shrimp fishery and other bottom-trawling operations in Pacific Mexican waters. It has been captured by divers for sport and for its large fin spines, which are made into jewellery; decreases in numbers of horn sharks have been noted in areas with intense diver activity in southern California. Horn sharks are often harassed and grabbed by divers, but when provoked may swim after their assailants and bite them. These sharks are kept in many public aquaria in the United States. They are hardy, attractive, readily maintained, will breed in captivity, and have been displayed for many years.

Local Names: California bull-head shark, Bullhead shark, Horned shark.

Remarks: Michael (1993) had a photobraph and brief account of what may be an undescribed bullhead shark in the southern Gulf of California, which he termed the Cortez bullhead shark (***Heterodontus* sp.**). According to Michael it is similar to ***H. francisci*** and ***H. mexicanus*** but differs from both species in having higher, more falcate dorsal fins, no dark spots, a lighter abdomen, and no light line on the interorbital space. It has low supraorbital ridges as in ***H. mexicanus***. The species has not, to the writer's knowledge, been collected, so its status is treated as uncertain here pending detailed comparison of material with the sympatric ***H. mexicanus*** and ***H. francisci***.

Literature: Daniel (1928); Beebe and Tee-Van (1941); Smith (1942); Roedel and Ripley (1950); Limbaugh (1963); Nelson and Johnson (1970); Miller and Lea (1972); Taylor (1972); Feder, Turner and Limbaugh (1974); Applegate et al. (1979); Chirichigno (1980); Compagno (1983, 1984); Michael (1993); Compagno, Krupp and Schneider (1995); Segura-Zarzosa, Abitia-Cárdenas and Galván-Magaña (1997).

Heterodontus galeatus (Günther, 1870)

Fig. 34

Cestracion galeatus Günther, 1870, *Cat. Fish. British Mus.*, 8: 416. Holotype: British Museum (Natural History), BMNH 1862.7.2.2, about 64 cm long, catalogue number according to Eschmeyer (1998, *Cat. Fish.: CD-ROM*), Australia.

Synonyms: None.

Other Combinations: ***Gyropleurodus galeatus*** (Günther, 1870), ***Molochophrys galeatus*** (Günther, 1870).

FAO Names: En - Crested bullhead shark; **Fr** - Requin dormeur à crête; **Sp** - Dormilón carenado.

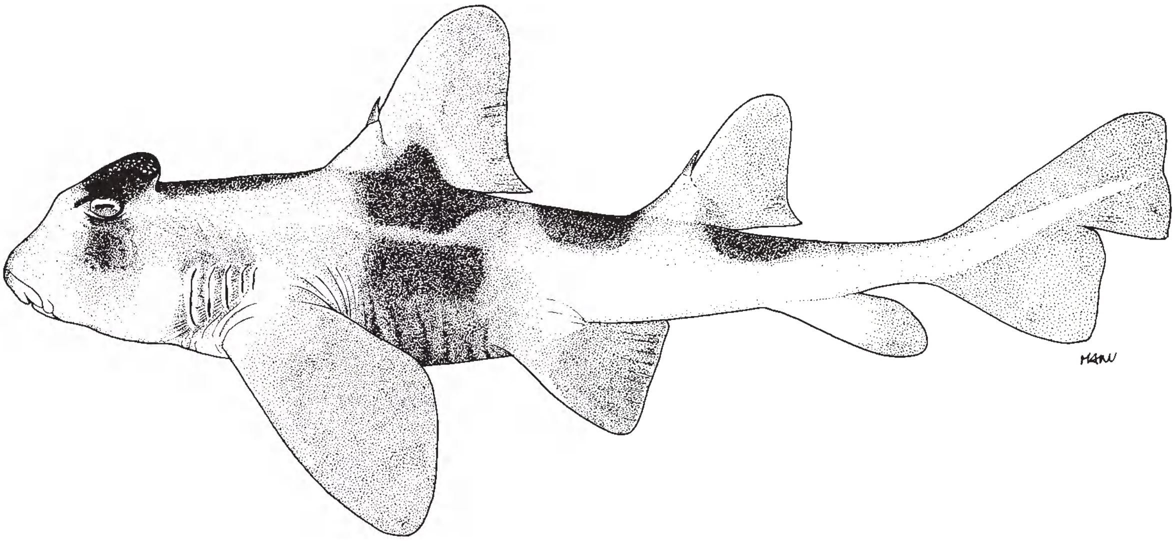


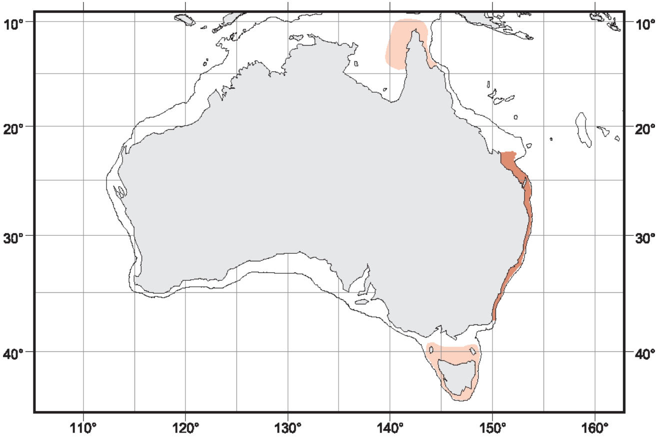
Fig. 34 *Heterodontus galeatus*

Field Marks: Dorsal fins with spines, anal fin present, supraorbital ridges greatly enlarged, colour pattern of dark broad bands on head, back and tail.

Diagnostic Features: Supraorbital ridges very high, more prominent than in any other ***Heterodontus***, abruptly truncated posteriorly; interorbital space deeply concave, depth between ridges about equal to eye length. Anterior holding teeth with a cusp and a pair of cusplets in adults, posterior molariform teeth strongly carinate and not greatly expanded and rounded. Pre-first dorsal-fin length 22 to 28%, and anal-caudal space 5 to 8%, of total length. Lateral trunk denticles fairly large and rough. Propterygium separate, not fused to mesopterygium. First dorsal-fin spine directed obliquely posterodorsally in adults; first dorsal-fin origin anterior to pectoral-fin insertions, slightly behind pectoral-fin midbases and well posterior to fifth gill openings; first dorsal-fin insertion well anterior to pelvic-fin origins and well behind pectoral-fin insertions; first dorsal-fin free rear tip about opposite to or slightly behind pelvic-fin origins; first dorsal fin moderately high and semifalcate or angular in adults, height 10.8 to 15.2% of total length, slightly larger than pelvic fins. Second dorsal-fin origin well in front of pelvic-fin rear tips, second dorsal fin somewhat falcate or angular and nearly as large as first dorsal fin. Anal fin subangular or rounded to weakly falcate, apex reaching lower caudal-fin origin when laid back; anal-caudal space between 1 and 2 times anal-fin base. Total vertebral count 106 to 108, precaudal count 71 or 72, monospondylous precaudal count 34 or 35, diplospondylous precaudal count 36 to 38, pre-first dorsal-fin spine count 16 to 18, and count from diplospondylous transition to second dorsal-fin spine 8 to 11. Egg cases with flat thin spiral flanges that are diagonal to case axis and a pair of long, slender tendrils on case apex, flanges with 6 or 7 turns. A large species, mature between 60 and 152 cm.

Colour: background colour of dorsal surface light brown or yellowish brown with five broad diffuse-edged brown or blackish saddles, but without light or dark spots; saddles not arranged in a harness pattern; head with a dark bar on interorbital surface and a single broad dark blotch under eye; fins without abrupt dark tips and white dorsal-fin apices; hatchlings without whorls on fins and body, colour pattern as in adults.

Distribution: Western South Pacific: East coast of Australia, from southern Queensland and New South Wales, with a doubtful record from Tasmania, and a possible record from the top of the Cape York Peninsula.



Habitat: A moderately common benthic and epibenthic shark of the southern Australian continental shelf at moderate depths, ranging from close inshore in the intertidal zone to 93 m. Found on reefs, in kelp and in beds of seagrass.

Biology: This shark often wedges its way between rocks in search of prey. The egg cases are dropped by females in seaweeds or sponges from 20 to 30 m depth on the bottom, during July and August, and hatch after about eight months. Eggs are commonest on the bottom in August and September but are found throughout the year. In captivity a newly hatched female matured and began to lay eggs at an age of 11.8 years and a length of about 70 cm. The crested bullhead shark feeds primarily on sea urchins (echinoids), but also crustaceans, molluscs and small fishes.

Size: Maximum said to be 152 cm long and attaining at least 130 cm, but most individuals are below 122 cm. Young hatch at about 17 cm. Males mature at about 60 cm and females at about 70 cm.

Interest to Fisheries and Human Impact: Interest to fisheries minimal, taken by bottom trawlers but not utilized commercially. Conservation status uncertain, distribution restricted to the warm east coast of Australia. Utilization by aquarium trade uncertain, but an obvious candidate because of its unusual appearance and striking colour pattern. Observed and photographed by divers, but not a special focus of ecotourism.

Local Names: Crested Port Jackson shark, Crested shark, Crested horn shark.

Literature: Whitley (1940); Fowler (1941); Smith (1942); McLaughlin and O'Gower (1971); Taylor (1972); Compagno (1984); Michael (1993); Last and Stevens (1994); Compagno and Niem (1998).

Heterodontus japonicus (Maclay and Macleay, 1884)

Fig. 35

Cestracion japonicus Maclay and Macleay, 1884, *Proc. Linnean Soc. New South Wales*, 1884, 8(4): 428, pl. 20. Holotype: Australian Museum, Sydney, AMS B.68, female from Tokyo, Japan.

Synonyms: ?***Cestracion philippi*** var. ***japonicus*** Dumeril, 1865: 426. Dumeril proposed this as a colour variant of ***Squalus philippi*** Bloch and Schneider, 1801 (= ***S. portusjacksoni*** Meyer, 1793) for Japanese specimens with transverse bands, but considered it equivalent to ***Centracion zebra*** Gray, 1831. Thus Dumeril may have confused two species, both of which occur in Japan. Taylor (1971: 107-108) requested the International Commission on Zoological Nomenclature to suppress Dumeril's name to remove the clearly defined ***Cestracion japonicus*** Maclay and Macleay, 1884, from possible junior homonymy if ***C. philippi*** var. ***japonicus*** is considered a synonym of ***C. zebra***. Dumeril's account could also be interpreted as providing a separate name for a Japanese variety of ***C. philippi*** with transverse bands apart from ***C. zebra*** (which Dumeril also synonymized with ***C. philippi***), and recognized as defined by subsequent workers.

Other Combinations: ***Gyropleurodus japonicus*** (Macleay and Macleay, 1884).

FAO Names: En - Japanese bullhead shark; **Fr** - Requin dormeur nekozame; **Sp** - Dormilón japonés.

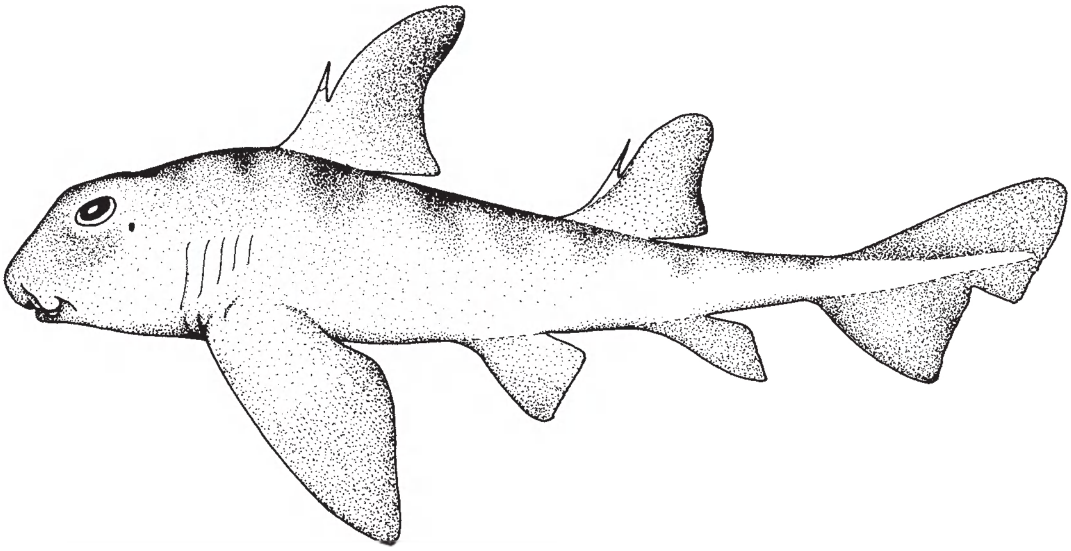
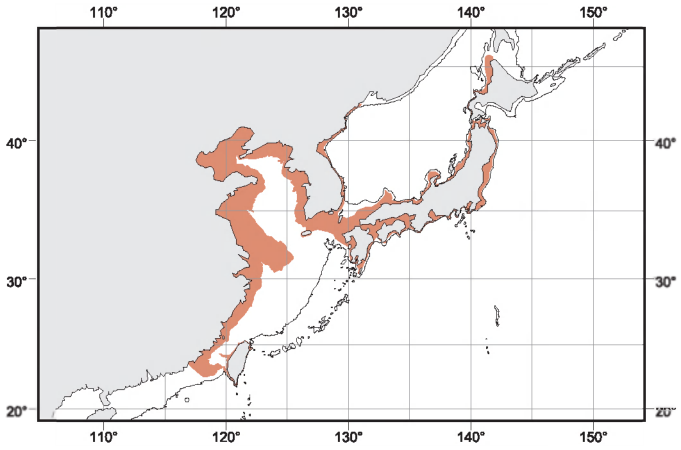


Fig. 35 *Heterodontus japonicus*

Field Marks: Dorsal fins with spines, anal fin present, first dorsal-fin origin over pectoral-fin bases, colour pattern of 11 to 14 broad, irregular-edged, dark saddles and vertical stripes on a light background.

Diagnostic Features: Supraorbital ridges moderately low, gradually ending posteriorly; interorbital space shallowly concave, depth between ridges about half eye length. Anterior holding teeth with a cusp and a pair of cusplets in adults, posterior molariform teeth not carinate and greatly expanded and rounded. Pre-first dorsal-fin length 21 to 25% and anal-caudal space 8 to 10% of total length. Lateral trunk denticles large and rough. Propterygium separate, not fused to mesopterygium. First dorsal-fin spine directed obliquely posterodorsally in hatchlings, juveniles and adults; first dorsal-fin origin anterior to pectoral-fin insertions and slightly behind pectoral-fin midbases, well posterior to fifth gill openings; first dorsal-fin insertion well anterior to pelvic-fin origins, well behind pectoral-fin insertions; first dorsal-fin free rear tip about opposite to or slightly ahead or behind pelvic-fin origins; first dorsal fin very high and broadly semifalcate in young but moderately high and semifalcate in adults, height 11 to 21% of total length, first dorsal fin much larger than pelvic fins. Second dorsal-fin origin over or slightly in front of pelvic-fin rear tips, broadly falcate and much smaller than first dorsal fin. Anal fin subangular and rounded to weakly falcate, apex well anterior to lower caudal-fin origin when laid back; anal-caudal space nearly or quite twice anal-fin base. Total vertebral count 109 to 116, precaudal count 72 to 78, monospondylous precaudal count 33 to 39, diplospondylous precaudal count 37 to 42, pre-first dorsal-fin spine count 15 to 17, and count from diplospondylous transition to second dorsal-fin spine 9 to 15. Egg cases with flat thin spiral flanges diagonal to case axis and having a pair of very short, slender tendrils on case apex, flanges with three turns. A large species, mature between 69 and 120 cm. **Colour**: background colour of dorsal surface tan to brown with 11 to 14 brown diffuse-edged markings from snout tip to origin of caudal fin, including broad saddles and narrower vertical bands usually between them, body without light or dark spots, bands and saddles not arranged in a harness pattern; head with a light-coloured bar on interorbital surface, and with a single broad dark blotch under eye that is indistinct in large adults; fins without abrupt dark tips and white dorsal-fin apices; hatchlings without whorls on fins and body, pattern as in adults although brighter.



Distribution: Western North Pacific: Japan, Korean peninsula, northern China, and Taiwan (Province of China). An East African record is apparently erroneous.

Habitat: A common, temperate-water bullhead shark of the western North Pacific continental shelf, occurring at moderate depths of 6 to 37 m, on or near the bottom. It prefers rocky areas (including reefs) and kelp-covered bottom.

Biology: This is a sluggish, slow-swimming shark, easily caught by divers. It slowly explores the bottom, swimming and 'walking' with its mobile paired fins.

Oviparous, laying its large spiral-cased eggs among rocks or in kelp, at depths of about 8 or 9 m; several females may lay their eggs in a single site, termed 'nests', although they apparently do not guard these sites after laying. In Japanese waters, eggs are laid from March through September, most abundantly in March through April; each female usually lays two eggs at a time, for 6 to 12 spawnings. Eggs hatch in about a year.

The Japanese bullhead shark feeds on crustaceans, molluscs (including top shells [Trochidae; Gastropoda]), small fishes and sea urchins. It can protrude its jaws a considerable distance while grabbing prey.

Size: Maximum total length about 120 cm. Size at hatching about 18 cm; males adult at 69 cm.

Interest to Fisheries and Human Impact: Interest to fisheries probably minimal, caught and eaten in Japan and presumably elsewhere in its range. Kept in public aquaria in Japan.

Local Names: Bull head, Japanese bull-head shark, Cat shark, Japanese horn shark, Cestracion shark, Sazaewari, Sazaiwari, Nekozame (Japan); Japanse bulkophaai (South Africa).

Literature: Fowler (1941); Smith (1942); Lindberg and Legeza (1959); Chen (1963); McLaughlin and O'Gower (1971); Taylor (1972); Nakaya and Shirai (1984); Compagno (1984); Michael (1993); Shen et al. (1993).

Heterodontus mexicanus Taylor and Castro-Aguirre, 1972

Fig. 36

Heterodontus mexicanus Taylor and Castro-Aguirre, 1972, *An. Esc. Nac. Cienc. Biol. México*, 19: 125, figs 1-5, 8-9. Holotype: Scripps Institution of Oceanography, SIO-70-90, 610 mm adult female, Cerro Colorado, Sonora, Gulf of California, Mexico.

Synonyms: None.

Other Combinations: None.

FAO Names: En - Mexican hornshark; **Fr** - Requin dormeur buffle; **Sp** - Dormilón búfalo.

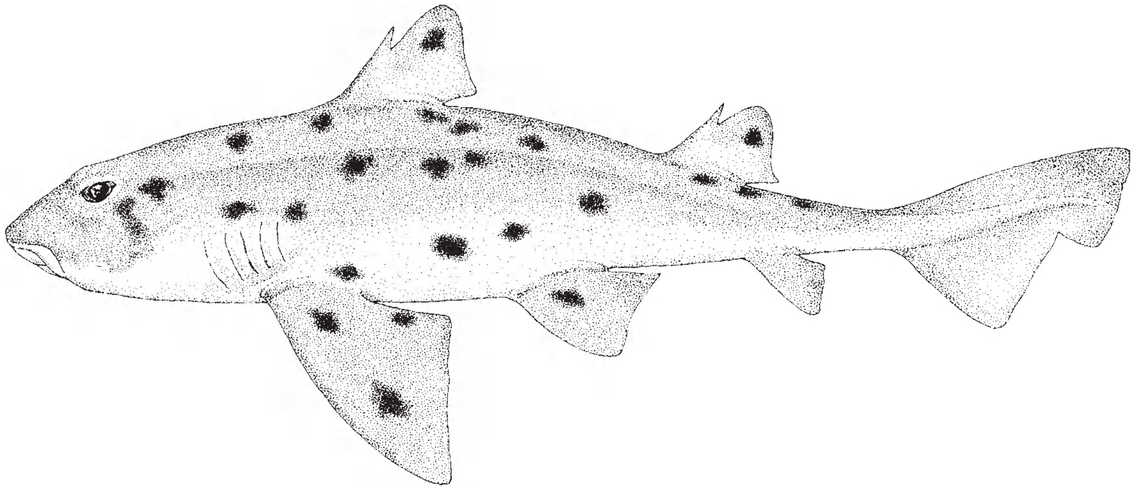
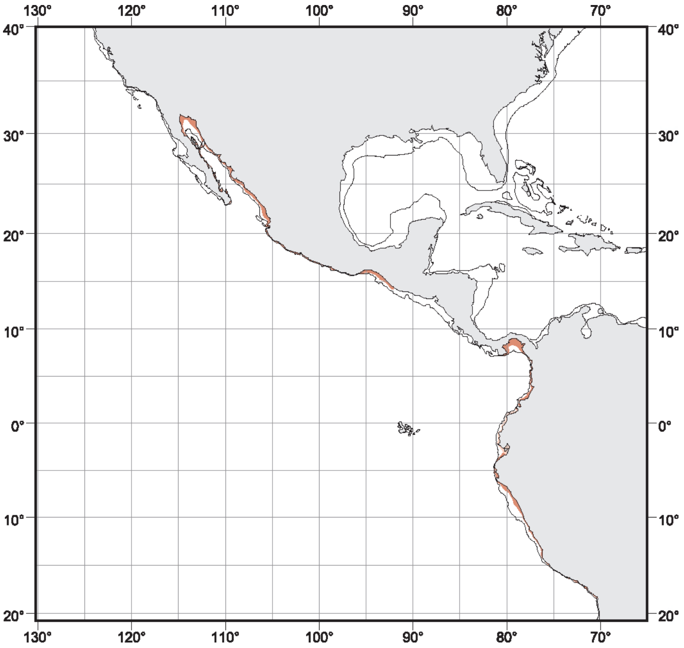


Fig. 36 *Heterodontus mexicanus*

Field Marks: Dorsal fins with spines, anal fin present, colour pattern of large dark spots of one-half eye diameter or more on light background, a light bar present on space between supraorbital ridges, first dorsal-fin origin over pectoral-fin bases.

Diagnostic Features: Supraorbital ridges low, gradually ending posteriorly; interorbital space shallowly concave, depth between ridges less than one-fourth eye length. Anterior holding teeth with a cusp and a pair of cusplets in adults, posterior molariform teeth strongly carinate and not greatly expanded and rounded. Pre-first dorsal-fin length 24 to 29% and anal-caudal space 6 to 9% of total length. Lateral trunk denticles large and rough, area behind first dorsal fin with about 70 to 130 denticles per cm^2 in adults. Propterygium fused to mesopterygium. First dorsal-fin spine directed obliquely posterodorsally in juveniles and adults; first dorsal-fin origin slightly anterior to pectoral-fin insertions, behind pectoral-fin midbases, and well posterior to fifth gill openings; first dorsal-fin insertion well anterior to pelvic-fin origins and well behind pectoral-fin insertions; first dorsal-fin free rear tip about opposite to or slightly ahead of pelvic-fin origins; first dorsal fin low and weakly falcate in adults, height 8 to 18% of total length, first dorsal fin about as large as pelvic fins; second dorsal-fin origin over or slightly in front of pelvic-fin rear tips, weakly falcate and nearly as large as first dorsal fin. Anal fin subangular and rounded to weakly falcate, with apex reaching lower caudal-fin origin or falling somewhat behind it when laid back; anal-caudal space between 1 and 2 times anal-fin base. Total vertebral count unknown, precaudal count 60 to 70, monospondylous precaudal count 30 to 34, diplospondylous precaudal count 30 to 38, pre-first dorsal-fin spine count 14 to 16, and count from diplospondylous transition to second dorsal-fin spine 9 to 14. Egg cases with thick, T-shaped paired spiral flanges, transverse to case axis, and a pair of long, slender tendrils on case apex; flanges with five turns. A small species, mature between 50 and 70 cm. **Colour**: background colour of dorsal surface light grey-brown with large black spots on body and fins, these one-half eye diameter or more in size; body without a dark harness pattern; head with a light-coloured bar on interorbital surface of head and 1 or 2 dusky indistinct blotches under eye; fins without abrupt dark tips and white dorsal-fin apices; hatchlings without whorls on fins and body.

Distribution: Eastern Pacific: Mexico (southern Baja California, the Gulf of California, and southern Pacific coast) south to Guatemala, Panama (Gulf of Panama), Colombia, probably Ecuador and Peru.



Habitat: A warm-temperate and tropical bullhead shark of littoral continental waters, found on rocky bottom including reefs and seamounts, on coral reefs, and on sandy areas from close inshore down to 20 to 50 m depth.

Biology: Common in the upper Gulf of California. Oviparous. The long tendrils and rigid, T-shaped spiral flanges on the egg cases of this shark suggest that wedging of the eggs in crevices through the action of flexible flanges has been replaced by anchoring of the cases to the substrate by the tendrils, unlike other bullhead sharks with flexible-flanged eggs. The heavy T-flanges may serve instead to protect the egg from impacts and egg-predators. Feeds on crabs and demersal fishes including midshipman (***Porichthys***, Batrachoididae).

Size: Maximum size about 70 cm. Egg cases about 8 to 9 cm long, young hatch at about 14 cm; males maturing between 40 and 50 cm and reaching at least 55 cm.

Interest to Fisheries and Human Impact: Interest to fisheries minimal. Small numbers are or were taken as a bycatch of the shrimp fishery in Mexico and processed into fishmeal along with other sharks. It is also caught in gill nets set for small sharks. Observed by divers in the Gulf of California, but not a special focus for ecotouristic diving.

Local Names: Buffalo hornshark, Mexican horn shark; Gata (Mexico).

Remarks: This shark had been collected in the Gulf of California many years ago by ichthyologists at the Scripps Institution of Oceanography and referred to under the unpublished manuscript names "H. seftoni" and "H. oligostictus". It was eventually published as ***H. mexicanus***.

Literature: Taylor (1972); Taylor and Castro-Aguirre (1972); Applegate et al. (1979); Chirichigno (1980); Compagno (1984); Franke and Acero (1991); Michael (1993); Compagno, Krupp and Schneider (1995).

Heterodontus portusjacksoni (Meyer, 1793)

Fig. 37

Squalus portus jacksoni Meyer, 1793, *Syst. Summar. Zool. Entdeck. Neuholland, Afrika*: 71. No type material, Botany Bay, New South Wales, Australia, based on the Port Jackson Shark of Phillip, 1789, *Voyage Botany Bay*: 283, fig.

Synonyms: ***Squalus jacksoni*** Suckow, 1799: 102. No type material, Botany Bay, Port Jackson, Australia, based on the Port Jackson Shark of Phillip, 1789: 283, fig. Reference from Fowler (1941). ***Squalus philippi*** Bloch and Schneider, 1801: 134. No type material, Botany Bay, Port Jackson, Australia, based on the Port Jackson Shark of Phillip, 1789: 283, fig. ***Squalus philippinus*** Shaw, 1804: 341. No type material?, southern Pacific Ocean, Botany Bay (Port Jackson, Australia), apparently based on the Port Jackson Shark of Phillip (1789: 283, fig.), and termed the "Phillipian shark" by Shaw. ***Squalus jacksonii*** Turton, 1806: 922. Variant spelling of ***Squalus jacksoni*** Suckow, 1799 or independently proposed? ***Cestracion philippi*** Lesson, 1830, 2: 97; 3, pl. 2. No type material, Botany Bay, Port Jackson, Australia, based on the Port Jackson Shark of Phillip, 1789: 283, fig. Proposed as a new name; specimen illustrated may not be this species. ***Cestracion heterodontus*** Sherrard, 1896: 42, 88, figs. Hobson's Bay, Victoria. Reference from Fowler (1941), uncertain if new name or error. ***Heterodontus bonae-spei*** Ogilby, 1908: 2. Holotype: Queensland Museum, No. QM I.1587, jaws only, "Table Bay, South Africa", possibly a specimen of ***H. portusjacksoni*** with a mistaken locality label according to Reif (1973: 165-167).

Other Combinations: None.

FAO Names: En - Port Jackson shark; **Fr** - Requin dormeur taureau; **Sp** - Dormilón toro.

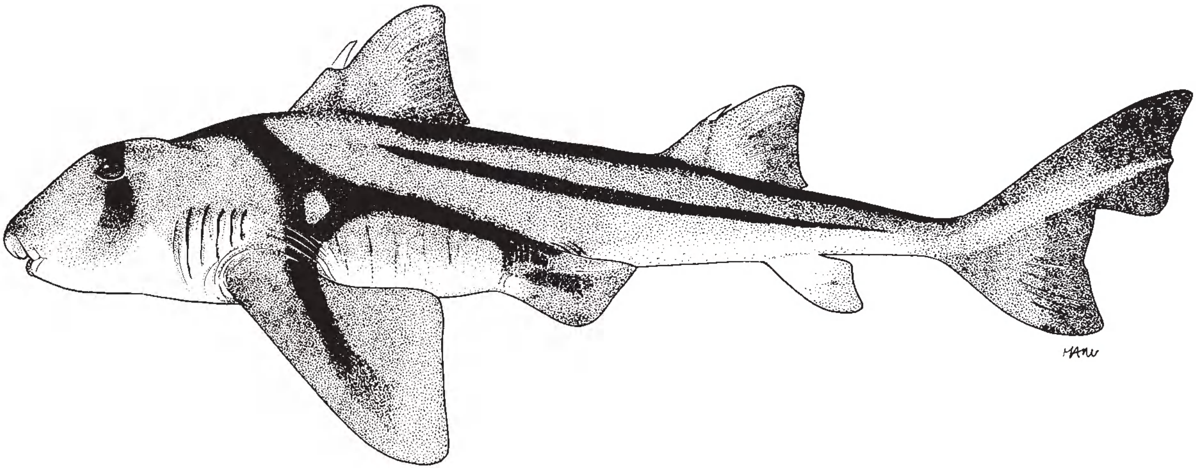
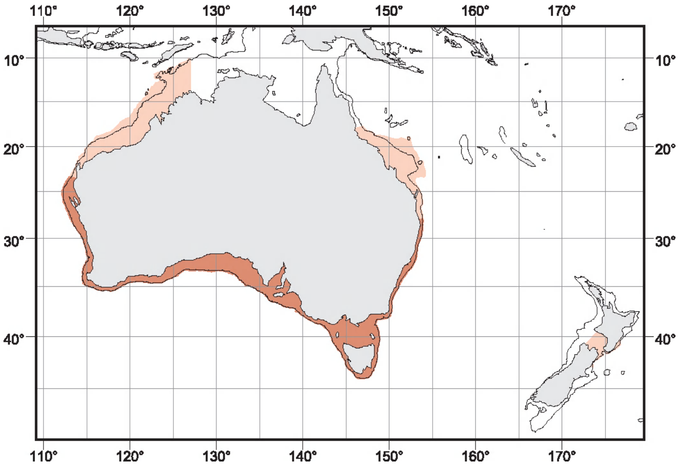


Fig. 37 *Heterodontus portusjacksoni*

Field Marks: Dorsal fins with spines, anal fin present, colour pattern with a conspicuous set of harness-like narrow dark stripes on the back, unique to the species.

Diagnostic Features: Supraorbital ridges moderately low, gradually ending posteriorly; interorbital space moderately concave, depth between ridges less than half eye length. Anterior holding teeth with a cusp and no cusplets in adults, posterior molariform teeth not carinate and greatly expanded and rounded. Pre-first dorsal-fin length 21 to 24% and anal-caudal space 10 to 13% of total length. Lateral trunk denticles fairly large and rough. Propterygium fused to mesopterygium. First dorsal-fin spine directed obliquely posterodorsally in juveniles and adults; first dorsal-fin origin well anterior to pectoral-fin insertions, about over or slightly behind pectoral-fin midbases, and somewhat posterior to fifth gill openings; first dorsal-fin insertion well anterior to pelvic-fin origins and well behind pectoral-fin insertions; first dorsal-fin free rear tip about opposite to pelvic-fin origins; first dorsal fin moderately high and rounded angular or falcate, height 12 to 16% of total length, first dorsal fin larger than pelvic fins; second dorsal-fin origin over or slightly behind pelvic-fin rear tips, second dorsal fin rounded to angular or falcate and nearly as large as first dorsal fin. Anal fin subangular and rounded or weakly falcate, apex well anterior to lower caudal-fin origin when laid back; anal-caudal space about three times anal-fin base. Total vertebral count 114, precaudal count 76 to 81, monospondylous precaudal count 37 to 39, diplospondylous precaudal count 37 to 43, pre-first dorsal-fin spine count 15 to 17, and count from diplospondylous transition to second dorsal-fin spine 9 to 14. Egg cases with flat thin spiral flanges diagonal to case axis and a pair of very short, slender tendrils on case apex; flanges with four or five turns. A large species, mature between 70 and 165 cm. **Colour**: background colour of dorsal surface grey to light brown or whitish with distinctive black striped harness marking; body and fins without light or dark spots; head with a narrow dark bar on interorbital surface and a single narrow dark to blackish band under eye; fins without abrupt dark tips and white dorsal-fin apices; hatchlings without whorls on fins and body, colour pattern as in adults.



Distribution: Western South Pacific: Temperate and subtropical southern Australia, from off New South Wales, Victoria, Tasmania, South and Western Australia (west coast), with questionable records from southern Queensland and the tropical north coast of Western Australia; also New Zealand (a single record, possibly as a straggler or waif from Australia).

Habitat: A common littoral, nocturnal bottom shark of the temperate Australian continental shelves and uppermost slopes, ranging from close inshore in the intertidal to at least 275 m.

Biology: Underwater observation and tagging of this nocturnal species has elucidated its life-history to a degree attained with few other species of sharks. While inshore, the Port Jackson shark favours caves with sandy floors and open trenches of shallow rocky reefs as daytime resting places, and almost all individuals in a given area will be found resting in relatively few of such sites. Strong selection is shown for favoured sites, and superficially identical sites nearby may have few or no sharks.

Port Jackson sharks can be solitary but often occur in small to large groups. Althose these sharks are evidently social and apparently are amenable to study underwater, relatively little is known of their sociobiology and behaviour patterns. This could be elucidated in the future by electronic tagging and night-observation with low-light video devices, as well as observations of captive colonies in semi-naturalistic habitats.

Pronounced fluctuations in abundance have been noted on shallow reefs off New South Wales, directly correlated with seasonal influxes of adults for breeding and inversely correlated by seasonal variations in temperature. These sharks are apparently social while resting, and favoured resting sites may have up to 16 sharks occupying them. Data from tagging suggests that seasonal reef populations are in a state of continuous flux, with individuals moving in and out of their favoured reefs throughout the breeding season. Apparently individuals are capable of homing to favoured resting sites after ranging considerable distances away from them during the breeding season. When sharks were experimentally removed from resting sites in Sydney Harbour to different localities up to 3 km away, they returned to their original resting sites. It has been suggested that these sharks have a highly-developed spatial memory, and apparently the means to locate favoured resting and breeding sites long distances apart along migration routes.

Port Jackson sharks are seasonal oviparous breeders, with juveniles segregating by size after hatching and adults segregating by sex. Mature females accompanied by some males move onto inshore reefs in late July and August in the Sydney area (New South Wales), and probably mating occurs at this time. Most mature males remain in deeper water offshore. During August and September (rarely in July and October) females lay 10 to 16 (commonly 10 to 12) eggs in rock crevices on shallow, sheltered reefs at depths from 1 to 5 m but occasionally down to 20 to 30 m. In captivity females lay a pair of cased eggs a day every 8 to 17 days. The broad spiral flanges of the egg cases serve as anchors to keep them wedged in the rocks. Females apparently favour traditional 'nest' sites, which several apparently use collectively for many years. Apart from rock crevices, females may occasionally lay egg cases on open sand, and egg cases have been found wedged under an underwater oil pipeline and in tin cans. Egg cases are oriented with their pointed ends into crevices, and females have been seen carrying egg cases, suggesting that females lay their eggs, pick them up at the broad end, and insert them into appropriate crevices. According to Michael (1993), adults have been observed eating their own egg-cases (as in ***H. francisci***).

Young hatch after about 9 to 12 months and move into nursery areas in bays and estuaries. Some may retreat into deeper water during summer, but most juveniles remain in mixed groups with a 1:1 sex ratio on the nursery grounds for several years. At the beginning of sexual maturity adolescents move into deeper water and segregate into male and female groups. After several years of adolescence, apparently spent at the outer edges of the continental shelves, these groups join the adult populations.

Adult males apparently move into deeper water near the end of the breeding season, followed by the adult females in late September or October. Some adults move offshore into deeper water, but others migrate. Small numbers of adults may return to the inshore breeding reefs as early as March or April of the next year, but most do not stay inshore and few sharks are present until the onset of the next breeding season. Observed ratios of adult males and females are not significantly at variance with a 1:1 ratio.

On the east coast of Australia the Port Jackson shark shows a pattern of migration southwards after breeding, with females migrating at least for 5 to 6 months and moving up to 850 km south of breeding reefs before returning to the same sites the next year. Some may range as far south as Tasmania from the Sydney area in New South Wales in the annual migration cycle. It is thought that migrating adult sharks move southwards along inshore coastal waters but return to their breeding reefs along deeper offshore waters.

Studies on blood proteins between Port Jackson sharks of different regions suggest that they form at least two populations, a southwestern one from Western Australia to northeastern Victoria and a northeastern one from New South Wales and possibly southern Queensland. There is blood protein evidence to suggest that sharks using favoured breeding sites in three localities in New South Wales represent genetically distinct subpopulations, and indicates that the high site specificity shown by tagging and recapturing of sharks in this area is probably of relatively long duration.

Data from captive sharks suggests that juveniles grow at about 5 to 6 cm per year and adults between 2 and 4 cm per year. Approximate estimates of age at maturity from captive growth data are 8 to 10 years for males and 11 to 14 years for females. So far, data is unavailable on growth rates in the wild from tagging and remeasuring of tagged individuals or from calibration and examination of fin spine or vertebral rings.

The Port Jackson shark feeds primarily on benthic invertebrates, mainly echinoderms. Prey items include sea urchins, starfish, polychaetes, large gastropods, prawns, crabs, barnacles, and small fishes. Occasionally garbage such as bits of mammalian fur, potato and orange peels are taken in by these sharks. Juveniles with their smaller, more pointed teeth apparently take more soft-bodied prey than adults. Food items in stomachs are usually broken into small pieces, indicating that the sharks actively grind their food with their powerful jaws and heavy molariform teeth. Food is apparently taken at night on the bottom, and by searching close to the substrate. Olfactory cues are thought to be important, but electrosense and lateral line sense may play a role in this also. Food is eaten after final contact with the mouth region. Juveniles at least are capable of digging food out of the sand by sucking in water and sand and blowing it out of the gill covers. Respiration can occur by pumping water into the first, enlarged gill slits and out the last four, which is thought to allow the shark to crush and grind its prey at leisure without having to take in water through its mouth and risk passage of food out the gill slits.

Predators of this shark are poorly known, but it is suspected that adults are highly protected by their sedentary habits, cryptic, nocturnal behaviour, fin spines, and disruptive colour patterns. Possible predators are large macropredatory sharks such as bluntnose sevengill and white sharks as well as large otariid seals. Juveniles in nursery grounds are thought to be more vulnerable to predation by other sharks and larger benthic teleosts. Adults are sometimes attacked by small predatory isopods, and eggs may be attacked by male Port Jackson sharks and possibly a gastropod drilling predator. As with other sharks, this has a sizeable parasite fauna, including cestodes (tapeworms), trematodes (flatworms), nematodes (roundworms), isopod larvae, copepods, fish lice, and leeches.

Size: Maximum total length reported as 165 cm, but apparently rare above 137 cm. Egg cases are 13 to 17 cm long and 5 to 7 cm wide at the broad end. Size at hatching 23 to 24 cm. Males are adolescent between 50 and 80 cm, mature between 70 and 80 cm, and reach at least 105 cm; females are adolescent between 65 and about 84 cm, mature between 80 and 95 cm, and reach at least 123 cm; adult females average about 25 cm longer than adult males.

Interest to Fisheries and Human Impact: Apparently of minimal interest to fisheries. Taken in commercial fisheries as bycatch in bottom trawls, shrimp nets, beach seines, anti-shark nets, bottom longlines and in shark gill nets on the south coast of Australia; also caught by sports anglers on rod-and-reel. Apparently not utilized as food. This shark is considered harmless to people. It is kept in public aquaria for display in Europe, the United States, and probably Australia, and is an obvious candidate for display because of its hardiness and attractive colour pattern. Divers observe this shark but it is not a special focus of ecotouristic diving. Conservation status uncertain.

Local Names: Bullhead shark, Bullhead, Pigfish, Oyster-crusher or Oyster crusher, Tabbigaw.

Remarks: Reif (1973) noted that the holotype of ***Heterodontus bonae-spei***, supposedly from South Africa, is most probably a specimen of ***H. portusjacksoni*** with an erroneous locality label. Eschmeyer (1998) noted that the name was unavailable because Ogilby (1908) did not distinguish it by characters but only by locality.

Literature: Ogilby (1908); Whitley (1940); Fowler (1941); Smith (1942); McLaughlin and O'Gower (1970, 1971); Taylor (1972); Reif (1973); O'Gower and Nash (1978); Michael (1993); Last and Stevens (1994); O'Gower (1995); Compagno and Niem (1998).

Heterodontus quoyi (Fréminville, 1840)

Fig. 38

Cestracion quoyi Fréminville, 1840, *Mag. Zool. Guerir.*, ser. 2(5): 1-3, pl. 3. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN-3445, adult male about 475 mm, type locality Galapagos Islands.

Synonyms: ***Cestracion pantherinus*** Valenciennes, 1846, pl. 10, fig. 2. Ibid., 1855, text: 350. Holotype the same specimen (MNHN-3445) as that of ***Cestracion quoyi***, Galapagos Islands. ***Gyropleurodus peruanus*** Evermann and Radcliffe, 1917: 2, pl. 1, fig. 1. Holotype: U.S. National Museum of Natural History, USNM-77691, 565 mm TL adult (gravid) female, Lobos de Tierra Island, Peru, confirmed by Howe and Springer (1993: 11).

Other Combinations: None.

FAO Names: En - Galapagos bullhead shark; **Fr** - Requin dormeur bouledogue; **Sp** - Dormilón de Galápagos.

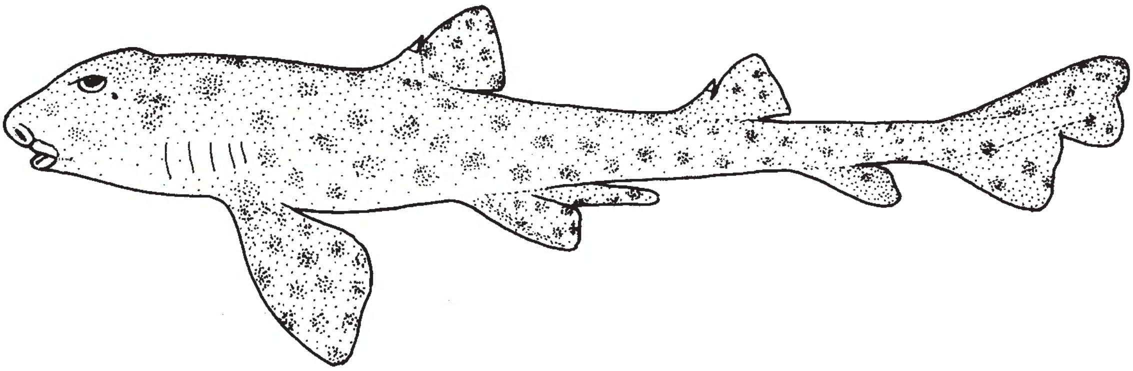
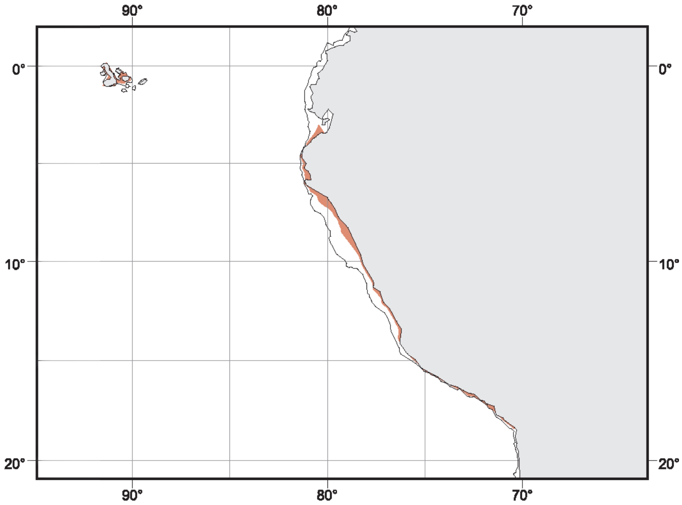


Fig. 38 *Heterodontus quoyi*

Field Marks: Dorsal fins with spines, anal fin present, first dorsal-fin origin over pectoral-fin inner margins, colour pattern of large dark spots.

Diagnostic Features: Supraorbital ridges low, gradually ending posteriorly; interorbital space very shallowly concave, depth between ridges less than one-fourth eye length. Anterior holding teeth with a cusp and a pair of cusplets in adults, posterior molariform teeth strongly carinate and not greatly expanded and rounded. Pre-first dorsal-fin length 32 to 36% and anal-caudal space 4 to 7% of total length. Lateral trunk denticles fairly large and rough. Propterygium separate, not fused to mesopterygium. First dorsal-fin spine directed obliquely posterodorsally in hatchlings to adults; first dorsal-fin origin behind pectoral-fin insertions, over pectoral-fin inner margins and far behind gill openings; first dorsal-fin insertion about opposite pelvic-fin origins and far behind pectoral-fin insertions; first dorsal-fin free rear tip over or behind midbases of pelvic fins and sometimes about opposite pelvic-fin insertions; first dorsal fin rounded and brush-shaped in young and low and rounded-subangular in adults, height 8 to 9% of total length, first dorsal fin subequal to pelvic fins; second dorsal-fin origin slightly to well behind pelvic-fin free rear tips, second dorsal fin rounded-angular and nearly as large as first dorsal fin. Anal fin rounded-angular, apex well anterior or reaching lower caudal-fin origin when laid back; anal-caudal space less than twice anal-fin base. Total vertebral count 103 to 109, precaudal count 67 to 72, monospondylous precaudal count 24 to 36, diplospondylous precaudal count 33 to 41, pre-first dorsal-fin spine count 19 to 20, and count from diplospondylous transition to second dorsal-fin spine 11 to 19. Identification of egg cases uncertain, but possibly like those of ***H. francisci***, with flat thin spiral flanges diagonal to case axis, without tendrils on case apices, and flanges with five turns. A small species, mature between 48 and 61 cm. **Colour**: background colour of dorsal surface light grey or brown with large black spots greater than half eye diameter, no dark harness pattern; head without a light-coloured bar on interorbital surface and with mottled dark spots or blotches under eye; fins without abrupt dark tips and white dorsal-fin apices; hatchlings without whorls on fins and body and similar in coloration to adults.



Distribution: Eastern Pacific from the coasts and offshore islands of Peru and the Galapagos Islands.

Habitat: A little-known but apparently common tropical and warm-temperate bullhead shark of inshore continental and insular waters, at moderate depths on the bottom. Lives on rocky and coral reefs, often seen resting on ledges of vertical rock surfaces at 16 to 30 m depth.

Biology: A poorly known, primarily nocturnal shark. Oviparous. Feeds on crabs; sometimes with marine algae in its stomach. One taken from the stomach of a tiger shark.

Size: Maximum total length 61 cm; an egg case possibly from this species was about 11 cm long; an apparently newly hatched male was 17 cm and an adult male was 48 cm long.

Interest to Fisheries and Human Impact: Not a commercial species (N. Chirichigno, pers. comm.), though presumably caught as discarded bycatch. Commonly seen by divers off the Galapagos Islands.

Local Names: Galapagos bull-head shark, Peruvian horn shark, Galapagos horn shark (English); Gato, Suño, Tiburón tamborín (Peru).

Remarks: N. Chirichigno (1980, pers. comm. to Compagno, 1984) suggested that there may be more than one species included under ***H. quoyi***. The ***quoyi***-like ***Heterodontus*** from Peru, with the first dorsal-fin origin slightly behind the pectoral-fin bases, includes two forms: one of these has concave posterior dorsal-fin margins, a long space about twice the anal-fin base length between the anal-fin base and lower caudal-fin origin, and an anal fin that falls well ahead of the lower caudal-fin origin when laid back; and a second form with convex posterior dorsal-fin margins, a short space much less than twice the anal-fin base length between the anal-fin base and lower caudal-fin origin, and an anal fin that reaches the lower caudal-fin origin when laid back. If distinct species, the first type is apparently the true ***H. quoyi***, while the second could be distinguished as ***H. peruanus***. I continue to hesitate to separate these two forms with the small amount of material I have examined, and follow Taylor (1972), who examined material from Peru and included them in one species.

Literature: Beebe and Tee-Van (1941); Smith (1942); McLaughlin and O'Gower (1971); Taylor (1972); Chirichigno (1980); Compagno (1984); Michael (1993); Compagno, Krupp, and Schneider (1995).

Heterodontus ramalheira (Smith, 1949)

Fig. 39

Gyropleurodus ramalheira Smith, 1949a, *Ann. Mag. Nat. Hist.* (ser. 12), 2(17): 367, fig. 1. Holotype in Natural History Museum, Maputo, Mozambique, 585 mm female, moderately deep water off Inhambane, Mozambique.

Synonyms: None.

Other Combinations: None.

FAO Names: En - Whitespotted bullhead shark; **Fr** - Requin dormeur chabot; **Sp** - Dormilón boquigrande.

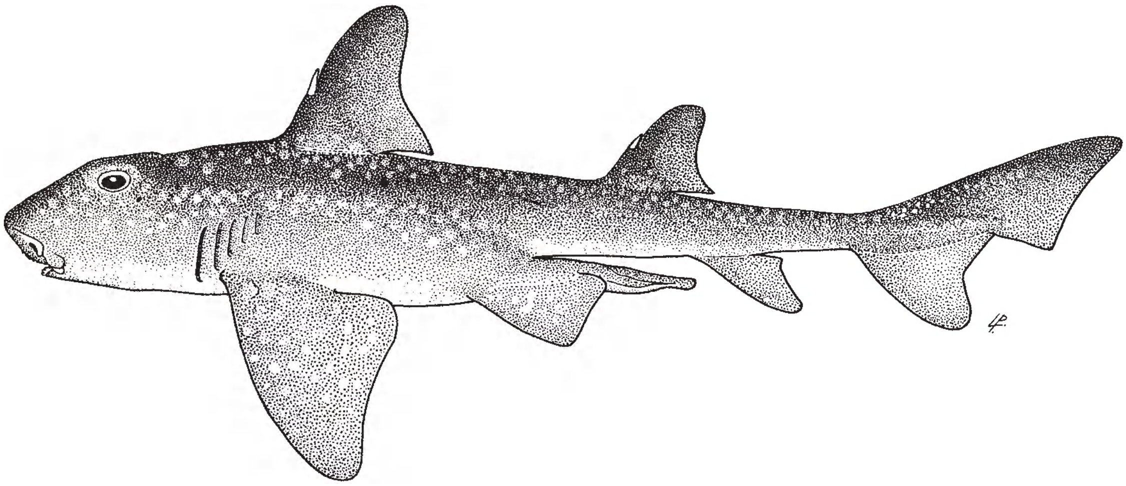


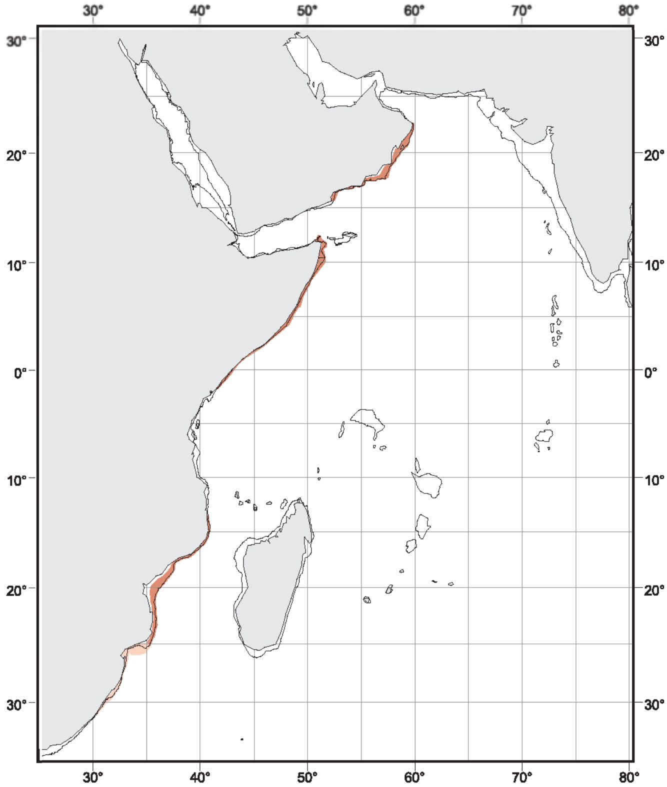
Fig. 39 *Heterodontus ramalheira*

Field Marks: Dorsal fins with spines, anal fin present, colour pattern of white spots on variegated darker background including dark saddles in adults, hatchling young with whorls of dark lines on a light background.

Diagnostic Features: Supraorbital ridges moderately high, abruptly truncated posteriorly; interorbital space moderately concave, depth between ridges about half eye length. Anterior holding teeth with a cusp and a pair of cusplets in adults, posterior molariform teeth strongly carinate and not greatly expanded and rounded. Pre-first dorsal-fin length 20 to 26% and anal-caudal space 8 to 10% of total length. Lateral trunk denticles large and rough. Propterygium separate, not fused to mesopterygium. First dorsal-fin spine directed somewhat forward in hatchlings and juveniles and vertical in adults; first dorsal-fin origin far anterior to pectoral-fin insertions, just behind or even over pectoral-fin origins and over third to fifth gill openings; first dorsal-fin insertion far anterior to pelvic-fin origins, just behind pectoral-fin insertions; first dorsal-fin free rear tip anterior to or opposite of pelvic-fin origins; first dorsal fin falcate in young and high and semifalcate in adults, first dorsal-fin height 11 to 21% of total length, first dorsal fin much larger than pelvic fins; second dorsal-fin origin over pelvic-fin inner margins and well in front of pelvic-fin rear tips, second dorsal fin falcate and much smaller than first dorsal fin. Anal fin angular and falcate, apex slightly anterior to lower caudal-fin origin when laid back; anal-caudal space slightly less than twice anal-fin base. Total vertebral count 104 to 116, precaudal count 67 to 73, monospondylous precaudal count 32 to 34, diplospondylous precaudal count 34 to 40, pre-first dorsal-fin spine count 10 to 14, and count from diplospondylous transition to second dorsal-fin spine 7 to 10. Egg cases unknown. A moderately large species, mature between 60 and 83 cm. **Colour**: background colour of dorsal surface dark reddish brown with white spots, lighter in hatchlings, without a dark harness pattern but with darker indistinct saddles; head without light-coloured bar on interorbital surface of head in adults but young with transverse parallel dark lines there, and a series of narrow dark parallel stripes under eye in hatchlings, changing to a dusky patch in larger juveniles and lost in adults; fins without abrupt dark tips and white dorsal-fin apices; hatchlings with a unique and striking pattern of numerous thin curved parallel dark lines in whorls on fins and body, lost with growth and absent in adults.

Distribution: Western and northern Indian Ocean, South Africa (KwaZulu-Natal), south-central Mozambique, Somalia, eastern shore of the Arabian Peninsula and southern Oman.

Habitat: A rare and little-known benthic shark of the outer continental shelf and uppermost slope of southern and East Africa and the eastern Arabian Peninsula, unusual for the family in being a deepish water species found at 40 to 275 m, with most records below 100 m and from trawler hauls. At least one station that recorded this shark was on sandy bottom.



Biology: Presumably oviparous, but egg cases have not been reported to date. Young individuals including a hatchling have been found off southern Mozambique at 110 m. Crabs were found in the stomachs of two individuals.

Size: Maximum about 83 cm; hatchling 18 cm; males immature at 39 cm, adolescent at 56 cm, adults to at least 69 cm; adult females 75 to 83 cm.

Interest to Fisheries and Human Impact: Interest to fisheries none, occasionally caught as bycatch of commercial bottom trawlers including shrimp trawlers off southern Mozambique and South Africa. Conservation status unknown, apparently rare or uncommon, only one specimen caught recently in experimental trawling off Mozambique (Sea Fisheries Research Institute, *R.V. ALGOA* cruise 014, 1994) with 52 offshore bottom trawl stations at depths of 37 to 517 m.

Local Names: Mozambique bullhead shark, Mosambiekse bulkophaai (South Africa); Turbarão dorminhoco de Moçambique.

Literature: Smith (1949a); Pinchuk (1969); Taylor (1972); Bass, D'Aubrey and Kistnasamy (1975d); Compagno (1984); van der Elst and Vermeulen (1986); Compagno, Ebert and Smale (1989); Bass (1986); Randall (1995); S. Dudley and P. van Blerck (pers. comm.).

Heterodontus zebra (Gray, 1831)

Fig. 40

Centracion zebra Gray, 1831, *Zool. Misc.*: 5. Holotype: British Museum (Natural History), BMNH 1953.5.10.4, dry specimen, female about 47 cm, from Swatow, China (confirmed by Eschmeyer, 1998, *Cat. Fish.*, CD-ROM, who gives the catalogue number). Also, ***Cestracion zebra*** Agassiz, 1853, *Proc. Am. Acad. Sci.*, 3: 65 (Eschmeyer, ibid.), possibly a correction of Gray's generic allocation rather than a new name.

Synonyms: ?***Cestracion philippi*** var. ***japonicus*** Dumeril, 1865: 426 (In part? See note above under ***H. japonicus***). ***Cestracion amboinensis*** Regan, 1906b: 436. Holotype: British Museum (Natural History), BMNH 1867.11.28.100 or 183, 580 mm specimen, Amboyna (confirmed by Eschmeyer, 1998: CD-ROM, who gives the catalogue number).

FAO Names: En - Zebra bullhead shark; **Fr** - Requin dormeur zebre; **Sp** - Dormilón acebrado.

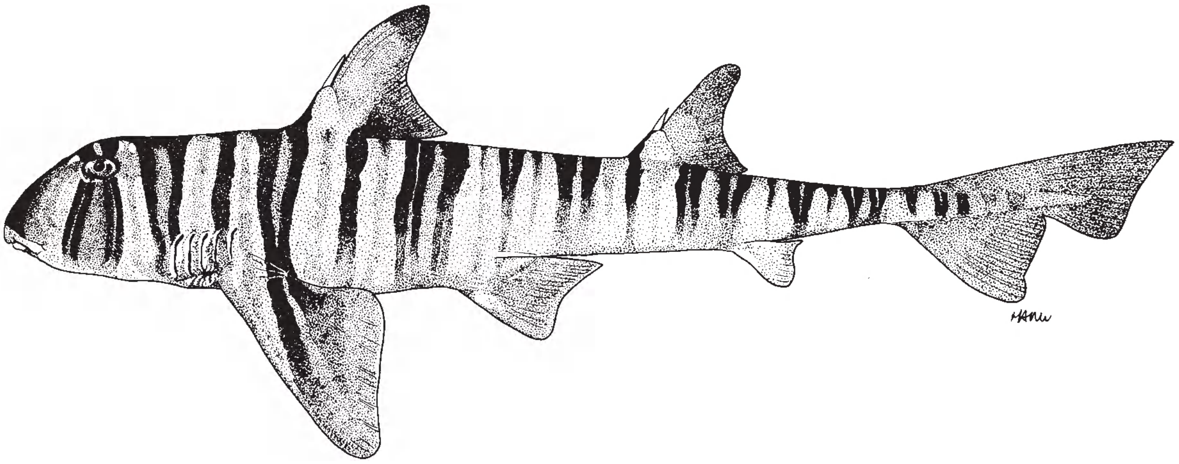


Fig. 40 *Heterodontus zebra*

Field Marks: Dorsal fins with spines, anal fin present, striking zebra-striped colour pattern of numerous narrow dark vertical saddles and bands on light background.

Diagnostic Features: Supraorbital ridges low, gradually ending posteriorly; interorbital space very shallowly concave with depth between ridges about one-fourth eye length. Anterior holding teeth with a cusp and probably a pair of cusplets in adults, posterior molariform teeth strongly carinate and not greatly expanded and rounded. Pre-first dorsal-fin length 21 to

27% and anal-caudal space 10 to 12% of total length. Lateral trunk denticles fairly small and smooth. Propterygium fused to mesopterygium. First dorsal-fin spine directed obliquely posterodorsally in young and adults; first dorsal-fin origin anterior to pectoral-fin insertions, slightly behind pectoral-fin midbases, and well posterior to fifth gill openings; first dorsal-fin insertion well anterior to pelvic-fin origins and well behind pectoral-fin insertions; first dorsal-fin free rear tip about opposite to or somewhat behind pelvic-fin origins; first dorsal fin very high and falcate in young and moderately high and falcate in adults, first dorsal-fin height 9 to 27% of total length, first dorsal fin much larger than pelvic fins; second dorsal-fin origin behind pelvic-fin rear tips, second dorsal fin falcate and much smaller than first dorsal fin. Anal fin subangular and rounded to falcate, apex slightly anterior to lower caudal-fin origin when laid back; anal-caudal space over twice anal-fin base. Total vertebral count 117, precaudal count 74 to 81, monospondylous precaudal count 34 to 38, diplospondylous precaudal count 39 to 45, pre-first dorsal-fin spine count 15 to 17, and count from diplospondylous transition to second dorsal-fin spine 10 to 16. Egg cases with flat thin spiral flanges nearly transverse to case axis, without tendrils on case apices but with short ones on opposite end, flanges with a single turn. A large species, mature between 64 and 122 cm. **Colour**: background colour of dorsal surface white or cream with a zebra-striped pattern of 22 to 36 brown or black, narrow vertical markings from snout tip to origin of caudal fin, with bold saddles and bands often separated by more diffused narrow bands, without light or dark spots, bands not arranged in a harness pattern; head with transverse dark and light bars on interorbital surface, and with a bilobate pair of dark bands separated by a light stripe under eye; fins without abrupt dark tips and white dorsal-fin apices; hatchlings without whorls on fins and body, colour pattern as in adults.

Distribution: Western Pacific: Japan, Korean peninsula, China, Taiwan (Province of China), Viet Nam, Indonesia (Sulawesi, Ambon), and tropical Australia (northern Western Australia).

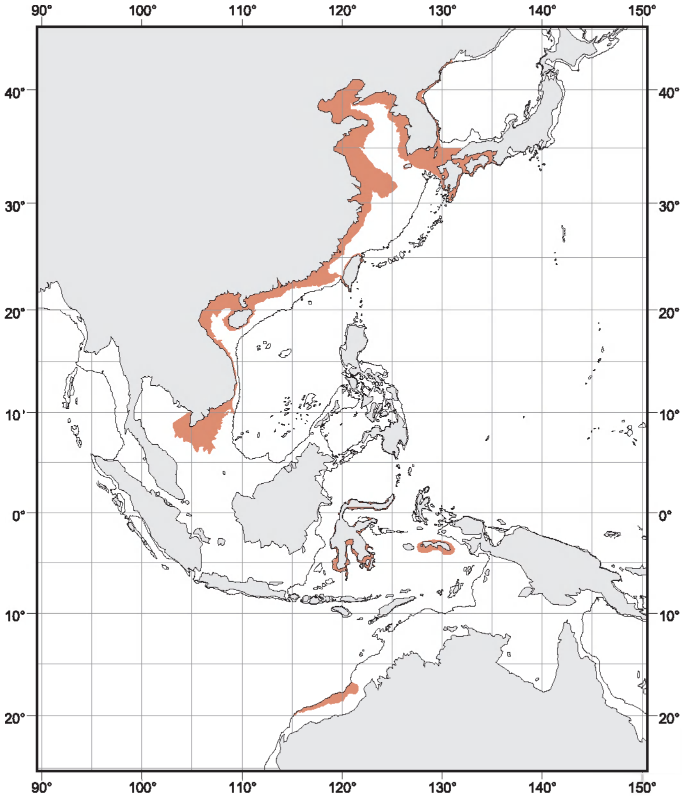
Habitat: A common but little-known bottom shark, found on the continental and insular shelves of the western Pacific from inshore down to at least 50 m in the South China Sea, but deeper and in 150 to 200 m off Western Australia.

Biology: Oviparous, details of spawning not recorded. Biology poorly known. Probably eats bottom invertebrates as with other members of the family.

Size: Maximum total length about 122 cm, hatchlings at least 15 cm, males immature at 44 cm and mature at 64 to 84 cm, females to 122 cm.

Interest to Fisheries and Human Impact: Probably of minimal interest to commercial fisheries. Caught as bycatch by commercial trawlers and possibly other fisheries in its range. Conservation status unknown but of some concern. Utilization in aquarium trade not recorded, but an obvious candidate because of its attractive colour pattern.

Local Names: Zebra horn shark, Zebra Port Jackson shark, Striped bullhead shark, Barred bull-head shark, Barred shark, Striped cat shark, Shima-nekozame (Japan); Maou urh sha or Cat shark, Mau i sha or Little shark (China).



Literature: Fowler (1941); Smith (1942); Lindberg and Legeza (1959); Chen (1963); Bessednov (1969); Taylor (1972); Compagno (1984); Nakaya and Shirai (1984); Last and Stevens (1994); Compagno and Niem (1998).

Heterodontus sp. A

Fig. 41

***Heterodontus* sp. A** J. Mee, pers. comm. for a bullhead shark collected off Oman, apparently representing an undescribed species. Also Randall, 1995, Coastal Fishes of Oman: 19, fig. 2.

Synonyms: None.

Other Combinations: None.

FAO Names: En - Oman bullhead shark; **Fr** - Requin dormeur d'Oman; **Sp** - Dormilón de Omán.

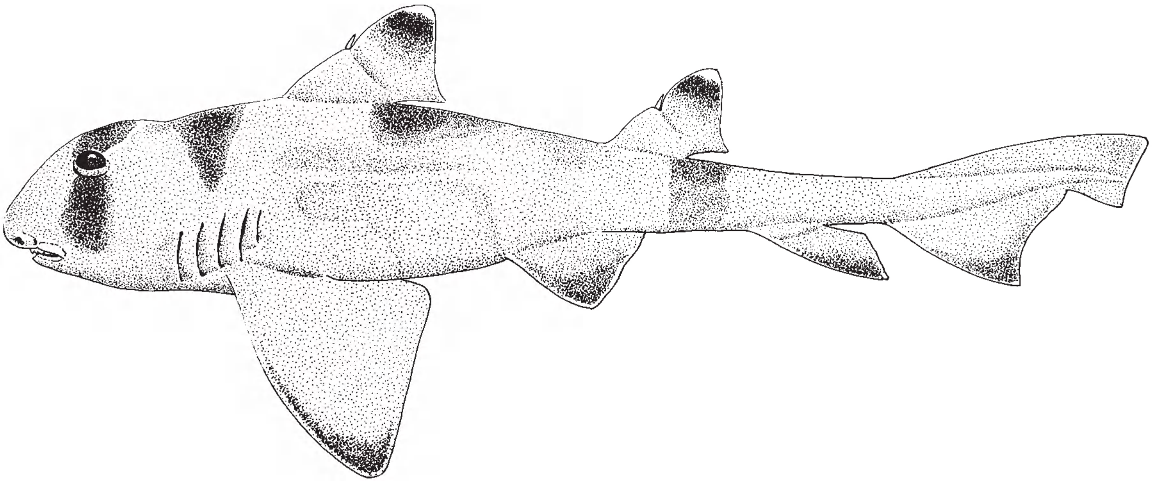


Fig. 41 *Heterodontus* sp. A

Field Marks: Dorsal fins with spines, anal fin present, first dorsal-fin origin over pectoral-fin inner margins, colour pattern of a few broad dark saddles on body, without narrow intermediate stripes or small dark spots, dorsal, caudal and pectoral fins with abruptly black tips, dorsal fins with white apical spots.

Diagnostic Features: Supraorbital ridges moderately low, gradually ending posteriorly. Interorbital space weakly concave, depth between ridges probably less than one-fourth eye length. Anterior holding teeth with a cusp and a pair of cusplets in adults, posterior molariform teeth unknown. Pre-first dorsal-fin length about 24% and anal-caudal space about 7% of total length. Lateral trunk denticles fairly rough. Propterygium condition unknown. First dorsal-fin spine directed obliquely posterodorsally in adults, first dorsal-fin origin in front of pectoral-fin insertions, somewhat behind pectoral-fin midbases, and well posterior to fifth gill openings; first dorsal-fin insertion well anterior to pelvic-fin origins and well behind pectoral-fin insertions; first dorsal-fin free rear tip slightly anterior to pelvic-fin origins; first dorsal fin low and rounded-angular in adults, height about 11% of total length, first dorsal fin about as large as pelvic fins; second dorsal-fin origin about opposite pelvic-fin insertions or rear tips, second dorsal fin weakly falcate and nearly as large as first dorsal fin. Anal fin subangular, with apex reaching lower caudal-fin origin when laid back; anal-caudal space less than twice anal-fin base. Total vertebral count 106, precaudal count 68, monospondylous precaudal count 35, diplospondylous precaudal count 33, prefirst dorsal-fin spine count 13, and count from diplospondylous transition to second dorsal-fin spine 8. Egg cases unknown. Possibly a small species, mature between 52 and 61 cm. **Colour**: background colour of dorsal surface tan to brown with 4 or 5 broad diffuse-edged brown saddles from snout tip to origin of caudal fin, without light or dark spots except dark fin tips, no harness pattern; head with a dark bar on interorbital surface and a single broad dark blotch under eye; fins tipped with dark brown or blackish, additionally a white spot on apices of dorsal fins; hatchling colour pattern unknown.

Distribution: Northern Indian Ocean: Oman.

Habitat: Caught off southern Oman, depth 80 m, presumably on soft bottom as specimens came from commercial trawlers.

Biology: Essentially unknown.

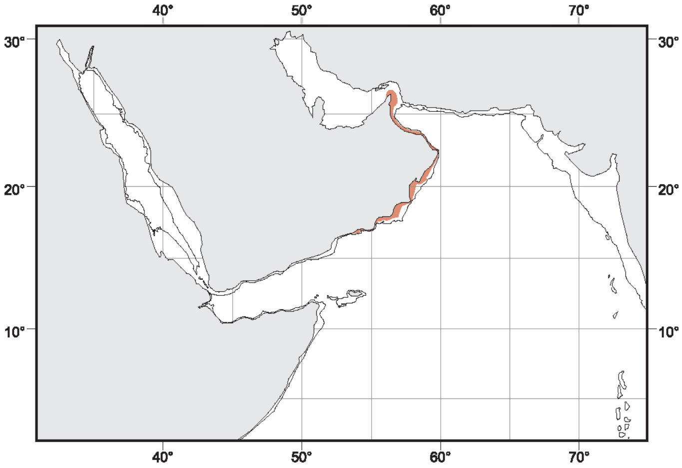
Size: Maximum size 61 cm. An adult male is 52 cm and an adult female 61.2 cm.

Interest to Fisheries and Human Impact: Caught in hauls by commercial trawlers off southern Oman.

Local Names: Oman bullhead shark.

Remarks: This is apparently an undescribed species of bullhead shark, superficially similar to *H. japonicus* but readily separable by its different colour pattern, very low dorsal fins, and possibly smaller size.

Literature: Randall (1995); J. Mee (pers. comm).



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2.2 Order LAMNIFORMES - Mackerel sharks

Order: Group Lamnae Garman, 1885, *Bull. Mus. Comp. Zool. Harvard*, 12(1): 30. Emended here to Order Lamniformes Garman, 1885.

Number of Recognized Families: 5.

Synonyms: Part 1 Squali, Abtheilung 2: Müller and Henle, 1838d: 27; Müller and Henle, 1839: 27. Part 1 Squali, Abtheilung 2, Unterabtheilung 3: Müller and Henle, 1839: 66. Ordo Plagiostomi, Subordo Squalini, Sectio Proktopterides, Tribus Dinotopterini: Bleeker, 1859: xi. Order Squali, Suborder Squali: Gill, 1862b: 394, 396. Order Squali, Suborder Galei: Gill, 1872: 22, 23. Order Plagiostomi diplospondyli, Suborder Plagiostomi asterospondyli, Group 2 Scylliolamnidae: Hasse, 1879: 51. Order Selachii, Suborder Asterospondyli: Woodward, 1889: 157. Order Asterospondyli: Gill, 1893: 130; Fowler, 1941: 4, 13; Smith, 1949: 37, 39. Order Asterospondyli, Suborder Galei: Jordan and Evermann, 1896: 19, 21. Order Euselachii, Suborder Pleurotremata, Division Galeoidei: Regan, 1906: 723. Order Selachii, Group 2, Division B, Subdivision 1, Suborder Scylliodei: Goodrich, 1909: 148. Order Pleurotremata, Suborder Galeoidei: Engelhardt, 1913: 97. Order Plagiostoma, Suborder Antacea, Group Carcharoidei: Garman, 1913: 10, 11. Order Plagiostoma, Suborder Antacea, Group Isuroidei: Garman, 1913: 10, 12. Order Euselachii, Suborder Galei, Series Lamnoidei: Jordan, 1923: 99. Order Plagiostomi, Suborder Galeiformes: Lozano y Rey, 1928: 280. Order Galea, Suborder Isurida, Superfamily Odontaspoidea: White, 1936: 4; White, 1937: 36, tab. 1. Order Galea, Suborder Isurida, Superfamily Isuroidea: White, 1936: 4; White, 1937: 36, tab. 1. Order Euselachii, Suborder Lamniformes: Bertin, 1939a: 9. Order Lamniformes: Berg, 1940: 137; Berg and Svetovidov, 1955: 65; Patterson, 1967: 670; Rass and Lindberg, 1971: 303; Lindberg, 1971: 8, 257; Compagno, 1973: 28; Applegate, 1974: 743; Nelson, 1976: 33; Compagno, 1984: 212; Nelson, 1984: 51; Gubanov, Kondyurin and Myagkov, 1986: 3, 49; Cappetta, 1987: 26, 85; Compagno, 1988: 382; Eschmeyer, 1990: 435; Nelson, 1994: 51; de Carvalho, 1996: 55; Shirai, 1996: 32; Eschmeyer, 1998. Order Lamniformes, Suborder Lamnoidei: Berg, 1940: 137; Berg and Svedovidov, 1955: 65; Patterson, 1967: 670; Lindberg, 1971: 8, 257; Nelson, 1976: 33; Nelson, 1984: 51. Order Euselachii, Suborder Galei, Superfamily Odontaspoidea: Whitley, 1940: 68. Order Euselachii, Suborder Galei, Superfamily Isuroidea: Whitley, 1940: 68. Order Selachii, Suborder Galeoidea: Romer, 1945: 576; Bigelow and Schroeder, 1948: 77, 95; Romer, 1966: 350. Order Lamnoidea, Suborder Galeoidea: Schultz and Stern, 1948: 224. Order Lamnida, Suborder Lamnina: Matsubara, 1955: 1-789. Order Galeiformes, Suborder Isuroidea: Arambourg and Bertin, 1958: 2029. Order Pleurotrema, Suborder Galeoidea: Norman, 1966: 7. Order Carchariida, Suborder Carchariina, Superfamily Carchariicae: Fowler, 1967a: 92, 140. Order Carchariida, Suborder Carchariina, Superfamily Lamnicae: Fowler, 1967a: 92, 104. Order Squatinida, Suborder Squaloidei: Glikman, 1967: 215. Superorder Lamnae, Order Odontaspidida: Glikman, 1967: 229, 230. Order Odontaspidida, Superfamily Odontaspidoidea: Glikman, 1967: 230. Order Odontaspidida, Superfamily Isuroidea: Glikman, 1967: 232. Order Odontaspidida, Superfamily Scapanorhynchoidea: Glikman, 1967: 233. Order Euselachii, Suborder Galeoidei: Blot, 1969: 702-776. Order Pleurotremata, Suborder Galeiformes: Budker and Whitehead, 1971: 5, tab. 2. Order Carcharhiniformes: Rass and Lindberg, 1971: 303; Gubanov, Kondyurin and Myagkov, 1986: 3, 61. Order Isuriformes: Chu and Meng, 1979: 114, tab. 2. Order Isuriformes, Suborder Carcharioidea: Chu and Meng, 1979: 114, tab. 2. Order Isuriformes, Suborder Isuroidea: Chu and Meng, 1979: 114, tab. 2. Order Isuriformes, Suborder Cetorhinoidea: Chu and Meng, 1979: 114, tab. 2. Order Isuriformes, Suborder Alopioidea: Chu and Meng, 1979: 114, tab. 2. Order Galeomorpha, Suborder Lamnoidea: Carroll, 1988: 599.

FAO Names: En - Mackerel sharks.

Field Marks: Large active pelagic sharks without nictitating eyelids, no barbels or nasoral grooves, nostrils free from mouth, long mouths that extend behind eyes, usually with enlarged anterior teeth and a gap or small intermediate teeth between anteriors and laterals on each side of the upper jaw, five broad gill openings, two spineless dorsal fins and an anal fin.

Diagnostic Features: Head conical to moderately depressed, not expanded laterally. Snout very short to moderately elongated, truncated to conical or blade-like and flattened, not greatly elongated and without lateral teeth or rostral barbels. Eyes usually on sides of head (dorsolateral in ***Carcharias***), without nictitating lower eyelids, secondary lower eyelids, or subocular pouches; upper eyelids not fused to eyeball. Nostrils of the ordinary shark type, transverse on snout, without barbels, nasoral grooves or circumnarial grooves, separate from mouth, anterior nasal flaps short and not reaching mouth. Five pairs of gill openings present on sides of head, with the posteriormost two in front of pectoral-fin origins or above them. Spiracles present and very small, well behind and about opposite to level of eyes. Mouth large, arched and elongated, extending well behind eyes. Labial furrows reduced or absent, when present on both jaws or on the lower jaw only. Teeth weakly to strongly differentiated along the jaws, with or without (***Megachasma***) enlarged anterior teeth but without enlarged molariform posterior teeth; usually with a gap or small intermediate teeth between anterior and lateral teeth in the upper jaw (absent in ***Megachasma***); teeth with osteodont histological structure. Trunk cylindrical, fusiform, or somewhat compressed, not flattened and ray-like. Caudal peduncle without thin lateral dermal ridges but with lateral keels variably present or absent. Dermal denticles covering entire body, not enlarged as thorns or spines. Pectoral fins small to moderately large, not expanded and ray-like, without triangular anterior lobes that cover the gill slits. Pectoral girdle (scapulocoracoid) high, U-shaped, with or (usually) without a medial joint, and with superscapulae directed posterodorsally and not contacting vertebral column. Pectoral-fin skeleton primitively tribasal, with propterygium in contact with radials and metapterygium without a proximal segment; pectoral fins primitively aplesodic, with radials confined to the fin bases, but plesodic in derived taxa and supporting the fin webs; radial count 15 to 46 with 2 to 13 segments. Pelvic fins small to moderately large, with vent continuous with their inner margins. Claspers with siphons in the abdomen but without large clasper sacs; clasper glans with a pseudosiphon, cover rhipidion, rhipidion (sometimes absent), and clasper spurs or spines; dorsal and ventral marginals of clasper skeleton rolled into a tube for the clasper canal. Two spineless dorsal fins present, with origin of first over abdomen and well in front of pelvic-fin origins; dorsal-fin skeleton with segmented radials but without segmented basal plates. Anal fin present. Caudal fin with a long dorsal lobe and the ventral lobe very strong to absent; vertebral axis elevated into the dorsal caudal lobe (heterocercal caudal fin). Vertebral calcification usually strong, secondary calcification usually in form of strong branched radii in intermedial spaces, sometimes with annular rings but without diagonal lamellae or other calcifications in the basal spaces (***Megachasma*** with vertebral calcification greatly reduced). Total vertebral count 109 to 477, precaudal vertebrae 50 to 125. Neurocranium with a short to greatly elongated, tripodal rostrum without ventral keel and open dorsally; nasal capsules spherical, oval or flattened and without subnasal fenestrae (basal communicating canals) or antorbital cartilages; orbits with complete preorbital walls (except ***Mitsukurina***), strong supraorbital crests (reduced to isolated preorbital and postorbital processes in ***Mitsukurina***), strong suborbital shelves, separate foramina for superficial ophthalmic nerves and hyomandibular nerves, and incomplete postorbital walls without lateral commissures for lateral head vein; occipital condyles low, occipital hemicentrum present between them. Jaws elongated, upper jaws (palatoquadrates) with or without short vertical orbital processes that articulate with cranial orbits in orbital notches of suborbital shelves or with basal plate; orbital processes when present do not penetrate supraorbital crests. Hyobranchial skeleton with narrow elongated basihyoid; posterior two pharyngobranchials and last epibranchial fused into a yoke-shaped element. Head muscles include elongated horizontal preorbitalis, elongated broad levator palatoquadrati that extend far behind the orbits, adductor mandibulae muscles not segmented and notched anteriorly for mouth gape; no craniomandibular muscle between the lower jaw and orbital walls; no mandibulocutaneous muscle between upper jaw and skin; and no postocular eyelid muscles. Intestinal valve of ring type, with 19 to 55 turns. Reproduction ovoviviparous (aplacental viviparous), foetal nutriment in at least some species from uterine cannibalism (eating of eggs and, in ***Carcharias taurus*** at least, eating other foetuses), but without placental vivipary or nutritive trophonemata.

Distribution: Circumglobal in temperate and tropical seas, with some lamnoids penetrating cold boreal and subantarctic waters. Some species favour temperate to cold boreal or subantarctic waters (basking shark, porbeagle and salmon shark) while most other species occur in warm-temperate to tropical seas; the white shark has one of the most extensive ranges of any cartilaginous fish.

Habitat: Mackerel sharks or lamnoids occur in a variety of marine habitats from shallow open and enclosed bays, rocky and coral reefs, and sandy beaches on the continental shelves to the epipelagic zone and possibly the mesopelagic zone of the open ocean, with a few species occurring on the continental and insular slopes. They range in depth from the intertidal to at least 1 600 m on the lower slopes, in the open ocean from the surface to at least 450 m, and on the abyssal plains over bottoms down to over 5 000 m depth. Although a few species are found in shallow bays and off beaches in the intertidal zone lamnoid sharks are not known to penetrate brackish estuaries and are not recorded from freshwater rivers and lakes.

Biology: The lamnoids are a small group of possibly 15 living species but are remarkably varied and often specialized in their form and habits. Except for the smallish crocodile shark, all living lamnoids are medium-sized to gigantic. Their ranks include sharks of littoral morphotype (Compagno, 1990a: sand tiger shark, ***Carcharias taurus***), but also high-speed tachypelagic predators (shortfin mako), macroceanic and microceanic specialists of the open ocean (longfin mako and crocodile shark), two very different filter feeders (basking and megamouth sharks), bathic and rhynchobathic deepwater specialists (bigeye sand tiger and goblin sharks), and an archipelagic shark or top predator (white shark). There are no living durophage (shell-crushing) or specialized bottom-dwelling lamnoids. The prey range of lamnoids is vast, from microscopic zooplankton to large bony fishes, marine mammals, other chondrichthyans, marine birds and reptiles, cephalopods, crabs, large gastropods, and carrion. Most lamnoids are active swimmers, some are highly migratory, and some may seasonally visit favoured areas including concentrations of food (fish banks, areas and current systems with plankton blooms, and seal colonies). At least some of the species are social (sand tiger shark, Lamnidae), and some may practice cooperative hunting. Mode of reproduction is known for only some of the lamnoid species which practice uterine cannibalism in the form of egg-eating or oophagy (Lamnidae, Alopiidae, crocodile shark, sand tiger shark, and possibly basking and megamouth sharks), but also foetus-eating or adelphophagy (sand tiger shark, possibly crocodile shark).

Interest to Fisheries and Human Impact: Several are important fisheries sharks in coastal and oceanic waters, particularly members of the families Alopiidae, Cetorhinidae, Lamnidae, and some Odontaspididae. These are regular components of targeted commercial or sport fisheries including some fisheries specifically targeting certain species (basking, shortfin mako and white sharks), and as bycatch of other fisheries targeting teleost fishes or marine invertebrates. Some species are rare to common and often discarded bycatch of high-seas and deepwater fisheries (crocodile shark, bigeye sand tiger, goblin shark). Lamnoids are caught in bottom and pelagic trawls, in pelagic and fixed gill nets (including anti-shark nets to protect bathing beaches), in fish traps, on bottom and pelagic longlines, in purse seines, with harpoons, and with hook-and-line and rod-and-reel. Many species are used for human consumption; the flesh of some species is excellent, and large fins are of high value in the oriental soup-fin trade. Several inshore and offshore species are caught by sportsfishing anglers, and some species (makos, white shark, porbeagle, threshers) are sought by big-game anglers and are recognized by the International Game Fish Association.

White sharks rarely but regularly bite swimmers, surfers, divers and boats, but less than a third of such incidents result in fatalities and very rarely result in consumption of the victim. Sand tigers and shortfin makos sporadically bite but do not consume people, and shortfin makos sometimes cause problems by jumping into sportsfishing boats after being hooked by anglers. *Jaws* and more recent shark-monster Hollywood films have inspired social phenomena leading to conservation problems for white sharks and sharks in general but have also been instrumental in promoting public awareness of the issues of shark conservation. Hollywood lamnoid stars have suffered from increased fishing pressure and demand for trophies and food including jaws, teeth, meat and fins, but have also received public support for their protection and conservation.

White sharks, shortfin makos, sand tiger sharks, and even the smalltooth sandtiger (***Odontaspis ferox***) are currently sought by ecotouristic divers and film-makers in the Indian Ocean, western Atlantic, western Pacific and eastern Pacific. Although the white shark has been subject to repeated and unsuccessful attempts to keep it in captivity in large public aquaria, the sand tiger shark is the only lamnoid that is readily kept for public viewing and is currently living in numerous aquaria in the USA, Europe and South Africa.

There are conservation concerns over several lamnoid species, including the white, basking and sand tiger sharks, some of which have declined locally from overfishing and possibly other environmental problems. Certain species yield products of extremely high value comparable to rhinoceros horns and elephant tusks, including the jaws, teeth and fins of white sharks and the fins of basking sharks. More abundant oceanic fisheries species, including makos and threshers, are in need of rational management, while less abundant to rare offshore species such as crocodile and bigeye sand tiger sharks are threatened as bycatch of fisheries driven by abundant, wide-ranging scombroid fishes. The conservation status of some uncommon to rare deepwater lamnoids, including the goblin, megamouth and bigeye sand tiger sharks, is poorly known and is of concern as these sharks are found in areas subject to intensive deepwater and oceanic fisheries and are not being monitored.

Local Names: Lamnoid sharks, Mackerel sharks.

Remarks: Garman (1885) was the first author to propose a higher group name applicable to this order but the concept of an order Lamniformes or equivalent ordinal taxon to include only lamnoid families is far more recent. Early writers and even some modern authors generally grouped orectoloboids and sometimes carcharhinoids and other shark groups together with the lamnoids. Garman's Lamnae included most living sharks except hexanchoids, heterodontoids and squatinoids. Garman (1913) later recognized two primarily lamnoid 'groups' (equivalent to infraorders or superfamilies) in his suborder Antacea (sharks), the Carcharoidei (for odontaspidids and mitsukurinids), and the Isuroidei, for alopiids, lamnids, cetorhinids, and the orectoloboid whale shark, but did not place the two groups in a common higher lamnoid group. White (1936, 1937) and Whitley (1940) essentially followed Garman's arrangement of dividing the lamnoids into two groups. An influential modern arrangement was Bigelow and Schroeder's (1948) order Selachii, suborder Galeoidea, which included the lamnoid, orectoloboid, and carcharhinoid families in a single undifferentiated group. This has been followed by several authors in various forms.

Jordan (1923) was the first author to propose an exclusive group for the lamnoids, the series Lamnoidei (equivalent to an infraorder or superfamily). Bertin's (1939a) suborder Lamniformes included all lamnoids but also (inexplicably) the carcharhinoid ***Pseudotriakis***. Rass and Lindberg (1971) used the order Lamniformes exclusively for all lamnoids except the basking shark, which was placed in the order Carcharhiniformes along with orectoloboids. Glikman (1967) proposed an order Odontaspidida for all lamnoids except the basking shark, which was placed in the order Squatinida in a suborder Squaloidei including the squaloids. Compagno (1973) and Applegate (1974) reinvented the order Lamniformes in its modern form, essentially the same as Jordan's series Lamnoidei, which has been followed by several authors including Compagno (1984, 1988, 1990b, 1999), Cappetta (1987), Eschmeyer (1990, 1998), Nelson (1994), de Carvalho (1996), and Shirai (1996). Chu and Meng (1979) used the order Isuriformes as an equivalent taxon to Lamniformes and Carroll (1988) used the order Galeomorpha, suborder Lamnoidei exclusively for lamnoids.

Continuing work on the morphology of sharks by the writer as an extension of previous work (Compagno, 1990b) supports the retention of the Lamniformes as a monophyletic but morphologically and ecologically varied group. The arrangement of lamnoid families recognized in Compagno (1984, 1990b, 1999) are retained here, but the possibility remains that the Odontaspididae is paraphyletic, and that the two genera, ***Carcharias*** and ***Odontaspis***, may be separable into two families, Carchariidae and Odontaspididae.

Key to Families:

1a. Snout greatly elongated and flattened, forming a dagger-like blade; no precaudal pits; ventral caudal lobe absent; anal fin broadly rounded (Fig. 42) . . . . **family Mitsukurinidae**


Fig. 42 ***Mitsukurina***

1b. Snout very short to moderately elongated, conical to flattened and broadly rounded but not blade-like; precaudal pits (upper pits, and often lowers) and ventral caudal lobe present; anal fin angular (Fig. 43) . . . . **→ 2**

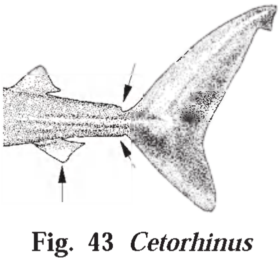


Fig. 43 ***Cetorhinus***

2a. Snout very short and broadly rounded in dorsoventral view; mouth terminal on head (Fig. 44); teeth in dental bands continuously varying, no row groups; internal gill openings with densely packed papillose gill rakers . . . . **family Megachasmidae**

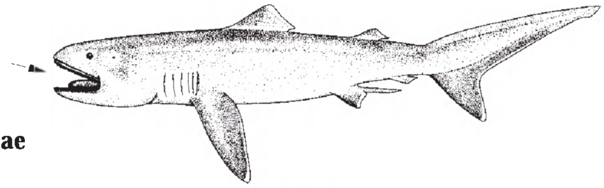


Fig. 44 *Megachasma*

2b. Snout longer and narrowly to broadly parabolic in dorsoventral view; mouth subterminal on head (Fig. 45); teeth differentiated into anteriors and lateroposteriors in upper jaw (Cetorhinidae), and anteriors, laterals and often intermediates and symphysials in other taxa; internal gill openings either without gill rakers or with rows of elongated gill raker denticles (Cetorhinidae). . . . . → **3**

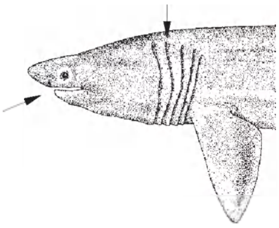


Fig. 45 *Cetorhinus*

3a. Caudal fin about as long as rest of shark; last two gill openings above pectoral-fin base (Fig. 46) . . . . **family Alopiidae**

3b. Caudal fin much shorter than rest of shark; all gill openings in front of pectoral-fin base (Fig. 47) . . . . → **4**

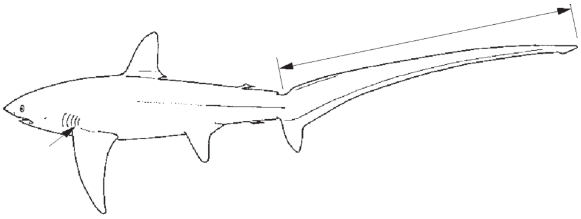


Fig. 46 *Alopias*

4a. Caudal fin asymmetrical, not lunate, ventral caudal lobe short, preventral caudal margin much shorter than dorsal caudal margin; caudal peduncle without lateral keels or with weak ones (Fig. 47) . . . . → **5**

4b. Caudal fin nearly symmetrical and lunate, with a long ventral lobe and preventral caudal margin nearly as long as dorsal caudal margin; caudal peduncle with very strong lateral keels (Fig. 48) . . . . → **6**

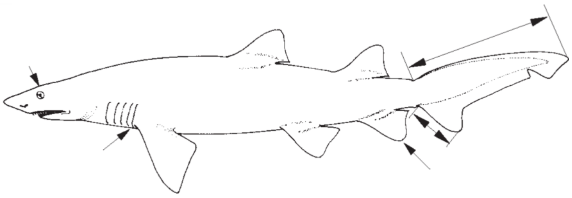


Fig. 47 *Carcharias*

5a. Eyes very large, body slender; anal fin narrow-based, pivoting; caudal peduncle with both upper and lower precaudal pits and low lateral keels on each side; gill openings extending onto dorsal surface of head (Fig. 49) . . . . **family Pseudocarchariidae**

5b. Eyes relatively small, body stout; anal fin broad-based, not pivoting; caudal peduncle with an upper precaudal pit but without a lower pit or lateral keels; gill openings not extending onto dorsal surface of head (Fig. 47) . . **family Odontaspididae**

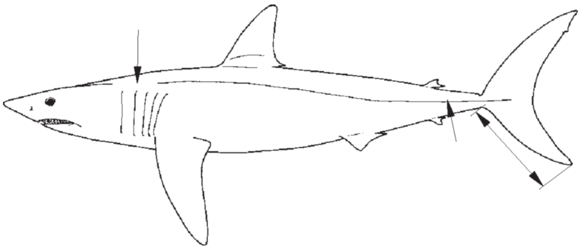


Fig. 48 *Isurus*

6a. Teeth relatively few, enlarged and blade-like, with less than 40 rows in each jaw; gill openings large but ending far lateral to mid-dorsal surface of head (Fig. 48); internal gill openings without gill rakers . . . . **family Lamnidae**

6b. Teeth numerous, minute, hooked and not blade-like, with over 150 rows in each jaw; gill openings extremely large, extending nearly to mid-dorsal surface of head (Fig. 45); internal gill openings with prominent gill rakers formed from modified dermal denticles . . . . **family Cetorhinidae**

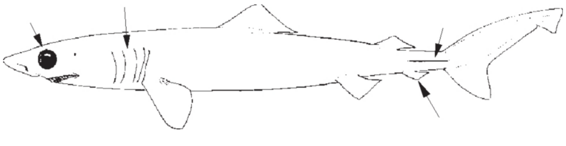


Fig. 49 *Pseudocarcharias*

2.2.1 Family ODONTASPIDIDAE

Family: Family Odontaspides Müller and Henle, 1839, *Syst. Beschr. Plagiost.*, pt. 2: 73. Emended to Family Odontaspididae Müller and Henle, 1839. The corrected form Odontaspididae was placed on the Official List of Family-Group Names in Zoology (Name no. 385) but Odontaspides was placed on the Official Index of Rejected and Invalid Family-Group Names in Zoology (Name no. 414) by the International Commission on Zoological Nomenclature (1965, Opinion 723, *Bull. Zool. Nomencl.*, 22: 33, 34). Odontaspididae was given special endorsement by the International Commission on Zoological Nomenclature (1987, Opinion 1459.6, *Bull. Zool. Nomencl.*, 44(3): 216) to take precedence over Carchariidae Müller and Henle, 1838 when the two are synonymized.

Type Genus: ***Odontaspis*** Agassiz, 1838.

Number of Recognized Genera: 2.

Synonyms: Subfamily Triglochidini Bonaparte, 1838: 208 (Family Squalidae). Type genus: ***Triglochis*** Müller and Henle, 1837. Family Carchariae Müller and Henle, 1838d: 27. Type genus: ***Carcharias*** Rafinesque, 1810. Rejected by the International Commission on Zoological Nomenclature (1965, Opinion 723: 33) but reinstated by the Commission (1987, Opinion 1459.5: 216) in the corrected form Family Carchariidae Müller and Henle, 1838 on the Official List of Family-Group Names in Zoology, with the special endorsement that it is not to be given precedence over Odontaspididae Müller and Henle, 1839 when considered a synonym of it. This name was widely used by earlier writers for members of the Carcharhinidae, following Müller and Henle's original usage, but Jordan and Gilbert (1883: 27) and many subsequent writers used it for members of the Odontaspididae with the assignment of ***Carcharias*** to this family. Family Carchariidae Jordan and Gilbert, 1883: 27. Emended spelling for Family Carchariae Müller and Henle, 1838. Type genus: ***Carcharias*** Rafinesque, 1810. Family Eugomphodidae Applegate, Espinosa, Menchaca and Sotelo, 1979: 130. Type genus: ***Eugomphodus*** Gill, 1862. Also *ibid.*: 30, as Eugonphodidae, error for Eugomphodidae.

FAO Names: En - Sand tiger sharks; **Fr** - Requins de sable; **Sp** - Solrayos, Toros.

Field Marks: Large heavy-bodied sharks with conical to slightly depressed pointed snouts, long mouths extending behind eyes, small to moderately large eyes without nictitating eyelids, moderately long gill openings in front of pectoral origins, large teeth with slender cusps and lateral cusplets, small intermediate teeth separating anterior and lateral teeth in the upper jaw, two large dorsal fins and an anal fin, small pectoral fins, a compressed caudal peduncle without keels but with an upper precaudal pit only, and an asymmetrical caudal fin with a strong but short ventral lobe.

Diagnostic Features: Head much shorter than trunk. Snout short to moderately long, pointed and bulbously conical or moderately depressed, not greatly elongated, flattened or blade-like. Eyes small to moderately large, length 1.4 to 4.1% of precaudal length. Gill openings moderately large, length of first 6.2 to 9.2% of precaudal length, not extending onto dorsal surface of head; all gill openings anterior to pectoral-fin bases; no gill rakers on internal gill slits. Mouth large, parabolic, ventral on head; jaws strongly protrusable to almost opposite snout tip but not greatly distensible laterally. Teeth large, anteriors narrow and awl-like but laterals moderately compressed and blade-like, in 34 to 56/36 to 46 (71 to 102 total) rows, less than 60 rows in either jaw; 2 or 3 rows of large anterior teeth on each side of upper jaw, three rows in lower jaw, the uppers separated from the smaller upper lateral teeth by 1 to 5 rows of small intermediate teeth (rarely absent); one or more pairs of symphysial teeth present in the lower jaw or both jaws. Trunk compressed-cylindrical and moderately stout, firm and not flabby. Caudal peduncle compressed and without keels but with a crescentic upper precaudal pit only. Dermal denticles moderately large and smooth, with flat crowns, small ridges and cusps, and with cusps directed posteriorly on lateral denticles. Pectoral fins moderately long and broad, much shorter than head in adults; pectoral skeleton aplesodic with radials confined to fin bases. Pelvic fins large, nearly or quite as large as first dorsal fin; fin skeleton aplesodic. First dorsal fin large, moderately high, erect and angular; first dorsal-fin skeleton aplesodic. Second dorsal and anal fins about as large as first dorsal fin or second dorsal smaller than first and as large or larger than anal fin; second dorsal and anal fins with broad nonpivoting bases. Caudal fin not lunate, dorsal lobe moderately long, less than half as long as rest of shark, ventral lobe short but strong. Neurocranium low to moderately high, with a short to moderately elongated rostrum, depressed internasal septum and widespread nasal capsules, small to large orbits with the supraorbital crests strong, small stapedial fenestrae, and with hyomandibular facets not extended outward. Vertebral centra strongly calcified with well-developed double cones and radii but no annuli. Total vertebral count 156 to 183, precaudal count 80 to 95, diplospondylous caudal count 71 to 88. Intestinal valve of ring type with 28 to 32 turns. Size large with adults 2.2 to at least 3.6 m.

Distribution: Odontaspidids have a wide but sporadic geographic distribution in virtually all warm-temperate and tropical seas, and further deepwater exploration and fisheries efforts with appropriate gear will undoubtedly reveal range extensions.

Habitat: Sand tiger sharks are tropical to warm-temperate, inshore to offshore, littoral and deepwater sharks. They occur in continental and insular waters from the outer shelves and down the slopes to possibly 1 600 m, on seamounts, and with one species (***Odontaspis noronhai***) also oceanic in the epipelagic and possibly the mesopelagic zone.

Biology: Sand tiger sharks are relatively slow but active littoral, epibenthic and oceanic swimmers. They feed on a wide variety of bony fishes, other sharks, rays, squids and bottom crustaceans. Development is ovoviviparous (aplacental viviparous), without a yolk-sac placenta but with uterine cannibalism in the genus ***Carcharias***, in the form of both oophagy and adelphophagy (egg and embryo-eating).

Interest to Fisheries and Human Impact: Sand tiger sharks, particularly ***Carcharias taurus*** and to a lesser extent ***Odontaspis ferox*** are or have been important for inshore and offshore fisheries wherever they occur, but are far less important and less abundant than requiem sharks (Carcharhinidae) or hammerheads (Sphyrnidae). ***Odontaspis noronhai*** is primarily a rare or uncommon bycatch of oceanic and slope line fisheries. In some areas of relative abundance, such as the east coast of North America and Australia, ***C. taurus*** has severely declined due to fishing pressure (including attacks by divers in Australia), but other areas that supported important fisheries (west Africa off Senegal, and the South China Sea) have not been monitored and local populations may need attention. Population trends in ***Odontaspis*** are essentially unknown, and potentially worrisome because of known catches by fisheries. Sand tiger sharks are presently protected in the eastern USA and Australia, and ***Carcharias taurus*** is to be decommercialized in South Africa and will only be fished by sports anglers.

These sharks are inoffensive and usually not aggressive to humans in the water and are the subject of ecotouristic viewing by divers in South Africa, Australia, the east coast of the USA, the Mediterranean Sea, and Malpelo Island in the eastern Pacific. Swimmers, divers and fishermen commonly encounter (or formerly encountered) ***C. taurus*** and more recently ***Odontaspis ferox*** in areas of abundance, but despite their impressive teeth there have been few incidents of ***Carcharias taurus*** biting people, and none currently known for ***Odontaspis***. As with other large sharks, sand tigers should be treated with respect and not harassed underwater.

Carcharias taurus is important for aquarium displays worldwide, but ***Odontaspis*** species have not been kept in captivity to the writer's knowledge. The former has the ideal combination of a fearsome, showy, large 'sharky' appearance, combined with docility, hardiness, and great longevity in captivity.

Local Names: Sand tiger sharks, Sand sharks, Ragged-tooth sharks, Grey or gray nurse sharks, Gray sharks, Patings, True sharks, Chuich'ih sha k'o; Mizuwani ka (Japan); Dlinnozubye akuly, Peschanye akuly (Russia); Tubaroes de areia.

Remarks: The family Odontaspididae was recognized by many authors following Müller and Henle (1839). However, considerable confusion was caused by these authors (Müller and Henle, 1838d), who proposed Carchariidae for carcharhinids but based it on Rafinesque's (1810) genus ***Carcharias***, which has as its type species the sand tiger shark ***C. taurus***. Several authors followed Müller and Henle in using Carchariidae for carcharhinids and Odontaspididae (or Odontaspidae) for sand tiger sharks (Bleeker, 1859; Dumeril, 1865; Günther, 1870; Regan, 1906; Engelhardt, 1913), while others used Odontaspididae for sand tiger sharks and other names for carcharhinids (Gray, 1851; Gill, 1862b, 1872; Bertin, 1939a; Berg, 1940; Berg and Svedovidov, 1955; Arambourg and Bertin, 1958; Norman, 1966). Carchariidae was reestablished and widely used as a family for sand tiger sharks rather than carcharhinids (Jordan and Gilbert, 1883; Gill, 1893; Jordan and Evermann, 1896; Garman, 1913; Jordan, 1923; Lozano y Rey, 1928; White, 1936, 1937; Whitley, 1940; Fowler, 1941, 1947; Bigelow and Schroeder, 1948; Matsubara, 1955; Garrick and Schultz, 1963; Romer, 1966; Pinchuk, 1972; Chu and Meng, 1979; Carroll 1988). However, this was curtailed by White, Tucker and Marshall (1961), who proposed to validate the name Odontaspididae over Carchariidae due to greater use in the palaeontological literature. The International Commission on Zoological Nomenclature (1965) suppressed Carchariidae for zoological literature. Various authors who published subsequent to this ruling have used Odontaspididae (Glikman, 1967; Patterson, 1967; Blot, 1969; Bailey et al, 1970; Budker and Whitehead, 1971; Lindberg, 1971; Rass and Lindberg, 1971; Compagno, 1973, 1981b, 1982, 1984, 1999; Nelson, 1976, 1984, 1994; Gubanov, Kondyurin and Myagkov, 1986; Cappetta, 1987; Eschmeyer, 1990; Robins et al., 1991a; Shirai, 1996; Helfman, Collette and Facey, 1997; Eschmeyer, 1998). Applegate et al. (1979) used Eugomphodidae. However, following a petition by Compagno and Follett (1986), the International Commission on Zoological Nomenclature (1987) reinstated Carchariidae as a valid family-group name for sand tiger sharks, but not having precedence over Odontaspididae unless removed from synonymy of that family. This leaves Carchariidae available for the genus ***Carcharias*** and its fossil relatives if considered a distinct family from Odontaspididae and ***Odontaspis***.

Although most writers have recognized only one genus of Odontaspididae (or Carchariidae), two genera are recognized here for the living species. This follows recent palaeontological and neontological work (Glikman, 1964, 1967; Herman, 1977; Compagno, 1981b, 1982, 1984; Cappetta, 1987) that treats the ***taurus*** and ***ferox*** groups of species as separate genera, but also morphological studies on the living species that revealed their distinctness (Compagno, 1984, 1990b; Compagno and Follett, 1987).

The oldest genus-group names for the ***taurus*** group are ***Carcharias*** Rafinesque, 1810, and ***Triglochis*** Müller and Henle, 1837, but these were rejected by the International Commission on Zoological Nomenclature (1965), following a proposal by White, Tucker and Marshall (1961). These authors reasoned that ***Carcharias*** Rafinesque, 1810 should be suppressed because the genus ***Odontaspis*** Agassiz, 1838 has been used far more frequently in the literature for odontaspidids (especially fossils) than ***Carcharias***. A key point to their reasoning is that "...since the respective nominal type species of ***Carcharias*** Rafinesque,1810, and ***Odontaspis*** J.L.R. Agassiz, 1838, are *congeneric*, it is the latter name which is threatened by the former" (emphasis added). However, subsequent work indicated that the two type species, ***taurus*** and ***ferox***, were not congeneric, and, provided two genera of living odontaspidids are recognized, ***Odontaspis*** is not threatened by ***Carcharias***. Compagno (1977, 1981b, 1982, 1984), Welton and Zinsmeister (1980) and various subsequent writers used the genus ***Eugomphodus*** Gill, 1862 as the next valid name that could substitute for ***Carcharias***. Cappetta (1987) used ***Synodontaspis*** in favour of ***Eugomphodus***, but the latter has priority. However, following the petition by Compagno and Follett (1986) the International Commission on Zoological Nomenclature (1987) reinstated the genus ***Carcharias*** Rafinesque, 1810.

The genus ***Odontaspis*** as presently delimited is restricted to ***O. ferox***, ***O. noronhai***, and fossil species (Compagno, 1984; Cappetta, 1987), while the genus ***Carcharias*** has a single living species, ***C. taurus***, and numerous fossil species.

Carcharias kamoharai Matsubara, 1936 (and its synonyms) have previously been placed in the genus ***Odontaspis*** or ***Carcharias*** (D'Aubrey, 1964a, b; Bass, D'Aubrey and Kistnasamy, 1975a), but this was placed in the genus ***Pseudocarcharias*** and the family Pseudocarchariidae (Compagno, 1973, 1984).

Phyletic studies by Compagno (1990b) based on external and skeletal morphology and dentition of living lamnoids, and a genetic study by Martin and Naylor (1997) suggested that Odontaspididae might be paraphyletic, with ***Carcharias*** and ***Odontaspis*** separate since the Cretaceous (Cappetta, 1987) and rating separate families. However, a phyletic study of the dentition of lamnoid sharks by Long and Waggoner (1996) suggested that Odontaspididae is monophyletic. Pending further study ***Odontaspis*** and ***Carcharias*** are retained in the family Odontaspididae following Compagno (1984).

Literature: Garman (1913); Fowler (1941, 1967a); Bigelow and Schroeder (1948); Garrick and Schultz (1963); Lindberg (1971); Shiino (1972, 1976); Compagno (1973, 1982, 1984, 1990b, 1999); D'Aubrey (1964a, b); Bass, D'Aubrey and Kistnasamy (1975a).

Key to Genera:

1a. Snout short and flattened; three rows of large upper anterior teeth on each side of symphysis; first dorsal fin about as large or slightly larger than second dorsal fin and anal fin; first dorsal fin closer to pelvic-fin bases than pectoral-fin bases (Fig. 50) . . . . ***Carcharias***

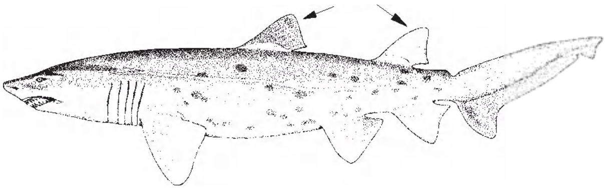


Fig. 50 *Carcharias*

1b. Snout long and conical; two rows of large upper anterior teeth on each side of symphysis; first dorsal fin noticeably larger than second dorsal fin and anal fin; first dorsal fin closer to pectoral-fin bases than pelvic-fin bases (Fig. 51) . . . . . ***Odontaspis***

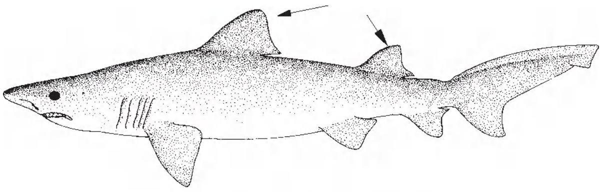


Fig. 51 *Odontaspis*

Carcharias Rafinesque, 1810

Genus: ***Carcharias*** Rafinesque, 1810, *Caratt. gen. sp. anim. piant. Sicilia, Palermo*, pt. 1: 10. Placed on the Official Index of Rejected and Invalid Generic Names in Zoology (Name no. 1746) by the International Commission on Zoological Nomenclature (1965, Opinion 723.5a, *Bull. Zool. Nomencl.*, 22(1): 33) following a proposal by White et al. (1961, *Bull. Zool. Nomencl.*, 18(4): 277-278). However, Compagno and Follett (1986, *Bull. Zool. Nomencl.*, 43(1): 89-92) argued for the reinstatement of ***Carcharias*** because its rejection on nomenclatural grounds interfered with taxonomic work on the family. This was accepted by the International Commission on Zoological Nomenclature with near-unanimity, and ***Carcharias*** was placed on the Official List of Generic Names in Zoology (1987, Opinion 1459.2, *Bull. Zool. Nomencl.*, 44(3): 216), with the special endorsement that it is not to be given precedence over ***Odontaspis*** Agassiz, 1838, whenever the two are considered synonyms.

Type Species: ***Carcharias taurus*** Rafinesque, 1810, by monotypy (International Commission on Zoological Nomenclature, 1912, Opinion 47, *Smithsonian Pub.*, (2060): 108).

Number of Recognized Species: 1.

Synonyms: Genus ***Triglochis*** Müller and Henle, 1837a: 113. Placed on the Official Index of Rejected and Invalid Generic Names in Zoology (Name no. 1747) by the International Commission on Zoological Nomenclature (1965, Opinion 723.5b: 33). Genus ***Eugomphodus*** Gill, 1862a: 60 (name only, but without allocated species); Gill, 1864: 260 (description). Type species, ***Eugomphodus griseus*** Gill, 1862, by monotypy, equals ***Carcharias griseus*** Storer, 1846 and ***C. griseus*** Ayres, 1843, and a junior synonym of ***Carcharias taurus*** Rafinesque, 1810. Subgenus ***Synodontaspis*** White, 1931 (Genus ***Odontaspis*** Agassiz, 1838): 51. Type species, ***Carcharias taurus*** Rafinesque, 1810 by original designation. Subgenus White, 1931 (Genus ***Odontaspis*** Agassiz, 1838): 63. Type species, ***Odontaspis platensis*** Lahille, 1928, by original designation.

Diagnostic Features: Snout short with preoral length 0.3 to 0.5 times mouth width and 3.2 to 4.7% (usually 4.0 or less) of total length; snout somewhat flattened but not bulbously conical. Eyes smaller and about 0.9 to 1.4% of total length, dorsolateral in position with prominent lateral head ridges below them. Upper symphysial teeth usually absent; three rows of large upper anterior teeth on either side of symphysis; anterior teeth with stout broad-tipped cusps and short and strongly hooked cusplets; anterior teeth enlarged with largest (second lower anterior) about 1.3 to 1.5% of total length; lateral teeth compressed, blade-like and with flattened cusps; posterior teeth strongly differentiated from lateral teeth, with cusps and cusplets reduced or absent and teeth molariform and carinate. Claspers tapering. First dorsal-fin base far posterior and closer to pelvic-fin bases than to pectoral-fin bases, with pre-first dorsal-fin length 48 to 58% of precaudal length; first dorsal-fin origin well behind inner margins of pectoral fins, insertion about over pelvic-fin origins. Second dorsal fin about as large as first dorsal fin. Anal fin about as large or slightly larger than dorsal fins; anal-fin origin under midbase of second dorsal fin. Irises of eyes light greenish.

Carcharias taurus Rafinesque, 1810

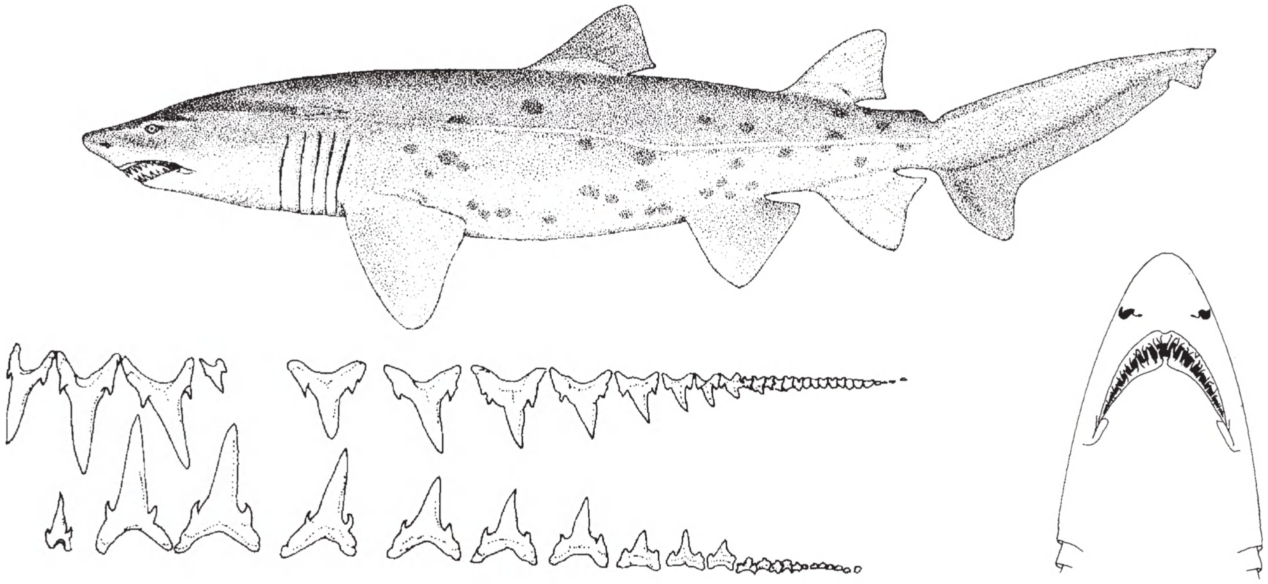
Fig. 52

Carcharias taurus Rafinesque, 1810, *Caratt. gen. sp. anim. piant. Sicilia, Palermo*, pt. 1:10, pl. 14, fig. 1. Holotype unknown; type locality, Sicily, Mediterranean Sea. Placed on the Official list of Specific Names in Zoology by the International Commission on Zoological Nomenclature (1987, Opinion 1459.4, *Bull. Zool. Nomencl.*, 44(3): 216).

Synonyms: ***Squalus americanus*** Mitchell, 1815: 483. No types known according to Eschmeyer (1998: CD-ROM). Type locality, New York. Not ***Squalus americanus*** Gmelin, 1788, = ***Dalatias licha*** (Bonnaterre, 1788). ***Squalus macrodous*** Mitchell, 1818: 328. Replacement name for ***S. americanus*** Mitchell, 1815. ***Squalus littoralis*** Le Sueur, 1818: 224. Holotype: 91 cm specimen, New York, possibly not extant. ***Squalus littoralis*** Mitchell, 1818: 328. Types unknown. Apparently a junior homonym of ***S. littoralis*** Le Sueur, 1818 according to Eschmeyer (1998: CD-ROM). ***Carcharias griseus*** Ayres, 1842: 58-59 (*nomen nudum*); Ayres, 1843a: 288 (no distinguishing features), Ayres, 1843b: 293, pl. 12, fig. 4. Type locality, Long Island, New York. No types according to Eschmeyer (1998: CD-ROM). ***Odontaspis americanus*** Abbott, 1861: 400 (new combination validates name?). ?***Carcharias tricuspidatus*** Day, 1878: 713, pl. 186, fig. 1. Figured from a skin about 373 cm TL, apparently lost (P.K. Talwar, pers. comm.), India (see remarks below). ?***Odontaspis cinerea*** Macleay, *in* Ramsay, 1880: 96. Port Jackson, New South Wales, name only, in footnote. ?***Carcharias cuspidatus*** Ogilby, 1888?: 1767. Reference in Fowler (1941: 122), but Ogilby, 1888 spelled it correctly as ***C. tricuspidatus***, hence possibly an error by Fowler? Australia. ***Lamna ecarinata*** Hemprich and Ehrenberg, 1899: 8, pl. 6, fig. 1. Holotype, Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin, ZMB 4532, a stuffed 846 mm female according to Paepke and Schmidt (1988: 163), Alexandria, Mediterranean Sea. ***Carcharias arenarius*** Ogilby, 1911: 37. Holotype: Queensland Museum, Brisbane, QM I.1884 (dry mount) according to Eschmeyer (1998: CD-ROM), Moreton Bay, Queensland. ***Carcharias owstoni*** Garman, 1913: 24. Holotype, Museum of Comparative Zoology, Harvard, MCZ-1278, 920 mm TL newborn or late foetal male, Sagami Sea, Japan. Status confirmed by Hartel and Dingerkus (1997) with catalogue number MCZ-1278-S. ?***Squalus lixa*** Larrañaga, 1923: 391. Reference from Eschmeyer (1998: CD-ROM); apparently a *species dubium* and *nomen nudum*, possibly referable to this species). ***Odontaspis platensis*** Lahille, 1928: 324, figs 13-16, pl. 3 (upper fig.). Syntypes: Possibly three syntypes, a 2.33 m specimen from Panela, near Montevideo, Uruguay, a jaw from Necochea, Quequen, Argentina, and a 2.27 m female (on which the description is primarily based) from Bahia Blanca, Argentina, status uncertain. ***Odontaspis tricuspitatus*** Fang and Wang, 1932: 241, fig. 12. Chefoo, China, apparently a spelling error for ***Carcharias tricuspidatus***.

Other Combinations: ***Eugomphodus taurus*** (Rafinesque, 1810), ***Odontaspis taurus*** (Rafinesque, 1810), ***Triglochis taurus*** (Rafinesque, 1810), ***Synodontaspis taurus*** (Rafinesque, 1810), ***Carcharias littoralis*** (Le Sueur, 1818), ***Odontaspis griseus*** (Ayres, 1843), ***Eugomphodus griseus*** (Ayres, 1843), ***Odontaspis littoralis*** (Le Sueur, 1818), ***Eugomphodus littoralis*** (Le Sueur, 1818), ***Carcharias americanus*** (Mitchell, 1815), ***Odontaspis tricuspidatus*** (Day, 1878), ***Carcharias platensis*** (Lahille, 1928).

FAO Names: En - Sand tiger shark; **Fr** - Requin taureau; **Sp** - Toro bacota.



UPPER AND LOWER TEETH OF LEFT SIDE

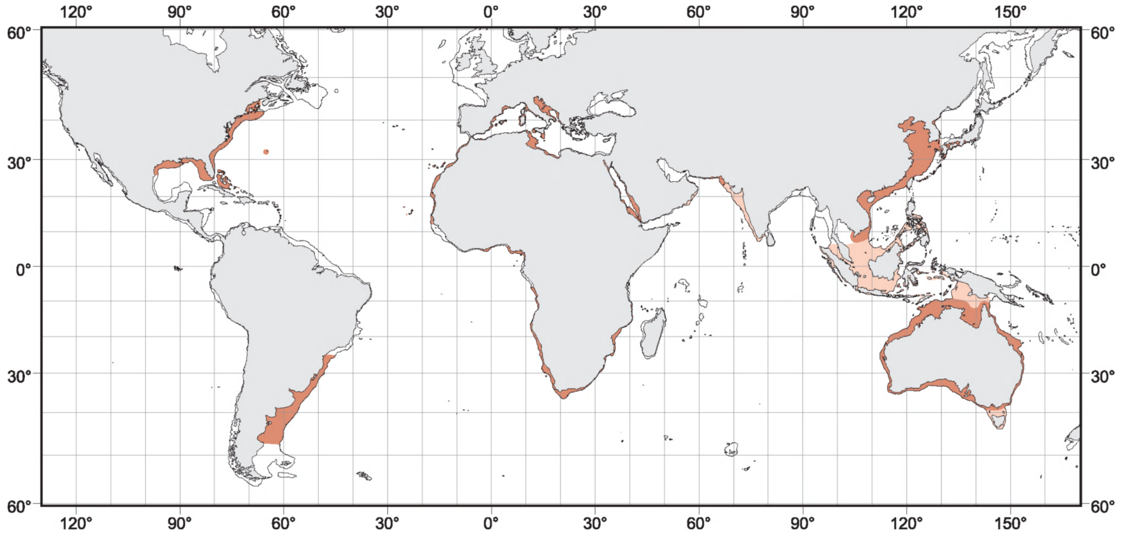
UNDERSIDE OF HEAD

Fig. 52 ***Carcharias taurus***

Field Marks: A large, bulky shark with a flattened-conical snout, eyes without nictitating eyelids, mouth long and extending behind eyes, teeth large with prominent narrow cusps and lateral cusplets, upper anterior teeth separated from lateral teeth by small intermediate teeth, anal fin and both dorsal fins equally large and broad-based, first dorsal fin on back closer to pelvic fins than to pectoral fins, upper precaudal pit present but lateral keels absent from caudal peduncle, caudal fin asymmetrical but with a strong ventral lobe. **Colour:** light brown, often with darker reddish or brownish spots scattered on body, eyes with light green irises.

Diagnostic Features: See genus *Carcharias* above.

Distribution: Wide-ranging in warm-temperate and tropical coastal waters of the Atlantic Ocean, Mediterranean Sea, and Indo-West Pacific Ocean; absent from the Central Pacific and eastern Pacific Oceans. Western Atlantic: Canada (Gulf of Maine: New Brunswick, rare), USA (Cape Cod, Massachusetts, New York, Rhode Island, Connecticut, New Jersey, Delaware, Maryland, Virginia, North Carolina, South Carolina to Florida, northern Gulf of Mexico including western Florida, Louisiana and Texas), Bahamas, Bermuda; southern Brazil to Uruguay and Argentina. Eastern Atlantic: Mediterranean to Canary Islands, Morocco, Western Sahara, Mauritania, Sao Tome and Principe, Cape Verde Islands, Senegal, Ghana, southern Nigeria to Cameroon, Angola, Namibia, and South Africa (Western Cape). Indo-West Pacific: South Africa (entire east coast), Mozambique, possibly Providence, Farquhar and Cerf Islands (western Indian Ocean), Red Sea, ?Oman, Pakistan, ?India. Western Pacific: ?Indonesia (Laiwui, Obi Major, Aru Islands), ?Malaysia, Viet Nam, ?Philippines, Japan, Taiwan (Province of China), China; Australia (Queensland, New South Wales, Victoria, South Australia, Northern Territory, Western Australia; Tasmanian records need confirmation).



Habitat: An inshore and offshore, littoral shark. This shark occurs in the surf zone off sandy and rocky beaches, in shallow bays, on offshore banks and reefs, in underwater caves, in troughs on sandy areas, and around coral and rocky reefs from the intertidal less than 1 m deep down to at least 191 m, with most at depths of 15 to 25 m. This species is often found near or on the bottom but also occurs in midwater or at the surface.

Biology: A common or formerly common to abundant shark, present in large aggregations during breeding. It is a strong but slow midwater swimmer that is more active at night. This shark is denser than water, but it swallows air at the surface and holds it in its stomach to maintain approximately neutral buoyancy. Like a bony fish with a swim bladder, it can readily halt and hover motionless in the water (*stalling*).

This species occurs as solitary individuals or in small to large aggregations or schools, ranging from 20 to at least 80 individuals in Australia and South Africa. It is strongly migratory in parts of its range, particularly in its northern and southern extremities where pronounced poleward migrations occur in summer and equatorial movements in autumn and winter (Australia, the east coast of the USA, and the east coast of South Africa). Aggregations of individuals occur for feeding, courtship, mating and birth. In Australia sexual segregation and separate migration of the sexes may occur off the east coast of Australia, with males predominant off southern Queensland during the winter and females off New South Wales. Off South Africa courtship and mating apparently occurs in the more tropical parts of its range, while pregnant females give birth in warm-temperate waters. In North America, nursery areas are not well-defined, and it may give birth along its entire range there during March and April.

The behaviour of this shark has been studied in captivity (Gordon, 1993), in a large shark tank housing sand tigers (young and adult), wobbegongs (***Orectolobus***), grey sharks (***Carcharhinus***), sevengills (***Notorynchus***), stingrays, and reef and pelagic teleosts. These studies have shown evidence of complex behaviour, including social interactions (with courtship and mating) between three adult sharks and asocial interactions with other marine vertebrates and divers. A dominance hierarchy was recorded among three adult sharks (two males and a female). Behaviour patterns observed include stalling (shark stops swimming and hovers above the bottom), *nosing* (male comes behind and below female, and places his snout just below her cloaca); *tailing* (male closely follows another male, his head interfering with normal caudal movement of the leading shark), *submissive behaviour* (or *bowing*, female swims slowly, with body angled about 15° downward, exposing the pelvic fins, and just prior to copulation), *cupping* and *flaring* (female depresses her pelvic fins into a cup-shape, then flares them outward, exposing the cloaca), *snapping* (males give quick bites to other fishes in the tank and then withdraws), *stalking* (close circling and passing of other fishes and divers), *clasper flexion* (movements of individual claspers forward and rearward), *clasper splaying* (claspers spread laterally), *clasper crossing* (claspers crossed with tips posterolateral), *shielding* (female swims close to bottom to protect her cloaca), and *scarring* (infliction of light bites by both males and females).

Most of the behaviours were observed during courtship and mating. The two adult males became reluctant to feed, and aggressive toward other fishes, particularly the grey sharks. The adult female slowed over large sand flats, cupped her pelvic fins when a male approached, and the two males lightened in colour and began 'defending' the sand flat area and presumably the female, snapping, stalking and tailing at immature sand tigers, other sharks and divers. Snapping and tailing resulted in one male driving off the other without scarring it. The dominant male then would bite the female on the anal fin forward to the pectoral fin, and the female would turn and bite the male, then return to patrol the sandy areas. Shielding also occurred, and cupping and flaring of the female's pelvic fins, while the male responded by nosing. Over a few days of courtship between the dominant male and the female, the dominant male eventually grabbed the female by the right flank and pectoral fin, contorted his body toward the female, and inserted his right clasper in her cloaca for a few minutes, then broke away and showed little further interest. Additional scarring on the female suggested that a secondary mating had occurred in one instance.

Reproduction in this species is better known than in most other lamnoids and features uterine cannibalism or cannibal vivipary. Gilmore, Dodrill and Linley (1983) give a detailed and fascinating account of the reproduction of the sand tiger shark, documenting the sequence of intrauterine nourishment in this species, in which a successful embryo progresses from using stored yolk through killing and eating other embryos to eating unfertilized eggs, for a 9 to 12-month gestation period. There are normally two young in a litter, one per uterus. Eggs leave the ovaries, and while in transit in the oviducts are fertilized and enclosed in groups of 16 to 23 in egg cases. However, at some time between fertilization and birth only one embryo of its group prevails, apparently by devouring its rivals, and this proceeds to eat fertilized eggs and smaller potential siblings *in utero* until birth. Unlike ovoviviparous non-cannibal and viviparous species, the yolk sac is reabsorbed at a small size, less than 17 cm, and the umbilical scar may be lost. At 17 cm, foetuses have sharp, functional teeth and are feeding; at about 26 cm, they can swim *in utero*; late foetuses are near 1 m long and one bit the hand of an investigating scientist (Stewart Springer). This species may breed every other year, with a rest year between pregnancies.

This species is thought to deposit two growth rings in its vertebrae per year, with males becoming adult at about five years and females at over six. Growth rings indicate animals growing to at least ten years old, with one adult male surviving nearly 17 years in captivity in South Africa. Growth is rapid over the first five years, but declines beyond 10 years and is virtually absent at 16 years.

The sand tiger primarily feeds on a wide variety of bony fishes (teleosts), with elasmobranchs an important secondary prey; crustaceans, cephalopods, and marine mammals are also taken. Bony fish prey includes herring (Clupeidae), anchovies (Engraulidae), hake (Merlucciidae), eels (Anguillidae), monkfish or anglers (Lophiidae), cusk eels (Ophidiidae), lizardfish (Synodontidae), sea catfish (Ariidae), croakers (Sciaenidae), Australian salmon (Arripidae), morwong (Cheilodactylidae), rock blackfish or opaleyes (Girellidae), bluefish, elf or taylor (Pomatomidae), mackerel and bonito (Scombridae), butterfishes (Stromateidae), snappers (Lutjanidae), wrasses (Labridae), mullet (Mugilidae), spadefish (Chaetodipteridae), sea robins (Triglidae), flatheads (Platycephalidae), duckbills (Percophidae), midshipmen (Batrachodidae), sea basses (Serranidae), porgies or sea bream (Sparidae), jacks (Carangidae), remoras (Echeneidae), flatfish (Pleuronectiformes) including soles (Soleidae), American soles (Achiridae), Atlantic flounders (Scophthalmidae), and righteye flounders (Paralichthyidae), and undoubtedly many others. Elasmobranch prey includes requiem sharks (Carcharhinidae), houndsharks (Triakidae), angel sharks (Squatinidae), skates (Rajidae) and their egg cases, and eagle rays (***Aetobatus*** and ***Myliobatis***, Myliobatidae). Invertebrate prey includes squid (Loliginidae), crabs, lobsters and hermit crabs (Paguridae). Plant material is rarely found in stomach contents, and presumably is accidentally ingested along with animal prey. Off Uruguay, Praderi (1985) found pinniped remains (7 individuals out of 12 identified as sea lion, ***Otaria***) in 2% of 557 stomachs of the sand tiger shark, as well as wounds attributable to this species on two Franciscana dolphins (***Pontoporia blainvillei***, not necessarily from predation). Schools of this shark have been observed feeding cooperatively, surrounding and bunching schooling prey and then feeding on them, and may use tail-slapping to scare and confuse schooling carangids. Australian and South African sharks sometimes have hydroid growths on their teeth, suggesting that the sharks were not feeding at the time.

Size: Maximum total length at least 318 cm, with recent records from shark meshing operations in Australia suggesting a maximum of at least 4.3 m. Older accounts attribute a size of at least 6.1 m to this species (Day, 1878), but this is unlikely. Size at birth 95 to 105 cm. Males maturing at about 190 to 195 cm with adults 220 to 257+ cm; females maturing at 220 cm or more and reaching 300+ cm, with immatures up to 225 cm.

Interest to Fisheries and Human Impact: This shark is generally fished commercially wherever it occurs, but particularly in the western North Pacific (where it is highly prized for food), off tropical west Africa, in the northern Indian Ocean (India and Pakistan), and in the western Atlantic (where it has a lesser value as a food-fish in the western North Atlantic but has been fished for hides and fins). Caught with line gear, but also with fixed bottom gill nets and in pelagic and bottom trawls. It is of only moderate importance to commercial fisheries in comparison to more abundant carcharhinids. The meat of this shark is utilized for human consumption (utilized fresh, frozen, smoked and dried-salted), carcasses for fishmeal, hides for leather (the skin is very thick and tough, but hides can be spoiled by mating scars), liver for oil, fins for the oriental sharkfin trade, and jaws and teeth for trophies and ornaments. In Australia (New South Wales) the flesh has been found to have high mercury levels (about ten times the permitted maximum), making the species unsuitable for human consumption.

The sand tiger is sought by anglers in fishing competitions because of its size (South Africa), but it is sluggish when hooked and generally does not give much of a fight. Divers using powerheads and poisoned spears found this slow-moving species an easy target in Australia and to a much more limited extent in South Africa. Such crude and barbaric sport, analogous to shooting domestic cattle with a pistol, caused a severe decline in the number of these sharks in Australia and has been banned since 1984. South African divers stopped shooting ragged-tooth sharks many years ago. Australian anglers agreed to a ban on catching sand tiger sharks in 1979. These sharks are caught live for the public aquarium trade, but the number of sharks involved in the trade is not recorded and is probably small. Separate catch statistics for this shark are not reported to FAO.

This species formerly had a bad reputation as a 'maneater' in Australian waters, but apart from shark-attack hyperbole this is apparently due to confusion with other species, particularly requiem sharks (Carcharhinidae) but possibly the white shark. Observations of this shark underwater suggest that it is primarily inoffensive and not aggressive toward people when not provoked, though its size and jagged dentition should invite respect. However, it occasionally harasses and rarely bites divers, particularly when they are spearfishing or possibly when adults are courting. This shark will steal fish off stringers and spears underwater, underlining the desirability of boating one's catch when this shark or others are about. Relatively few valid instances of this shark biting people have been reported, and minimalist bites on divers off South Africa and elsewhere suggest non-predatory behaviour and possibly agonistic activity similar to scarring bites delivered to conspecifics, other species of sharks and occasionally to divers in aquaria. Divers view aggregations of these sharks off Australia (particularly off New South Wales), South Africa and the east coast of North America. There are regular charter tours that include places frequented by congregations of these sharks. Interest in ecotouristic diving on sand tiger sharks is high in Australia, leading to potential problems such as too many divers driving away sharks in a given area, and feeding of sharks resulting in possible incidents of biting. Management of diving contact with sand tiger sharks may be required in the future, as with white sharks. Capture, tagging and live release of sand tiger sharks by recreational anglers and scientists occurs in South Africa and elsewhere, and sonic tagging is planned in Australia to trace movements.

This shark is prized as an exhibit in large aquaria and oceanaria and is regularly shown in the United States, Europe, Australia and South Africa. It is very hardy and docile in captivity, grows to adult size and can live for decades in aquaria, can be kept with other sharks and fishes (although it sometimes may prey on fishes and will bite and sometimes kill other sharks), and makes an impressive display because of its showy, toothy, 'sharky' appearance, large size, and amenability to being approached and even fed underwater by divers. An aquarium in Cape Town, South Africa allows ecotouristic divers to swim with these sharks in their giant oceanic tank. Adults will court and even give birth in adequate tank facilities.

The conservation status of this species is of concern because of its vulnerability to fisheries and recorded declines off eastern North America and Australia. It is listed as a vulnerable species by IUCN in its Red List of Threatened Animals. It congregates in large numbers in coastal areas during the breeding season, and is readily accessible to commercial fishers who can catch it with little effort. It began to decline dramatically off New South Wales, Australia, in the 1960s due to fisheries, including shooting by sports divers, and catches in anti-shark nets dropped thirty-fold. It was fully protected off

New South Wales in 1984, and later off Queensland and in all Commonwealth waters of Australia, as well as in federal waters of the eastern coast of the USA. However, despite it having a midrange intrinsic rebound potential (Smith, Au and Show, 1998), the population off New South Wales has not shown signs of recovery and a new recovery plan is being drafted by the Australian Government (Environment Australia, 2000a).

A burgeoning fishery for sand tigers along the east coast of the United States during the 1990s caused local catches to plummet off North Carolina, Florida and Chesapeake Bay, and the species was given total protection from sports and commercial fisheries in 1997.

There is a proposal under consideration by the South African Sea Fisheries Research Institute (now Marine and Coastal Management) to decommercialize catches of this species, allowing it only to be fished by sports anglers. Unfortunately, relatively little is known of trends in other places in which sand tiger sharks have been heavily fished, including the western North Pacific, western South Atlantic and eastern North Atlantic.

Local Names: Sand shark, Sand tiger shark, Sand tiger (USA); Tiburón, Sarda, Tiburón de leznas (Argentina); Lamio, Verdoun, Odontaspide taureau (France); Odontaspe tauro, Carcharia tauro, Triglochide tauro, Pisci cani (Italy); Pez toro (Spain); Psina zmijozuba sivka (Adriatic); Sarda (Canaries); Requin sable, Requin sable tachete (Senegal); Grey nurse shark, Grey nurse, Sand shark, Shovel-nosed shark (Australia); Shirowani, Umiwani, Owston's sand shark (Japan); Shovelnose shark, Sand tiger, Yellow shark, Brown shark, Grey shark, Tiger shark, Grey-nurse (English); Ragged-tooth or Raggedtooth shark, Spotted ragged-tooth or Raggedtooth shark, Raggie, Yellow belly, Blue nurse shark, Spikkel-skeurtandhaai (South Africa); Indian sand tiger, Requin taureau bambak, Toro bambaco, Blue nurse shark, Blue nurse, Dundanee (India); Ca nham nhon, Ca nham nhan (Viet Nam).

Remarks: Included as synonyms of ***Carcharias taurus*** are a number of regional species that have often been considered valid in the older literature, but which are most likely local representatives (or at most local subspecies) of a single, wide-ranging species. The dentitional characters most often used to distinguish several of these species (see Bigelow and Schroeder, 1948) apparently vary considerably within samples from a given area (Applegate, 1965; Sadowsky, 1970; Taniuchi, 1970). Regional names include ***Squalus americanus*** and its synonyms from the western North Atlantic, ***Odontaspis platensis*** from the western South Atlantic, ***Carcharias tricuspidatus*** from the Indian subcontinent, ***C. owstoni*** from the western North Pacific, and ***C. arenarius*** from Australia. Abe et al. (1968, 1969), Sadowsky (1970), Taniuchi (1970), and Whitley and Pollard (1980) have all used the species name ***taurus*** for the local representatives of the species formerly named ***owstoni***, ***arenarius*** and ***platensis***. ***Carcharias taurus*** itself has been placed in different genera as ***Odontaspis taurus***, ***Eugomphodus taurus*** and ***Synodontaspis taurus***.

Carcharias tricuspidatus was distinguished by Compagno (1984) from ***C. taurus*** by characters from Day's (1878) original description. A problem was that these characters could not be confirmed in recent accounts or specimens of this species from the Indian subcontinent. Compagno (1984) suggested that ***C. tricuspidatus*** may be a junior synonym of ***C. taurus*** as with other regional species of ***Carcharias***. Day's (1878) original description stated that ***C. tricuspidatus*** lacked labial furrows and pictured it as having a broadly rounded snout (***C. taurus*** has a rounded-angular snout and well-developed labial furrows). However, since the species was described from a skin, now lost, it is possible that the reported snout shape is in error and that the labial furrows were overlooked. Day's (1878, pl. 186, fig. 13) drawing of the snout of his ***C. tricuspidatus*** may even be based on ***Negaprion acutidens***, though the lateral view and tooth illustrated are very similar to those of ***Carcharias taurus***. An alternative is that the drawing is inaccurate and sketchy, as with several others of Day's shark drawings, and might reflect problems Day had in interpreting the holotype. During a trip to India in 1982, the writer was unable to examine any specimens of ***Carcharias*** from India (which is apparently much less common there than large carcharhinids) and was unable to confirm or deny the validity of this species. Compagno (1984) left this as a species dubium, but further consideration leads me to place it as a tentative synonym of ***C. taurus*** as suggested by ***C. taurus*** material I examined in the Pakistan collection of the Los Angeles County Museum of Natural History.

Literature: Rafinesque (1810); Day (1878); Garman (1913); Whitley (1940); Bigelow and Schroeder (1948); Springer (1948); Cadenat (1956); D'Aubrey (1964a,b); Applegate (1965); Abe et al. (1968, 1969); Lineaweaver and Backus (1970); Taniuchi (1970); Sadowsky (1970); Bass, D'Aubrey and Kistnasamy (1975a); Gilmore, Dodril and Linley (1983); Compagno (1984); Govender, Kistnasamy and van der Elst (1991); Gordon (1993); Michael (1993); Musick, Branstetter and Colvocoresses (1993); Branstetter and Musick (1994); Last and Stevens (1994); Pollard, Smith and Smith (1996); Hoese and Moore (1998); McEachran and Fechhelm (1998); Smith, Au and Show (1998); Castro, Woodley and Brudek (1999); Gelsleichter, Musick and Nichols (1999); Environment Australia (2000a).

Odontaspis Agassiz, 1838

Genus: ***Odontaspis*** Agassiz, 1838, *Recher. Poiss. Foss.*, 3: 86, 87. Placed on the Official List of Generic Names in Zoology (Name no. 1659) by the International Commission on Zoological Nomenclature (1965, Opinion 723.3c, *Bull. Zool. Nomencl.*, 22(1): 33).

Type Species: ***Carcharias ferox*** Risso, 1826 by monotypy, equals ***Squalus ferox*** Risso, 1810. This genus takes precedence over ***Carcharias*** Rafinesque, 1810 when the two are considered synonyms, by special endorsement of the International Commission on Zoological Nomenclature (1987, Opinion 1459.3, *Bull. Zool. Nomencl.*, 44(3): 216).

Number of Recognized Species: 2.

Synonyms: None.

Field Marks: Large bulky sharks with bulbous conical snouts, eyes without nictitating eyelids, mouth long and extending behind eyes, teeth moderately large with prominent narrow cusps and lateral cusplets, upper anterior teeth separated from lateral teeth by small intermediate teeth, anal fin and second dorsal fin smaller than first dorsal fin, all three broad-based, first dorsal fin on back closer to pectoral fins than to pelvic fins, only upper precaudal pit present but lateral keels absent from caudal peduncle, caudal fin asymmetrical but with a strong ventral lobe. **Colour:** blackish to light brown, eyes with black irises.

Diagnostic Features: Snout longer with preoral length 0.8 to 1.2 times mouth width and 4.4 to 7.8% (usually over 5%) of total length; snout long and bulbously conical. Eyes moderately large and about 1.6 to 2.8% of total length, lateral in position without lateral-head ridges below them. A pair of upper symphysial tooth rows present or absent; two rows of large upper anterior teeth on either side of symphysis; anterior teeth with slender narrow-tipped cusps and long straight or weakly curved but not hooked cusplets; anterior teeth smaller with largest (second lower anterior) about 1% of total length; lateral teeth little compressed and not blade-like and with little-flattened cusps; posterior teeth grading into lateral teeth, with prominent cusps and cusplets and not molariform. Claspers cylindrical and blunt-tipped. First dorsal-fin base more anterior and closer to pectoral-fin bases than to pelvic-fin bases and with pre-first dorsal-fin space 43 to 49% of precaudal length; first dorsal-fin origin over inner margins of pectoral fins, insertion well anterior to pelvic-fin origins. Second dorsal fin about half as large as first dorsal fin. Anal fin subequal to or somewhat smaller than second dorsal; anal-fin origin under or behind second dorsal-fin insertion. Irises of eyes black.

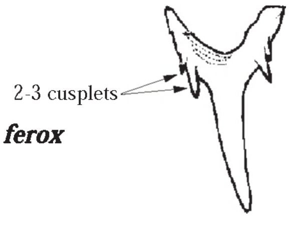
Local Names: Deepwater sand tigers.

Remarks: Following Compagno (1984) and Cappetta (1987), this account restricts the genus ***Odontaspis*** to species related to ***O. ferox***, including the living ***O. ferox***, ***O. noronhai***, and fossil species. ***O. noronhai*** needs further study of its anatomy to clarify differences between it and ***O. ferox*** and between ***Odontaspis*** and ***Carcharias***. Data on vertebral counts, vertebral calcification patterns, cranial and fin skeletal morphology, and clasper morphology were unavailable for ***Odontaspis noronhai***.

Key to Species:

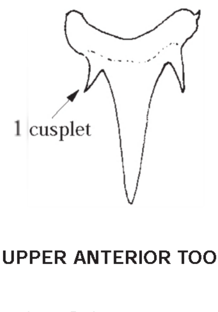
1a. Teeth mostly with two or three cusplets on each side of cusp (Fig. 53); colour grey or grey-brown above, lighter below, often with darker spots on sides but without a white-tipped first dorsal fin . . . . ***Odontaspis ferox***

1b. Teeth mostly with only one cusplet on each side of cusp (Fig. 54); colour dark reddish brown to blackish brown or black above and below, first dorsal fin often with a white blotch on its tip . . . . ***Odontaspis noronhai***



UPPER ANTERIOR TOOTH

Fig. 53 ***Odontaspis ferox***



UPPER ANTERIOR TOOTH

Fig. 54 ***Odontaspis noronhai***

Odontaspis ferox (Risso, 1810)

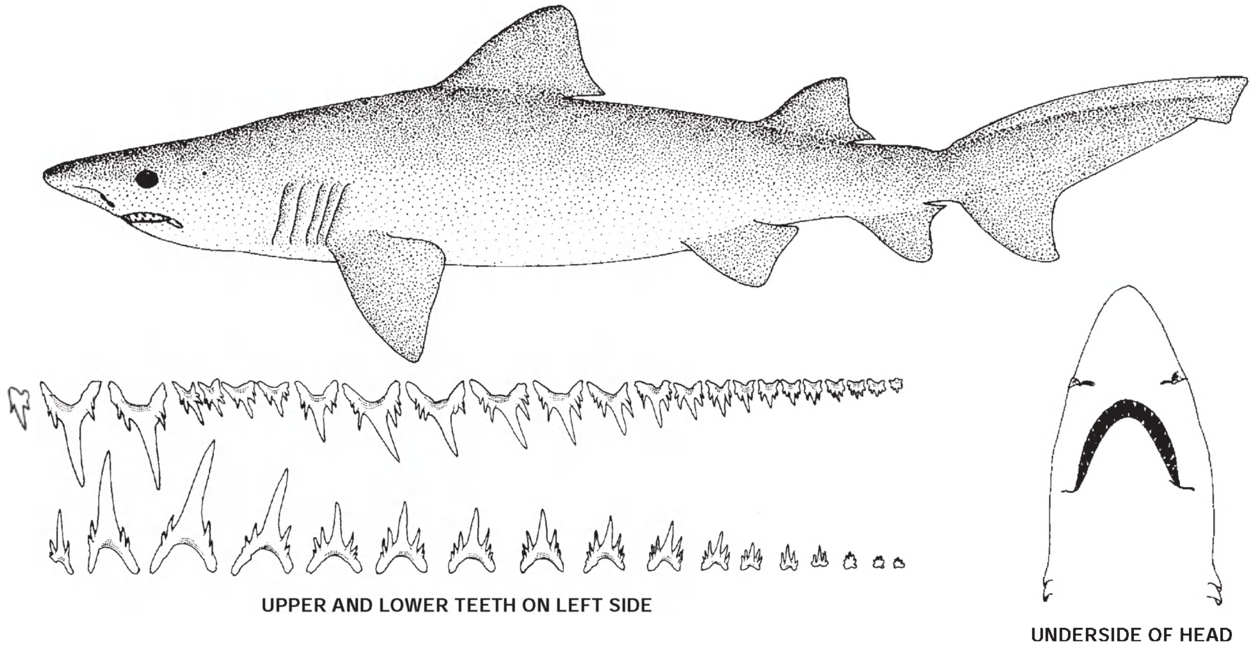
Fig. 55

Squalus ferox Risso, 1810, *Ichthyol. Nice, Paris*: 38. Holotype unknown; type locality off Nice, France, in the Mediterranean Sea. Also, ***Carcharias ferox*** Risso, 1826, *Hist. nat. Princip. Prod. Europe Méred., Paris, Poissons*, 3: 122. Description virtually verbatim that of ***Squalus ferox*** Risso, 1810, and quite evidently a generic translocation, not a new species name. Placed on the Official List of Specific Names in Zoology (Name no. 2057) by the International Commission on Zoological Nomenclature (1965, Opinion 723.4.c: 33).

Synonyms: ***Odontaspis herbsti*** Whitley, 1950: 234, fig. 1, pl. 17, fig. 1. Holotype: Australian Museum, Sydney, AMS-IB.2136, 168 cm immature male, Gabo Island, New South Wales, 137 m depth.

Other Combinations: None.

FAO Names: En - Smalltooth sandtiger; **Fr** - Requin féroce; **Sp** - Solrayo.



UPPER AND LOWER TEETH ON LEFT SIDE

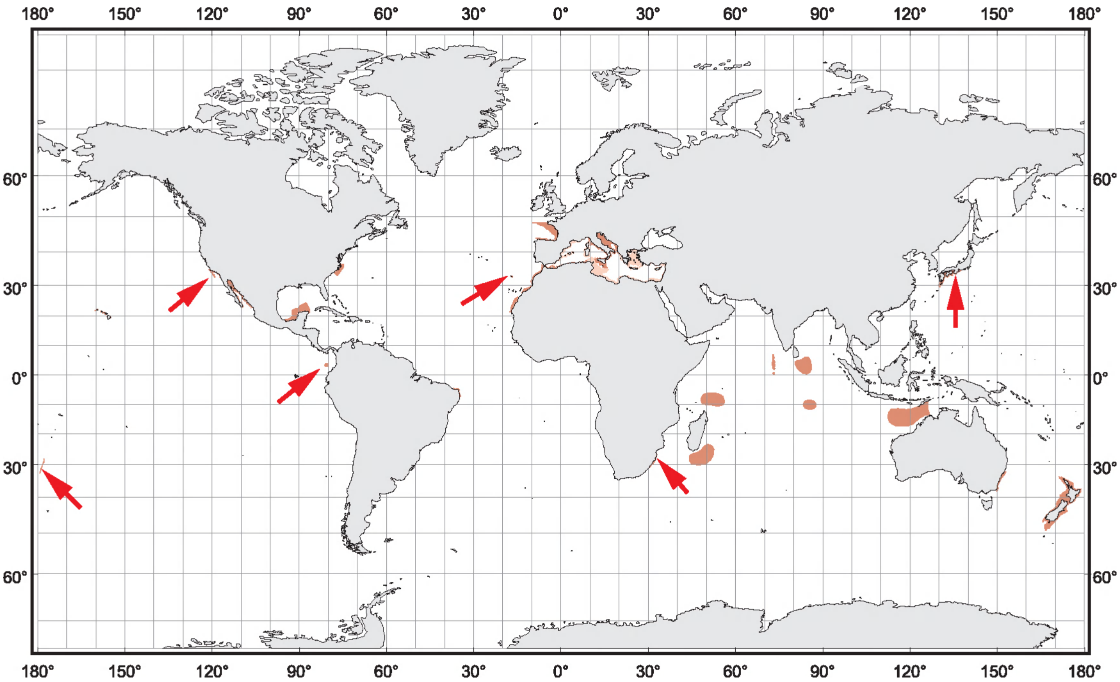
UNDERSIDE OF HEAD

Fig. 55 *Odontaspis ferox*

Field Marks: A large, bulky shark with a long bulbously conical snout, eyes moderately large without nictitating eyelids, mouth long and extending behind eyes, teeth moderately large with prominent narrow cusps and two or more pairs of lateral cusplets, upper anterior teeth separated from lateral teeth by 2 to 5 rows of small intermediate teeth, anal fin and second dorsal fin smaller than first dorsal fin but broad-based, first dorsal fin on back and closer to pectoral fins than pelvic fins, upper precaudal pit present but lateral keels absent from caudal peduncle, caudal fin asymmetrical but with a strong ventral lobe, colour medium grey or grey-brown above, usually lighter below, sometimes with darker spots scattered on body.

Diagnostic Features: Two to five (mostly four) rows of small intermediate teeth between upper anterior and lateral tooth rows; a pair of upper and a pair of lower symphysial teeth present; tooth rows numerous, 48 to 56/36 to 46 (88 to 102 total); root lobes of anterolateral teeth deeply arched and narrow; anterolateral teeth usually with 2 or 3 pairs of lateral cusplets. Pectoral fins angular. First dorsal apex subangular in adults. Anal fin with height 4.6 to 6.0% of total length. Anal fin with strongly concave posterior margin. Caudal fin with ventral caudal lobe short but stout. **Colour:** medium grey or grey-brown above, lighter below, with darker dusky spots on sides of some individuals; fins dusky with blackish edges in young but uniform dusky in adults, first dorsal fin without a white blotch.

Distribution: Possibly circumglobal in warm-temperate and tropical waters but spottily distributed. Western Atlantic: Mexico (Campeche Bank), United States (North Carolina), Brazil (NE Natal). Eastern North Atlantic: France (Bay of Biscay), Madeira, Morocco, Western Sahara, Mediterranean (Algeria, Italy, Adriatic, Lebanon). Western Indian Ocean: South Africa (KwaZulu-Natal), NE and SE of Madagascar in open ocean?, Maldives, open ocean SSE of Sri Lanka, SW of Sumatra and W of northern Australia. Western Pacific: Japan (Oshina Islands, SE Honshu off Izu-Shichito Islands), Australia (New South Wales), New Zealand and Kermadec Islands. Central Pacific: Hawaiian Islands (Oahu; record of "***O. owstoni***" from Pedestal Seamount in the Hawaiian range possibly this species or ***O. noronhai***?). Eastern Pacific: United States (southern California), Mexico (Gulf of California, Baja California), Colombia (Malpelo Island). A cosmopolitan distribution has been proposed for this species (Bonfil, 1995) and further exploration of deepish waters around the world might unveil its presence in still unknown parts of its range.



Habitat: This shark is a little-known inhabitant of deepish water in warm-temperate and tropical seas, on or near the bottom on continental and insular shelves and upper slopes at depths of 13 to 420 m, also possibly epipelagic zone in 140 to 180 m over the ocean floor. Sometimes observed by divers near dropoffs on coral reefs.

Biology: An active-swimming offshore shark, caught and seen as individuals and in small groups. Reproduction is sketchily known in the species, with litter size unknown. An adult female from the Gulf of California had its right ovary filled with hundreds of small eggs and suggests that the species practices uterine cannibalism in the form of oophagy. It is not known if developing foetuses attack and devour each other until only one is left in each uterus as in ***Carcharias taurus***, or if larger litters are possible.

This species feeds on small bony fishes, squid and shrimp. The teeth of this species and of ***Odontaspis noronhai*** are noticeably smaller and less robust than those of ***Carcharias taurus*** (with this species having larger anterior teeth than ***Odontaspis noronhai***), suggesting that both species take smaller and possibly less active prey than ***Carcharias taurus***. Also, the dentitions of both species are more weakly differentiated along the jaws, with their lateral teeth less specialized for cutting than ***Carcharias taurus*** and their posterior teeth not differentiated into specialized crushers. This suggests a more uniform diet of softer prey than in ***C. taurus***.

Apparently the offshore and deepish-water habitat of this species does not allow this shark to regulate its buoyancy by gulping air as in ***C. taurus***; it does however, have a longer body cavity than ***C. taurus***, with a very large, oily liver, and presumably uses this organ as its primary hydrostatic structure.

Off Lebanon, adult individuals confronted by scuba divers may approach quite closely or slowly flee, and have been seen to hover (*stall*), *gape*, do a *U-turn* and do *tail-shake* (shaking their caudal fins vigorously) which may indicate ambiguity or mild agonistic reactions to divers or possibly conspecifics. Individuals have been seen with scars possibly from courtship or possibly low-intensity *scarring*. They occur singly and in small groups and seem to prefer swimming near the bottom, in sandy areas and on rocky reefs, sometimes following gullies or depressions in the reef (I.K. Fergusson, L.J.V. Compagno, K.J. Graham, F. Fakhoury, W. Noshie and W. Noshie, unpublished data).

Size: Maximum total length at least 410 cm and possibly larger; size at birth above 105 cm; male mature at 275 cm, females adult at 364 cm. Specimens recently seen by divers at Malpelo Island are said to be considerably larger than the known maximum, but specimens have not been measured or photographed in such a way as to confirm this.

Interest to Fisheries and Human Impact: This uncommon to rare but wide-ranging species is primarily fished in the Mediterranean Sea and off Japan with bottom gill nets, line gear, and bottom trawls, and less commonly elsewhere. It forms a discarded or utilized bycatch of deepwater line and net fisheries in areas where it occurs. It is used in Japan for human consumption and for its liver, which is very large and oily, and has a reasonably high squalene content. Its flesh is considered far inferior to that of ***Carcharias taurus*** in Japan. This shark has not been recorded as biting people, and recent underwater observations by ecotouristic divers in the Mediterranean and off Malpelo Island in the eastern Pacific suggest that it is essentially docile although sometimes inquisitive when confronted by people. Its conservation status is essentially unknown. It has been protected in Australia since 1984.

Local Names: Bumpytail ragged-tooth shark, Bumpytail ragged-tooth, Ragged-tooth, Knopstert-skeurtandhaai (South Africa); Sand tiger shark, Herbsts or Herbst's nurse shark, Smalltooth sand tiger (Australia); Tiger ragged-tooth (Malpelo Island); Cagnia, Can da denti, Cagnassown de foundo, Carcaria feroce, Lamia, Odontaspe feroce, Pisci cani, Smidiru, Squalo feroce, Triglochide feroce (Italy); Salroig, Surraig, Solraig (Spain); Smalltooth sand tiger, Ragged-tooth shark (Azores); Psina zmij ozuba ruzicua (Adriatic); Ragged-tooth shark (USA, California), Fierce shark, Ôwanizame (Japan).

Remarks: Garrick (1974) recognized ***Odontaspis herbsti*** for members of the genus from New Zealand, Australia, California and Madeira that differed from the Mediterranean ***O. ferox*** only in lacking spots. This was followed by Bass, D'Aubrey and Kistnasamy (1975a) for South African spotless individuals, but Robins et al. (1980: 69) note that specimens from California may have spots or lack them. Observations of live ***O. ferox*** underwater in the Mediterranean Sea and off Malpelo Island also reveals individuals with and without spots (I.K. Fergusson, L.J.V. Compagno. K.J. Graham, F. Fakhoury, W. Noshie and W. Noshie, unpublished data). Apparently presence of spots reflects individual variation in a single species. ***Carcharias taurus*** is also variable in presence or absence of spots.

Literature: Risso (1810); Garman (1913); Maul (1955); Tortonese (1956); Daugherty (1964); D'Aubrey (1964a, b); Abe et al. (1968); Garrick (1974); Bass, D'Aubrey and Kistnasamy (1975); Taniuchi (1983); Compagno (1984); Nakaya (1984); Quero (1984); Gubanov (1985); Seigel and Compagno (1986); Springer (1990); Anderson and Ahmed (1993); Michael (1993); Last and Stevens (1994); Bonfil (1995, 1997); Menni, Hazin and Lessa (1995); Pollard, Smith, and Smith (1995); Villavicencio-Garayzar (1996); Santos, Porteiro and Barreiros (1997); Sheehan (1998); I.K. Fergusson, L.J.V. Compagno, K.J. Graham, F. Fakhoury, W. Noshie and W. Noshie (unpublished data); R. Bonfil (pers. comm.); D. Perrine (pers. comm.); C. Roessler (pers. comm.).

Odontaspis noronhai (Maul, 1955)

Fig. 56

Carcharias noronhai Maul, 1955, *Notul. Nat. Acad. Nat. Sci. Philadelphia*, (279): 3, figs. 1-4. Holotype: Museu Municipal do Funchal, Madeira, MMF-2691, 1 710 mm female, from off Camara de Lobos, Madeira, between 600 and 1 000 m depth and most likely at 800 to 1 000 m depth.

Synonyms: None.

Other Combinations: None.

FAO Names: **En** - Bigeye sand tiger; **Fr** - Requin noronhai; **Sp** - Solrayo ojigrande.

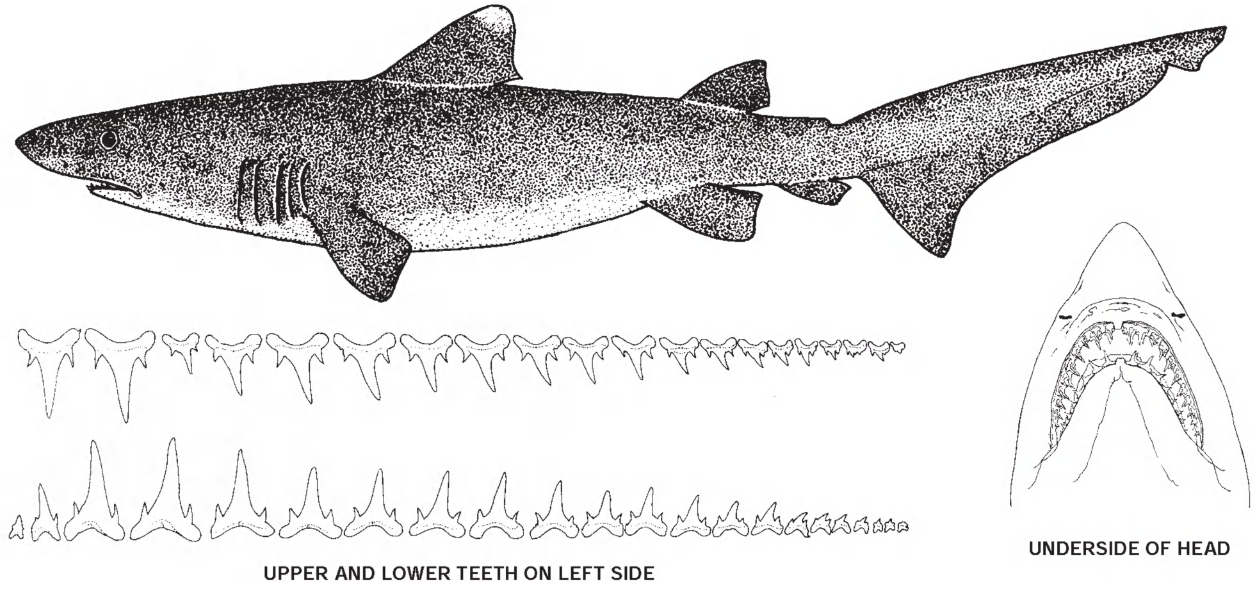
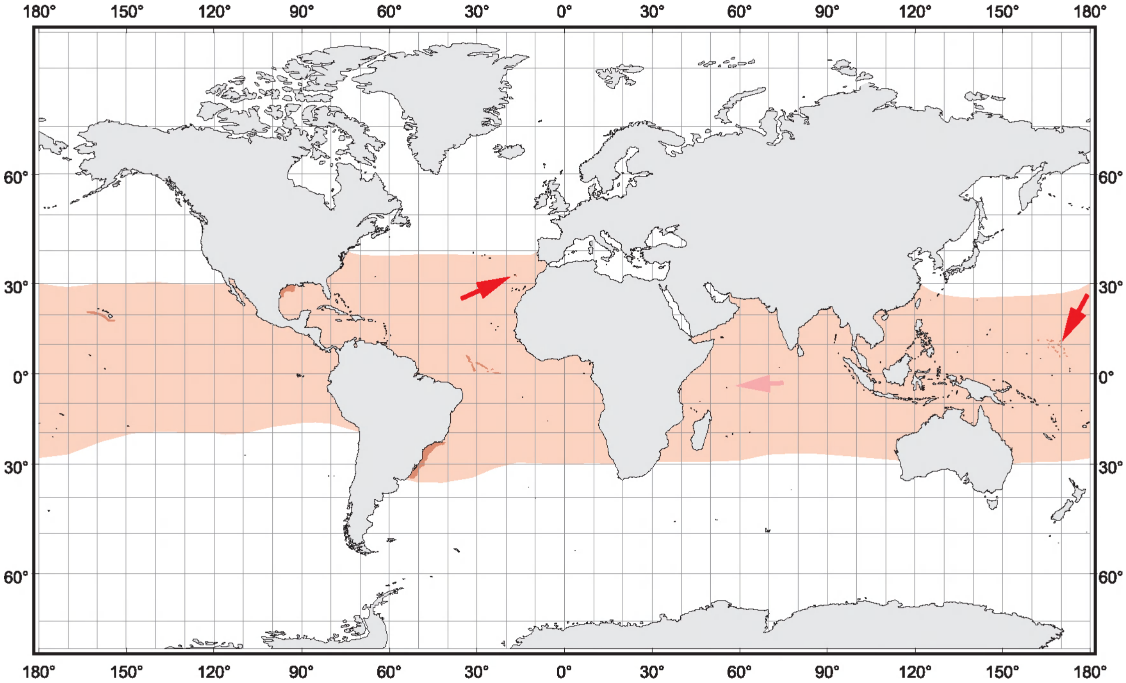


Fig. 56 ***Odontaspis noronhai***

Field Marks: A large, bulky shark with a long bulbously conical snout, eyes very large without nictitating eyelids, mouth long and extending behind eyes, teeth moderately large with prominent narrow cusps and a single pair of lateral cusplets, upper anterior teeth separated from lateral teeth by one or two rows of small intermediate teeth, anal fin and second dorsal fin smaller than first dorsal fin but broad-based, first dorsal fin on back and closer to pectoral fins than to pelvic fins, upper precaudal pit present but lateral keels absent from caudal peduncle, caudal fin asymmetrical but with a strong ventral lobe, colour uniform blackish, dark chocolate brown or reddish brown, without spots, first dorsal fin with a light apical blotch.

Diagnostic Features: One row (occasionally two rows) of small intermediate teeth between upper anterior and lateral tooth rows; a pair of rows or a single row of upper symphysial teeth present, but sometimes absent; usually 2 to 4 pairs of lower symphysial tooth rows present; tooth rows 34 to 43/37 to 46 (71 to 83 total); root lobes moderately arched and broad; anterolateral teeth with a single pair of lateral cusplets. Pectoral fin rounded. First dorsal-fin apex broadly rounded in adult. Anal fin with height 2.4 to 4.5% of total length. Anal fin with straight posterior margin. Caudal fin with ventral caudal lobe hardly developed. **Colour:** background colour of surface black, chocolate brown or dark reddish brown dorsally and ventrally, without dark spots on sides of body; fins black, first dorsal fin often with a white blotch at tip.

Distribution: Possibly circumglobal in all warm seas but as presently known sporadically distributed with very few records in the Atlantic and Central Pacific. Western North Atlantic: USA (Texas, Gulf of Mexico). Central Atlantic off Mid-Atlantic Ridge just north of the Equator. Western South Atlantic: Southern Brazil. Eastern North Atlantic: Madeira. ?Western Indian Ocean: possibly Seychelles. Pacific: South of Hawaiian Islands, USA; off Marshall Islands, possibly South China Sea.



Habitat: Apparently an inhabitant of the continental and insular slopes near the bottom at 600 to 1 000 or more metres and well off it near the surface at 100 m in water 640 m deep, and in the epipelagic and mesopelagic zone of the open ocean at 60 to 450 m in water 4 500 to 5 300 m deep. Its uniform dark coloration, similar to many deepwater oceanic teleosts, suggests a mesopelagic rather than epipelagic habitat, and it could be primarily an oceanic shark rather than a primarily slope-dwelling epibenthic species.

Biology: This is a poorly known deepwater shark. One was caught at night near the Marshall Islands at 75 m with a longline set over water between 4 500 and 5 300 m deep, suggesting that it may migrate vertically to the epipelagic zone at night and descend in the daytime but this cannot be confirmed at present. It may also be migratory and seasonal in distribution, as Brazilian catches were made only during the springtime. Reproduction unknown, feeding habits little known; one specimen had squid beaks and fish otoliths in its stomach. One caught near Hawaii writhed and snapped vigorously when captured.

Size: Maximum at least 3.6 m; males possibly adolescent at 217 cm, three males adult at 326 to 342 cm long; a female immature at 321 cm and another adult at about 326 cm.

Interest to Fisheries and Human Impact: Incidental and apparently rare bycatch of pelagic longliners but little-utilized. The holotype was taken on a vertical longline set by fishermen for black scabbardfish (***Aphanopus carbo***). Presumably taken occasionally by deepwater fisheries with line and net gear, including pelagic gill nets, purse seines and deep-set longlines. It may live mostly below the depths normally fished by horizontal pelagic longlines and purse seines, and is possibly too large to be a regular bottom or pelagic trawl catch. Conservation status unknown.

Local Names: Bigeye sand tiger, Black sand tiger, Oceanic sand tiger.

Remarks: Compagno (1981a) recognized this species on the type description (Maul, 1955) but suggested that it possibly was only an extreme variant of ***O. ferox***. However, descriptions of additional specimens convinced the writer that it is a valid species, readily separable from ***O. ferox*** (Compagno, 1984; Sadowsky et al., 1984; Branstetter and McEachran, 1986; Humpreys, Moffitt and Seki, 1989). Some characters used by Compagno (1984), including the position of the first dorsal-fin origin, more vertical position of the first dorsal-fin margin, and position of the second dorsal-fin origin relative to the pelvic-fin bases, apparently do not hold due to individual variation in ***O. noronhai*** and ***O. ferox***.

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A set of jaws possibly from the Seychelles (D. Ward, pers. comm.) has the dentitional characters of this species, and is the basis for the Indian Ocean record of ***O. noronhai***. Sadowsky et al. (1984) indicated that a possible alternative locality for this jaw set was the South China Sea.

Literature: Maul (1955); D'Aubrey (1964b); Sadowsky, Amorim and Arfelli (1984); Compagno (1984); Quero (1984); Branstetter and McEachran (1986); Humphreys, Moffitt and Seki (1989); Springer (1990); McEachran and Fechhelm (1998); D. Brogan (pers. comm.); D. Guitart-Manday (pers. comm.); V. Sadowsky (pers. comm.).

2.2.2 Family MITSUKURINIDAE

Family: Family Mitsukurinidae Jordan, 1898, *Proc. Calif. Acad. Sci. ser. 3 (Zool.)*, 1: 201.

Type Genus: ***Mitsukurina*** Jordan, 1898.

Number of Recognized Genera: 1.

Synonyms: Family Scapanorhynchidae White, 1936: 4. Type genus: ***Scapanorhynchus*** Woodward, 1889, a Cretaceous fossil genus (see remarks below).

FAO Names: En - Goblin sharks; **Fr** - Requins lutin; **Sp** - Tiburones duende.

Diagnostic Features: Head as long as trunk or slightly shorter. Snout greatly elongated, blade-like and flattened. Eyes small, length 1.0 to 2.4% of precaudal length. Gill openings short, length of first 4.6 to 5.9% of precaudal length, not extending onto dorsal surface of head; all gill openings anterior to pectoral-fin bases; no gill rakers on internal gill slits. Mouth large, parabolic, ventral on head; jaws strongly protrusable to about opposite snout tip but not greatly distensible laterally. Teeth large, anteriors and laterals very narrow and awl-like, in 35 to 53/31 to 62 (66 to 115 total) rows; three rows of large anterior teeth on each side of upper and lower jaws, the uppers separated from the smaller upper lateral teeth by a gap without intermediate teeth; a pair of lower symphysial teeth present. Trunk compressed and moderately slender, very soft and flabby. Caudal peduncle compressed and without keels or precaudal pits. Dermal denticles small and rough, with erect spike-like crowns with narrow cusps and ridges; cusps of lateral denticles pointing perpendicular to surface of skin. Pectoral fins short and broad, much shorter than head in adults; pectoral skeleton aplesodic with radials confined to fin bases. Pelvic fins large, larger than dorsal fins; fin skeleton aplesodic. Dorsal fins small, low, and rounded, or semi-angular, first and second dorsals equal-sized and smaller than the large, rounded anal fin; first dorsal skeleton aplesodic. Second dorsal and anal fins with broad, nonpivoting bases. Caudal fin not lunate, dorsal lobe long but half length of rest of shark or less, ventral lobe not developed. Neurocranium low, with a greatly elongated compressed rostrum, depressed internasal septum and widespread nasal capsules, small orbits with the supraorbital crests reduced to isolated preorbital and postorbital processes, tiny stapedial foramina, and with hyomandibular facets not extended outward. Vertebral centra strongly calcified, with well-developed double cones and radii but no annuli. Total vertebral count 122 to 125, precaudal count 53 to 56, diplospondylous caudal count 68 to 69. Intestinal valve of ring type with 19 turns. Size large, with adults 2.6 to 3.6 m long.

Local Names: Goblin sharks, Chien wên sha k'o; Mitsukurizame-ka (Japan); Akuly domovye (Russia).

Remarks: The living genus ***Mitsukurina*** has often been synonymized with the Upper Cretaceous fossil genus ***Scapanorhynchus*** Woodward, 1889 (Woodward, 1899; Regan, 1906a; Goodrich, 1909; Engelhardt, 1913; Garman, 1913; White, 1936, 1937; Berg, 1940; Fowler, 1941; Romer, 1945, 1966; Bigelow and Schroeder, 1948; Berg and Svedovidov, 1955; Matsubara, 1955; Garrick and Schultz, 1963; Norman, 1966; Bass, D'Aubrey and Kistnasamy, 1975a), but the two are apparently generically distinct (Signeux, 1949; Arambourg and Bertin, 1958; Glikman, 1967; Cappetta, I980, 1987; Compagno, 1973, 1984). The type species of ***Scapanorhynchus***, ***S. lewisi*** (Davis, 1887) is known from whole-bodied specimens that show many differences from ***Mitsukurina owstoni*** (Cappetta, 1987). Thus ***Scapanorhynchus lewisi*** has angular dorsal fins, a very long, low subangular anal fin, a more angular, much larger pectoral fin, a caudal fin with a discrete ventral caudal lobe and a more angular terminal lobe, more normal denticles with flattened, expanded tricuspidate crowns, and somewhat different teeth with less expanded and flattened root lobes and often stouter cusps. Some palaeontologists (Glikman, 1967; Shelton P. Applegate (pers. comm.)) place ***Scapanorhynchus*** in a separate family (Scapanorhynchidae) from ***Mitsukurina***, but others (Herman, 1977; Cappetta, 1980, 1987; Carroll, 1988) include them both in the Mitsukurinidae. Despite dentitional and other differences, the presence of a greatly expanded, paddlefish-like rostrum, anteriorly extended subethmoid fossa, elongated anal fin, and bent palatine processes on the palatoquadrates in both genera is strongly suggestive of a relationship between them.

Jordan (1898) proposed a new family, Mitsukurinidae, for the living goblin shark, which was recognized by several subsequent authors (Jordan, 1923; Lozano y Rey, 1928; Whitley, 1940; Glikman, 1967; Compagno, 1973, 1981b, 1984, 1999; Carroll, 1988; Nelson, 1994; Shirai, 1996; Helfman, Collette and Facey, 1997; Eschmeyer, 1998). Following White (1936, 1937), many workers used the family Scapanorhynchidae for the goblin shark (Fowler, 1941, 1947, 1967a, b; Romer, 1945; Bigelow and Schroeder, 1948; Matsubara, 1955; Budker and Whitehead, 1971; Lindberg, 1971; Rass and Lindberg, 1971; Pinchuk, 1972; Bass, D'Aubrey and Kistnasamy, 1975a; Nelson, 1976; Gubanov, Kondyurin and Myagkov, 1986), but Mitsukurinidae Jordan 1898 has priority (Compagno, 1984). Cappetta (1987) and Carroll (1988) also include the fossil genus ***Anomotodon*** Arambourg, 1952 in the Mitsukurinidae, and include as a synonym of Mitsukurinidae the family Anomotodontidae Herman, 1979. Several authors (Regan, 1906a; Engelhardt, 1913; Garman, 1913; Bertin, 1939a; Berg, 1940; Fowler, 1941; Berg and Svedovidov, 1955; Arambourg and Bertin, 1958; Norman, 1966; Romer, 1966; Patterson, 1967; Blot, 1969; Nelson, 1984; Eschmeyer, 1990), included ***Mitsukurina*** as a separate genus or as a synonym of ***Scapanorhynchus*** in the family Odontaspididae or Carchariidae, while Goodrich (1909) included it in the Lamnidae.

Mitsukurina shows a curious mix of numerous primitive and derived characters that isolate it from other living lamnoids. Compagno (1990b), using morphological characters for a phyletic analysis of Lamniformes, and Long and Waggoner (1996), using dental morphology, suggested that Mitsukurinidae is the sister group of all other living Lamniformes. Recent molecular phyletic studies (Naylor et al., 1997; Martin and Naylor, 1997) have not given unambiguous results on the relationship of Mitsukurinidae to other lamnoids, but one possibility is that Mitsukurinidae is sister to all other taxa. Morphological and molecular studies apparently support the retention of ***Mitsukurina*** in its own family.

This family includes only a single living species, ***Mitsukurina owstoni***, along with fossil species of ***Anomotodon***, ***Mitsukurina*** and ***Scapanorhynchus***. Morphological definition of the family is based on the living species.

Mitsukurina Jordan, 1898

Genus: ***Mitsukurina*** Jordan, 1898, *Proc. Calif. Acad. Sci. ser. 3 (Zool.)*, 1: 199.

Type Species: ***Mitsukurina owstoni*** Jordan, 1898, by monotypy.

Number of Recognized Species: 1.

Synonyms: None.

Diagnostic Features: See family Mitsukurinidae above.

Mitsukurina owstoni Jordan, 1898

Fig. 57

Mitsukurina owstoni Jordan, 1898, *Proc. Calif. Acad. Sci. ser. 3 (Zool.)*, 1: 200, pls. 11-12. Holotype: Zoological Museum, University of Tokyo, 107 cm immature male, near Yokohama, Japan, in deep water. Holotype lost, according to Eschmeyer (1998, *Cat. Fish.*: CD-ROM).

Synonyms: ***Odontaspis nasutus*** de Braganza, 1904: 49, 104, pl. 1, figs. 1-1c. Type locality, Mare de Sezimbra, Portugal, 603 m. Types unknown according to Eschmeyer (1998). ***Scapanorhynchus jordani*** Hussakof, 1909: 257, text-figs., pl. 44. Syntypes (2): American Museum of Natural History, AMNH-00004SW, jaws, model on display from 1 300 mm female; 1 155 mm female, formerly in the Zoological Department at Columbia University. Type locality, Japan. ***Scapanorhynchus dofleini*** Engelhardt, 1912: 644. Holotype: Zoologischen Staatssammlung München, 2 100 mm female, Mayegawa, Sagami Sea, Japan. Locality of holotype unknown according to Eschmeyer (1998: CD-ROM). ***Scapanorhynchus mitsukurii*** White, 1937: 29 (error for ***Mitsukurina owstoni*** Jordan, 1898). Japan.

Other Combinations: ***Scapanorhynchus owstoni*** (Jordan, 1898).

FAO Names: En - Goblin shark; **Fr** - Requin lutin; **Sp** - Tiburón duende.

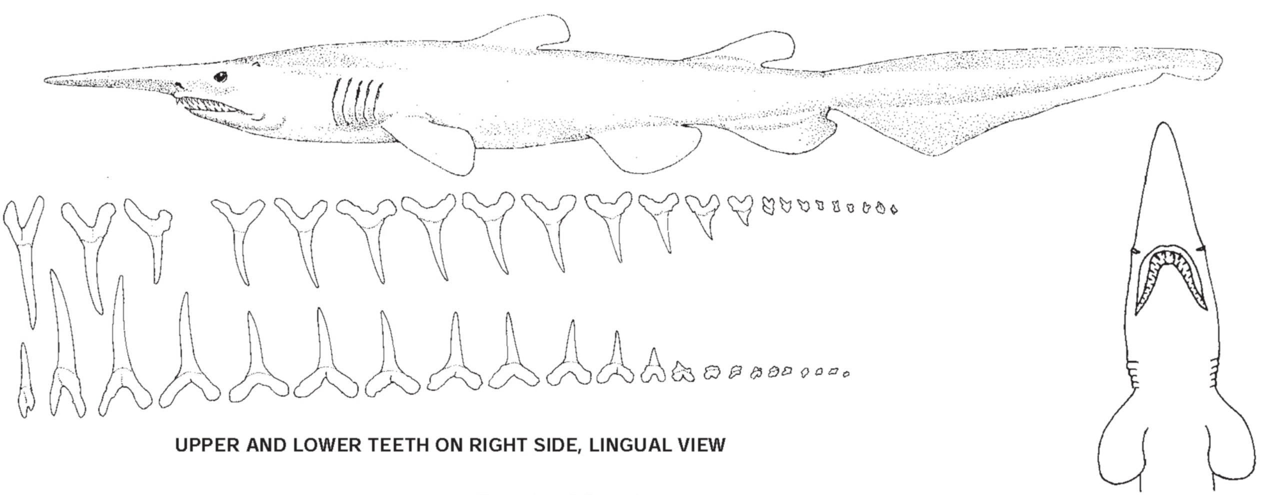
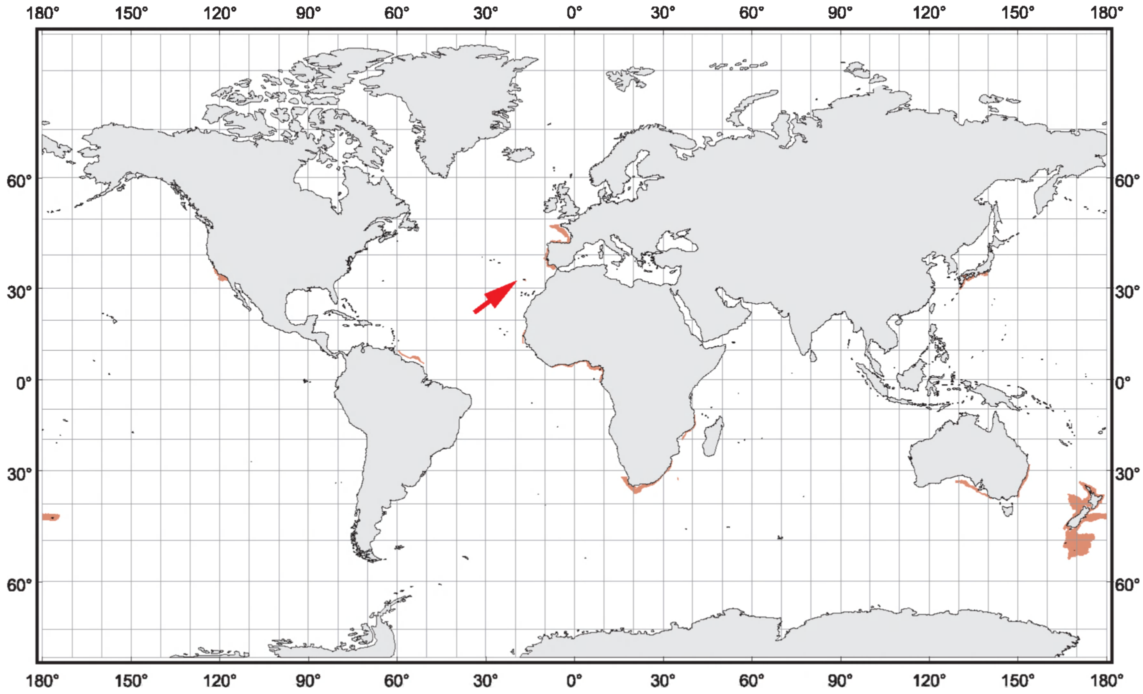


Fig. 57 *Mitsukurina owstoni*

Field Marks: This unmistakable shark has a flat blade-like elongated snout, tiny eyes without nictitating eyelids, soft flabby body, slender very long-cusped teeth in long highly protrusable jaws, two spineless dorsals and an anal fin, and a long caudal fin without a ventral lobe. **Colour:** live and newly-captured individuals are pinkish white, but usually fade to brownish in alcohol.

Diagnostic Features: See family Mitsukurinidae above.

Distribution: Western Atlantic: Guiana, Surinam, French Guyana. Eastern Atlantic: France (Bay of Biscay), Madeira, Portugal, Senegal, Gulf of Guinea, South Africa (Western Cape). Western Indian Ocean: South Africa (Eastern Cape, KwaZulu-Natal), Mozambique (Mozambique seamount range). Western Pacific: Japan, Australia (South Australia, New South Wales), New Zealand. Eastern Pacific: USA (southern California).



Habitat: A poorly known, bottom-dwelling shark that inhabits the outer continental shelves and upper slopes and is found off seamounts, but rarely occurs at the surface or in shallow water close inshore. Most records are on or near the continental slopes between 270 and 960 m deep but down to at least 1 300 m, sometimes in shallower shelf waters at 95 to 137 m. Seamount records suggest that the species is oceanic or semioceanic in addition to its known occurrences off continental slopes.

Biology: Very little is known of the biology of this bizarre shark, which is rare in most places where it is known apart from Japan and possibly Portugal. The long flexible caudal fin, without a ventral lobe, the soft, flabby body, and small, soft paired and unpaired fins, suggest that the goblin shark is a relatively inactive, slow swimming species with a density close to seawater. Its remarkable blade-like snout is superficially similar to those of the chondrostean paddlefishes (Polyodontidae), and like these fishes may use it as a forward-projecting prey detector. Its slender, pick-like anterior and lateral teeth suggests small, soft-bodied prey including fishes, shrimp and squid, and one specimen was found with fish remains in its stomach. As in ***Carcharias taurus***, the posterior teeth of the goblin shark are modified for crushing.

The jaws of the goblin shark are highly specialized for rapid projection from the head as in some mesopelagic teleosts, propelled in part by a double set of elastic tensioning ligaments at the mandibular joints. The first set of ligaments are at the hinge joint between the ceratohyal head and Meckel's cartilage on each side; and the second set extends across the head of the hyomandibula in a cavity between the ceratohyal and Meckel's cartilage on each side. The ligaments are stretched when the jaws are retracted rearward into the mouth but are relaxed when the jaws are shot forward, and apparently function (along with the long preorbitalis muscles) like a catapult to project the jaws forward and snap up small animals.

This shark is often illustrated and preserved with the jaws more or less protruded but a live goblin shark in captivity in the Marine Science Museum, Tokai University, Shimizu, Japan, held its jaws tightly retracted while swimming (Shiobara, 1990, Y. Shiobara, pers. comm. and photographs). Early catch records (Bean, 1905) suggested that mature females visited the east coast of Honshu during the springtime only. Mode of reproduction unknown; a pregnant female has never been reported.

Size: Maximum total length at least 384 cm. Size at birth unknown, smallest recorded specimen 107 cm; mature males 264, 320 and 384 cm, females reaching 373 cm, one mature at 335 cm. Weight 210 kg at 384 cm.

Interest to Fisheries and Human Impact: Interest to fisheries minimal, taken as untargeted bycatch of deepwater trawl fisheries and occasionally taken with deepwater longlines, deep-set gill nets, and possibly purse seines. Utilized dried-salted for human consumption. Harmless to people. A spectacular aquarium exhibit, but seldom kept in captivity; one lived for a week in an aquarium at Tokai University, Shimizu, Japan. Conservation status unknown.

Local Names: Nasuta (Portugal), Elphin or Elfin shark, Japanese goblin shark, Tenguzame or Tengu (goblin) shark, Mitsukurizame or Mitsukuri's shark (Japan); Kabouterhaai (South Africa).

Literature: Jordan (1898); Bean (1905); Hussakof (1909); Garman (1913); Fowler (1941); Bigelow and Schroeder (1948); Stead (1963); Bass, D'Aubrey and Kistnasamy (1975a); Uyeno, Nakamura and Mikami (1976); Piotrovsky and Prut'ko (1980); Uyeno, Matsuura and Fujii (1983); Cadenat and Blache (1981); Quero (1984); Compagno (1984); Davison and van Berkel (1985); Stevens and Paxton (1985); Shcherbachev (1987); Compagno, Ebert and Smale (1989); Springer (1990); Shiobara (1990); Compagno, Ebert and Cowley (1991); Last and Stevens (1994); Shinohara and Matsuura (1997); P. Duarte (pers. comm.); D.A. Ebert (pers. comm.); Y. Shiobara (pers. comm.); J.D. Stevens (pers. comm.); J. Ugoretz (pers. comm.).

2.2.3 Family PSEUDOCARCHARIIDAE

Family: Family Pseudocarchariidae Compagno, 1973, *J. Linn. Soc.(Zool.)*, 53, suppl. 1: 28.

Type Genus: ***Pseudocarcharias*** Cadenat, 1963.

Number of Recognized Genera: 1.

Synonyms: Family Pseudocarcharinidae Shirai, 1996: 34. Probably error for Pseudocarchariidae.

FAO Names: En - Crocodile sharks; **Fr** - Requins crocodile; **Sp** - Tiburones cocodrilo.

Diagnostic Features: Head much shorter than trunk. Snout moderately long, pointed and bulbously conical, not greatly elongated or flattened and blade-like. Eyes very large, length 3.6 to 4.9% of precaudal length. Gill openings moderately long, length of first 5.4 to 8.2% of precaudal length, extending onto dorsal surface of head; all gill openings in front of pectoral-fin bases; no gill rakers on internal gill slits. Mouth large, parabolic, ventral on head; jaws strongly protrusable to almost opposite snout tip but not greatly distensible laterally. Teeth large, the anteriors narrow and awl-like, the laterals more compressed and blade-like, with 26 to 29/21 to 26 (45 to 52 total) rows; two rows of enlarged anterior teeth on each side of upper jaw, the uppers separated from the smaller upper lateral teeth by a row of small intermediate teeth; three rows of lower anteriors on each side, the first two rows enlarged but the third about as large as laterals; symphysials absent. Trunk cylindrical and slender. Caudal peduncle slightly depressed and with low lateral keels and upper and lower crescentic precaudal pits present. Dermal denticles small and smooth, with flat crowns, small ridges and cusps, and with cusps directed posteriorly on lateral denticles. Pectoral fins small, short and broad, much shorter than head in adults; pectoral skeleton aplesodic with radials confined to fin bases. Pelvic fins large, somewhat smaller than pectoral and first dorsal fins; fin skeleton aplesodic. First dorsal fin small, low, and angular; fin skeleton aplesodic. Second dorsal fin smaller than first but larger than anal fin; second dorsal fin with a broad nonpivoting base but anal fin pivotable. Caudal fin not lunate, dorsal lobe moderately long but less than half as long as rest of shark, ventral lobe short but strong. Neurocranium moderately high, with a short to moderately elongated rostrum, depressed internasal septum and narrowly separated nasal capsules, large orbits with the supraorbital crests strong, small stapedial fenestrae, and with hyomandibular facets not extended outward. Vertebral centra strongly calcified, with well-developed double cones and radii but no annuli. Total vertebral count 146 to 158, precaudal count 80 to 88, diplospondylous caudal count 60 to 71. Intestinal valve of ring type with 24 to 27 turns. Size small with adults 0.74 to 1.10 m.

Local Names: Crocodile sharks, Tubarões crocodilos (Mozambique).

Remarks: The single living genus and species in this family, ***Pseudocarcharias kamoharai***, was formerly placed in the family Odontaspididae and genus ***Odontaspis*** or ***Carcharias*** (Matsubara, 1936; Teng, 1959; D'Aubrey, 1964a, b; Bass, D'Aubrey and Kistnasamy, 1975a). Anatomical work by the writer has shown that this species is very distinct and rates a separate family Pseudocarchariidae. Characters of the family are presented and discussed in Compagno (1973, 1977, 1982, 1984, 1990b, 1999). Pseudocarchariidae has been recognized by a number of subsequent writers (Last and Stevens, 1994; Nelson, 1994; Shirai, 1996; Helfman, Collette and Facey, 1997). Eschmeyer (1990) reduced its rank to a subfamily Pseudocarchariinae of the family Odontaspididae, but subsequently recognized it as a full family (Eschmeyer, 1998).

Pseudocarcharias was proposed by Cadenat (1963) as a subgenus of ***Carcharias*** Rafinesque, 1810 but was synonymized with ***Carcharias*** by D'Aubrey (1964a, b) and ***Odontaspis*** Agassiz, 1838 by Bass, D'Aubrey and Kistnasamy (1975a). It is strongly divergent from either ***Odontaspis*** or ***Carcharias*** as delimited here and has been recognized by many writers (Abe et al., 1969; Compagno, 1973, 1977, 1981a,b, 1982, 1984, 1990b, 1999; Krefft, 1980; Fujita, 1981; Cadenat and Blache, 1981; Nakaya, 1984; Springer, 1990; Cigala-Fulgosi, 1992; Last and Stevens, 1994). The synonymy of the species follows D'Aubrey (1964a, b), Bass, D'Aubrey and Kistnasamy (1975d) and Compagno (1973, 1984).

Compagno (1990b) suggested, on morphological characters, that Pseudocarchariidae might be the sister group of Megachasmidae, Alopiidae, Cetorhinidae, and Lamnidae within Lamniformes. Recent molecular phyletic studies (Naylor et al., 1997; Martin and Naylor, 1997) have not given unambiguous results on the relationship of Pseudocarchariidae to other lamnoids, but suggest relationships with Odontaspididae and Megachasmidae. Long and Waggoner (1996), using dental morphology for a phyletic analysis of Lamniformes, suggested that Pseudocarchariidae is the immediate sister group of Alopiidae plus Lamnidae within the Lamniformes.

Pseudocarcharias Cadenat, 1963

Genus: Subgenus ***Pseudocarcharias*** Cadenat, 1963 (Genus ***Carcharias*** Rafinesque, 1810), *Bull. Inst. Francaise Afrique Noire*, ser. A, 25(2): 526 (proposed as a subgenus of ***Carcharias*** Rafinesque, 1810, but used throughout in generic form).

Type Species: ***Pseudocarcharias pelagicus*** Cadenat, 1963, by original designation, a junior synonym of ***Carcharias kamoharai*** Matsubara, 1936.

Number or Recognized Species: 1.

Synonyms: None.

Diagnostic Features: See family Pseudocarchariidae above.

Pseudocarcharias kamoharai (Matsubara, 1936)

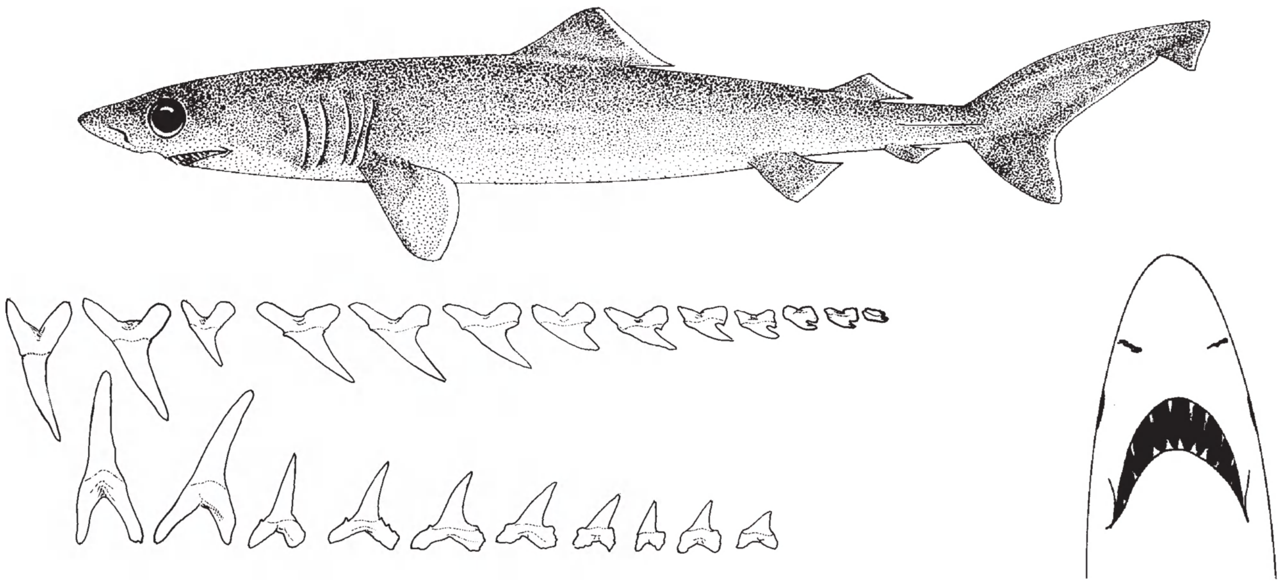
Fig. 58

Carcharias kamoharai Matsubara, 1936, *Zool. Mag. Tokyo*, 48(7): 380. Holotype: Imperial Fisheries Institute, Japan, Kyoto University, Department of Fisheries, Faculty of Agriculture, Japan (housed at Maizuru, Japan) FAKU, Fish Spec. 1823, 735 mm male, Koti Fish Market, Koti, Japan, apparently lost according to Eschmeyer (1998, *Cat. Fish.*: CD-ROM).

Synonyms: ***Carcharias yangi*** Teng, 1959: 1, fig. 1. Holotype, Taiwan Fisheries Research Institute, TFRI 2895, 1 000 mm TL adult male, Su-ao fish market, from off Su-ao, Taiwan (Province of China). Type status confirmed by Eschmeyer (1998: CD-ROM). ***Pseudocarcharias pelagicus*** Cadenat, 1963: 529, figs. 1-5. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN 1963-1, 975 mm adult male, off the Guinea coast, West Africa. Type status confirmed by Eschmeyer (1998: CD-ROM).

Other Combinations: ***Odontaspis kamoharai*** (Matsubara, 1936).

FAO Names: **En** - Crocodile shark; **Fr** - Requin crocodile; **Sp** - Tiburón cocodrilo.



UPPER AND LOWER TEETH ON RIGHT SIDE, LINGUAL VIEW

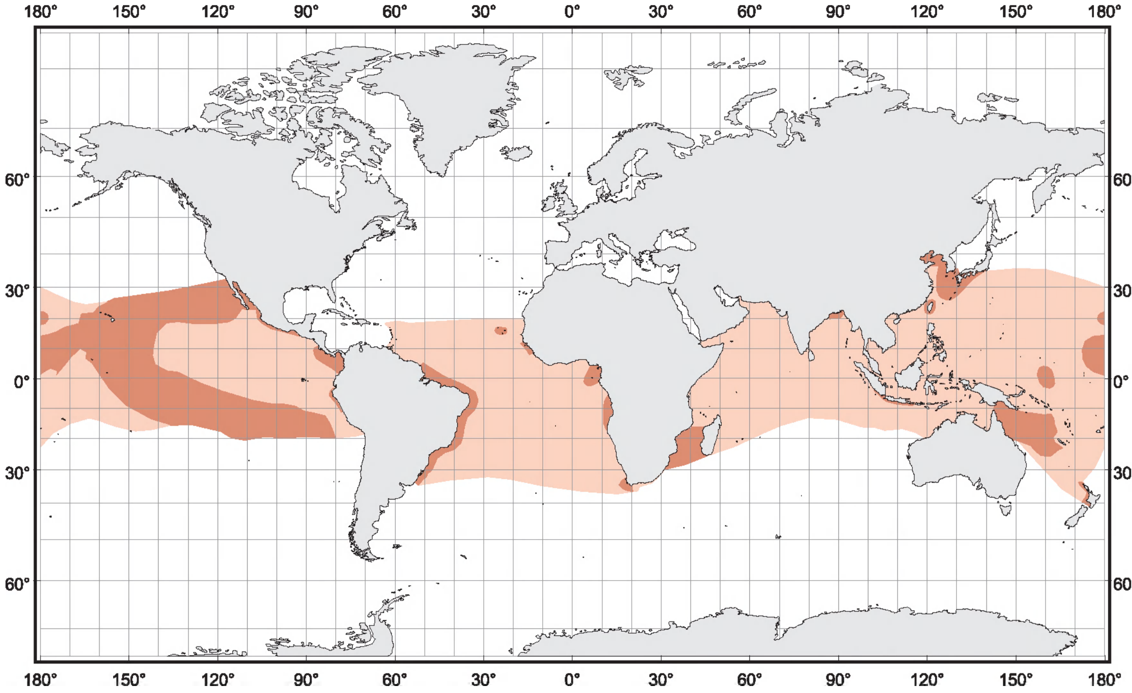
UNDERSIDE OF HEAD

Fig. 58 *Pseudocarcharias kamoharai*

Field Marks: A small, very distinctive oceanic shark, with huge eyes lacking nictitating eyelids, long gill slits, slender, spindle-shaped body, long-cusped prominent teeth in a long angular mouth with highly protrusable jaws, small pectoral fins, two small spineless dorsal fins and an anal fin, weak keels and precaudal pits on the caudal peduncle, an asymmetrical caudal fin with a long ventral lobe. **Colour:** grey or grey-brown dorsal surface, lighter ventral surface, and light-edged fins.

Diagnostic Features: See family Pseudocarchariidae above.

Distribution: Oceanic and circumtropical. Western Atlantic: Off Brazil. Eastern Atlantic: Southeast of Cape Verde Islands, between them and Guinea-Bissau, Guinea, Angola, and South Africa (Western Cape, vicinity of Cape Town and Cape Peninsula). Western Indian Ocean: Mozambique Channel between southern Madagascar, southern Mozambique and KwaZulu-Natal, South Africa, possibly south within Agulhas Current to off Eastern Cape. ? Eastern Indian Ocean: Bay of Bengal (possibly erroneous). Western North Pacific: Off Japan, Taiwan Island and Korean Peninsula; area between Marshall, Howland and Baker, Palmyra, Johnston and Hawaiian Islands. Western South Pacific: Australia (northeastern Queensland), west of New Zealand (North Island), Coral Sea, Indonesia (south of Sumatra near Sunda Straits and off Java). Central Pacific: Marquesas Islands, Hawaiian Islands, open ocean between Marquesas and Hawaiian Islands, open ocean between Hawaiian Islands and Baja California, around Line Islands, open water between Line Islands and southern Peru. Eastern Pacific: Mexico (off west coast of Baja California), Costa Rica, Panama and northern Peru.



Habitat: A rare to locally abundant oceanic, epipelagic and possibly mesopelagic shark, usually found offshore and far from land but sometimes occurring inshore and near the bottom, at depths from the surface to at least 590 m. Its bicolorate, countershaded colour pattern, lack of an expanded iris and prominent green or yellow retinal reflection, and frequent occurrence in pelagic longline catches suggests that it primarily inhabits the epipelagic zone. There are several records of strandings in the Cape Town area, South Africa, possibly due to upwelling of cold water that may stun these sharks but in at least one instance as a discarded catch of an offshore longliner.

Biology: The long body cavity, large liver, and small fins of this shark (microceanic habitus, Compagno, 1990a) give it a superficial resemblance to ***Isistius***, ***Squaliolus***, ***Euprotomicrus***, ***Scymnodalatias***, and other oceanic squaloids, as well as ***Odontaspis noronhai***, and like these sharks its extremely large and oily liver is probably important in maintaining neutral buoyancy. Its habits are little known, but its firm body musculature, tough skin, small precaudal fins, and large caudal fin suggests that it is a relatively active species, which is also suggested by its behaviour when captured. Off Cape Point, South Africa, one jumped out of the water after a bait and was caught. It snaps strongly and vigorously when captured (S. Kato, pers. comm.) and can bite very hard. The large but nonreflective eyes of the crocodile shark suggest nocturnal activity in the epipelagic zone, and possibly a diel pattern of movement toward the surface at night and away from it in the day.

The crocodile shark is ovoviviparous and a uterine cannibal, with the young having yolk sacs at 3 to 4 cm long but reabsorbing them and subsisting on eggs and possibly other young beyond this size. Number of young in a litter four, two per uterus; egg cases formed in the oviducts have 2 to 9 fertilized eggs, but apparently only two of these survive, possibly through elimination of extra rivals. An interesting question is why two young survive in each uterus in this shark and some other lamnoids, while in ***Carcharias taurus*** only one foetus per uterus is normally produced.

Feeding habits of this shark are sketchily known. Its long, flexed teeth, strong and long jaws, and its vigorous activity when captured adapt it to moderately large, active oceanic prey. Of seven specimens examined by the writer for stomach contents, the stomachs of four were empty and three others had a number of small bristlemouths (gonostomatids), possibly lanternfish (myctophids), unidentified fish scales, small shrimp, and squid beaks, including onychoteutids (***Moroteuthis robsoni***), mastigoteuthids (***Mastigoteuthis***), pholidoteuthids (***Pholidoteuthis ?boschmai***), and cranchiids (***Megalocranchia?***) in their stomachs (M. Roeleveld and M. Lipinski, pers. comm., on identification of squid beaks). The jaws of the crocodile shark can be protruded for a considerable distance from its head.

Size: This is the smallest living lamnoid, with maximum size at least 110 cm; size at birth about 41 cm; males adult at 74 to 110 cm; adolescent females examined 96 to 110 cm and adults recorded at 89 to 110 cm and presumably greater.

Interest to Fisheries and Human Impact: This shark is primarily caught as a discarded bycatch of pelagic longline fisheries for scombroids, but details are sketchy. Abe et al. (1969) noted that the species is often caught on tuna longlines, but discarded because of its small size and meat that is apparently unsuitable for the Japanese market. The liver of this species is very large and very high in squalene, and hence is of potential value. It also has been caught on squid jigs and occasionally washes up on beaches in the Cape Town area of South Africa. It may also be a discarded bycatch of pelagic squid fisheries as well as of pelagic net fisheries for scombroid fishes.

The crocodile shark is small and has never bitten people in the water, but should be treated with respect because of its strong jaws. It apparently has not been kept by large public aquaria but its small size and poorly-known behaviour suggests it may be more amenable to captivity than larger pelagic lamnoids and might be an interesting animal to observe in captivity.

Conservation status is uncertain but of concern because of its epipelagic habitat and because it is an apparently widespread, discarded, and largely unrecorded bycatch of the burgeoning pelagic longline fisheries. It is too small to be of much value for fins, and is little-utilized for flesh, but has a large mouth and strong teeth and is readily caught on longline hooks fished near the surface. It does not appear to be abundant anywhere with the known exception of the Mozambique Channel in the western Indian Ocean during the 1960s, and catch records are very limited and largely confined to a small number of specimens (less than 50) deposited in museums. It was assessed as Limited Risk (Near Threatened) for the Red List of the IUCN Shark Specialist Group (L.J.V. Compagno and J.A. Musick, pers. comm.).

Local Names: Kamohara's sand shark, Mizu-wani, Mizuwani, Water crocodile, Water alligator (Japan); Japanese ragged tooth shark, Grootoog-skeurtandhaai, Bigeye ragged-tooth (South Africa).

Literature: Matsubara (1936);Teng (1959); Lindberg and Legeza (1959); Cadenat (1963); Chen (1963); D'Aubrey (1964a, b); Merrett (1965); Abe et al. (1969); Abe (1973); Bass, D'Aubrey and Kistnasamy (1975a); Compagno (1973, 1981, 1982, 1984, 1990a, b); Krefft (1980); Fujita (1981); Cadenat and Blache (1981); Nakaya (1984); Sadowsky, Amorim and Arfelli (1987); Kashkin (1989); Fischer et al. (1990); Springer (1990); Cigala-Fulgosi (1992); Last and Stevens (1994); Long and Seigel (1996); L.J.V. Compagno and J.A. Musick (pers. comm.); S. Kato, (pers. comm.).

2.2.4 Family MEGACHASMIDAE

Family: Family Megachasmidae Taylor, Compagno and Struhsaker, 1983, *Proc. California Acad. Sci.*, ser. 4, 43(8): 87, 89.

Type Genus: ***Megachasma*** Taylor, Compagno and Struhsaker, 1983.

Number of Recognized Genera: 1.

Synonyms: None.

FAO Names: En - Megamouth sharks; **Fr** - Requins grande gueule; **Sp** - Tiburones bocudos.

Diagnostic Features: Head very elongated and about length of trunk. Snout extremely short, flattened and broadly rounded, not elongated and blade-like. Eyes moderately large, length 1.6 to 1.8% of precaudal length. Gill openings moderately long, length of first 6.4 to 8.6% of precaudal length, not extending onto dorsal surface of head; last two gill openings over pectoral-fin bases; unique gill rakers of finger-like dermal papillae with cartilage cores fringing internal gill slits. Mouth very large and arcuate, terminal on head; jaws greatly protrusable anteriorly beyond snout tip but not greatly distensible laterally. Teeth small, continuously varying and more or less awl-shaped, in 55 to 115/75 to 121 (130 to 236 total) rows, no differentiation between anterior, intermediate, lateral, or symphysial teeth. Trunk cylindrical and somewhat compressed, stout, and relatively flabby. Caudal peduncle compressed and without lateral keels but with small fossate-shaped upper precaudal pit only. Dermal denticles very small and smooth, with flat crowns, small ridges and cusps and with cusps directed posteriorly on lateral denticles. Pectoral fins large, narrow and elongated, much shorter than head in adults; pectoral skeleton plesodic with radials extending far into fin webs. Pelvic fins moderate-sized, smaller than pectoral and first dorsal fins; fin skeleton probably aplesodic, not extending into fin web. First dorsal fin moderately large, semierect and angular; fin skeleton aplesodic. Second dorsal fin less than half size of first but moderately large. Anal fin smaller than second dorsal fin and with its base slightly behind second dorsal-fin base, bases of both fins not pivotable. Caudal fin not lunate, dorsal lobe long but less than half as long as rest of shark, ventral lobe short but strong. Neurocranium depressed, with short wide rostrum, greatly depressed internasal septum and widespread nasal capsules, small orbits with strong supraorbital crests, small stapedial fenestrae, and with hyomandibular facets not extended outward. Vertebral centra weakly calcified, with rudimentary radii and double cones and no annuli. Total vertebral count 151, precaudal count 64, diplospondylous caudal count 82 to 87. Intestinal valve of ring type with 23 or 24 turns. Size very large with adults 4.5 to 5.5 m long.

Remarks: Taylor, Compagno and Struhsaker (1983) proposed a new monotypic family of lamnoid sharks, Megachasmidae, for the new genus and species of megamouth shark (***Megachasma pelagios***), and suggested that it might be either the sister group of all other lamnoids or could be grouped with more derived lamnoids having plesodic pectoral fins. The family Megachasmidae has received recognition from various authors, including Compagno (1984, 1990b, 1999), Gubanov, Kondyurin and Myagkov (1986), Eschmeyer (1990, 1998), Nelson (1994), Last and Stevens (1994), Shirai (1996), and Helfman, Collette and Facey (1997). Maisey (1985) adopted the second suggestion of the megamouth shark being related to derived plesodic lamnoids, but maintained that the megamouth shark was the sister group of the basking shark and confamilial with it in the family Cetorhinidae on derived characters of its jaw suspension, cranial morphology, dentition and filter-feeding. Robins et al. (1991a) followed Maisey's classification. Compagno (1990b) noted that Maisey's derived characters for grouping the basking and megamouth sharks did not hold, and listed numerous characters separating these sharks. He suggested on morphological grounds that the Megachasmidae was distinct from Cetorhinidae, that Cetorhinidae was the immediate sister group of Lamnidae, that Megachasmidae was a valid taxon, that filter-feeding was independently derived in the basking and megamouth sharks, and that the Megachasmidae, on the basis of plesodic pectoral fins, was the sister group of all other plesodic lamnoids (Alopiidae, Cetorhinidae and Lamnidae). Two molecular studies confirmed the separation of the Megachasmidae and Cetorhinidae and refuted the common evolution of filter-feeding in these sharks, but disagreed on the relationships of Megachasmidae within the Lamniformes. Martin and Naylor (1997), using cytochrome b mitochondrial genes, suggested that ***Cetorhinus*** was sister to the Lamnidae but could not resolve the position of ***Megachasma*** robustly except for its arising from the basal root of lamnoids; their work suggested no common grouping of plesodic lamnoids but a possible relationship of ***Megachasma*** to ***Pseudocarcharias*** plus ***Odontaspis***. Morrissey, Dunn and Mulé (1997) using the 12S messenger RNA mitochondrial gene suggested that ***Megachasma*** was the sister of all other lamnoids that they examined. Long and Waggoner (1996), using dental morphology for a phyletic analysis of Lamniformes, suggested that the basking and megamouth sharks were immediate sister groups within the Lamniformes, and formed a sister taxon to Odontaspididae, Pseudocarchariidae, Alopiidae, and Lamnidae. As noted in Compagno (1990b), similarities in tooth morphology between these sharks could be the result of parallelism and may not reflect a common immediate origin within the Lamniformes. Particularly problematical is the absence of disjunct monognathic heterodonty in ***Megachasma***, while ***Cetorhinus*** retains disjunct upper anteriors and a gap between laterals and anteriors as in all other lamnoids. Although the phylogeny of Lamniformes remains unsettled, morphological and molecular studies support the retention of the Megachasmidae as distinct from the Cetorhinidae or any other lamnoid family.

Megachasma Taylor, Compagno and Struhsaker, 1983

Genus: ***Megachasma*** Taylor, Compagno and Struhsaker, 1983, *Proc. California Acad. Sci.*, ser. 4, 43(8): 87, 96.

Type Species: ***Megachasma pelagios*** Taylor, Compagno and Struhsaker, 1983, by original designation.

Number of Recognized Species: 1.

Synonyms: None.

Diagnostic Features: See family Megachasmidae above.

Megachasma pelagios Taylor, Compagno and Struhsaker, 1983

Fig. 59

Megachasma pelagios Taylor, Compagno and Struhsaker, 1983, *Proc. California Acad. Sci.*, ser. 4, 43(8): 87, 96, figs. 1-15. Holotype: Bernice P. Bishop Museum, BPBM-22730, 4 460 mm adult male, off Oahu, Hawaiian Islands, 21° 51′ N, 157° 46′ W, about 42 km northeast of Kahuku Point, at 165 m depth in water about 4 600 m deep.

Synonyms: None.

Other Combinations: None.

FAO Names: En - Megamouth shark; **Fr** - Requin grande gueule; **Sp** - Tiburón bocudo.

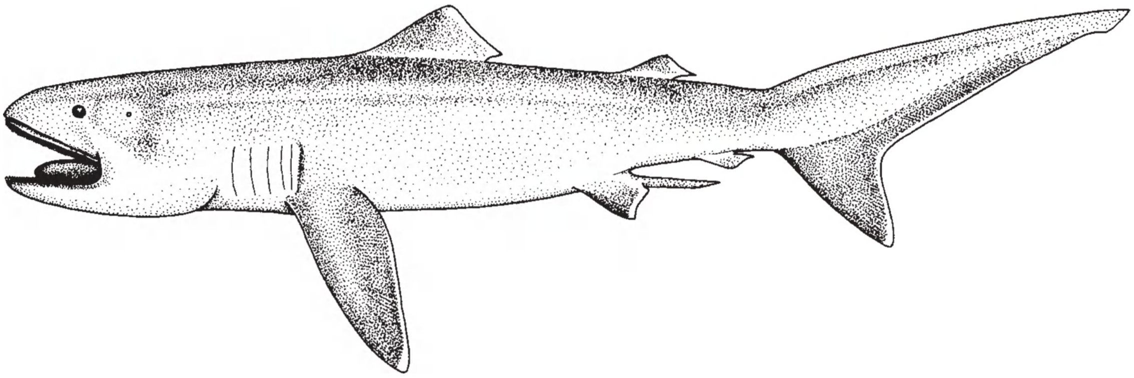
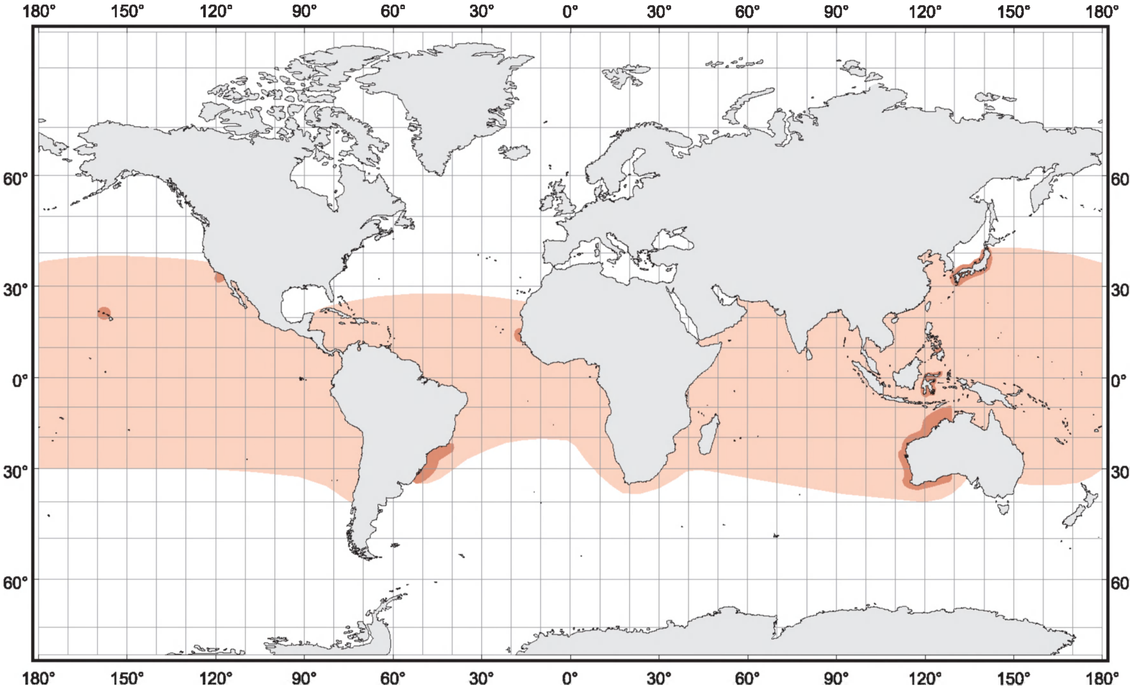


Fig. 59 ***Megachasma pelagios***

Field Marks: One of three species of gigantic filter-feeding non-batoid sharks, unmistakable with its extremely short but broadly rounded snout, very large and long head, huge terminal mouth that extends behind the eyes, numerous small hooked teeth, moderately long gill slits, internal gill slits lined with dense rows of papillose gill rakers, eyes without nictitating eyelids, two dorsal fins and an anal fin, caudal peduncle without keels, caudal fin asymmetrical not lunate, but with a short and strong ventral lobe, and no light spots. **Colour:** upper surface of body grey or grey-black above, without light spots, underside white, mouth dusky blackish with dark spotting on lower jaw, and dorsal surfaces of pectoral and pelvic fins blackish with conspicuous light margins.

Diagnostic Features: See family Megachasmidae above.

Distribution: Spottily known from less than 20 specimens but probably circumtropical and wide-ranging. Western Atlantic: Brazil. Eastern Atlantic: Senegal. Southeastern Indian Ocean: Australia (Western Australia). Western North Pacific: Japan, Philippines (Macabalan Bay, Cagayan de Oro), Indonesia (Sulawezi, Nain Island, Bunaken Archipelago). Central Pacific: Hawaiian Islands (Oahu). Eastern Pacific: USA (southern California near San Clemente and off Catalina Island and San Diego).



Habitat: A coastal and oceanic, epipelagic and neritic species, found in water as shallow as 5 m in a shallow bay and in water 40 m deep on the continental shelf, with at least one washed ashore alive on a sandy beach; also offshore in the epipelagic zone at 8 to 166 m depth in water 348 to 4 600 m deep. The coloration and catch records of the megamouth shark are suggestive of epipelagic rather than deepwater habitat, as is the composition of its liver oil (Itabashi, Yamaguchi and Nakaya, 1997).

Biology: This is a seldom reported, possibly rare or uncommon shark, with most examples from off Japan and southern California. As the megamouth shark has greatly reduced teeth, very numerous gill-raker papillae on its internal gill openings, and stomach packed with very small prey, it can be properly considered a specialized filter feeder like the basking shark (***Cetorhinus maximus***), whale shark (***Rhincodon typus***), and the devil rays (Mobulidae). However, the flabby body, soft fins, asymmetrical caudal fin without keels, and weak calcification of the megamouth shark suggested that it is much less active than the whale and basking sharks (Compagno, 1984, 1990b) and the mobulids. Observations and tracking of a live specimen off southern California confirmed its relative sluggishness (Nelson et al., 1997).

The only known prey of the megamouth shark are epipelagic and mesopelagic euphausiid shrimp, copepods, and jellyfish. The first megamouth shark from Hawaii had been feeding on an euphausiid shrimp, ***Thysanopoda pectinata***, that averages 3.1 cm in length. The shrimp has a diel migration pattern with a range of 300 to 1 100 m depth during the day; at night it is commonest at 150 to 500 m with a maximum range of 75 to 525 m. When captured during the night the shark was apparently at the upper depths where these shrimp are commonest. It may have been feeding on them when it fouled itself by its mouth and teeth on a pair of parachutes being used as sea anchors by a US Navy research vessel. The second megamouth shark from California had euphausiids, copepods and deepwater jellyfish (***Atolla vanhoeffeni***) in its stomach. Two female sharks from Japan had macerated euphausiids in their stomachs (probably ***Euphausia nana***). The feeding structures of this shark may allow it to feed on other pelagic invertebrates and even small midwater fishes, but so far the limited stomach contents available suggests that this shark primarily targets euphausiid shrimp as prey.

There has been considerable speculation on the feeding habits of this shark. Taylor, Compagno and Struhsaker (1983) compared the basking, whale, and megamouth sharks, and suggested that the megamouth shark slowly swam through schools of euphausiid shrimp with jaws widely open, occasionally closing its mouth and contracting its pharynx to concentrate prey before swallowing it. These authors noted the presence of a bright silvery mouth lining, which they suggested was possibly bioluminescent but could not prove it because of inadequate histological evidence. The second specimen had tissue in its lower jaw that may be luminescent (Lavenberg and Seigel, 1985) and could along with the reflective upper jaw tissue serve as a 'light trap' for luring prey to the proximity of its mouth (Diamond, 1985). Compagno (1990b) noted that the protrusability of the jaws in the megamouth shark may allow it to use its mouth as a bellows to suck in prey, and that open-mouthed cruising through prey concentrations was optimal for the basking shark but not the megamouth shark.

Taylor, Compagno and Struhsaker (1983) suggested that the soft flabby body and fins, low-flow filter apparatus, and small gill openings of the megamouth shark indicated that it was less active than the whale and basking sharks. Oikawa and Kanda (1997) considered gill histology and filament area in the megamouth shark compared to the shortfin mako and other species, and suggested that the megamouth shark was less active. An adult male megamouth shark of about 4.9 m length was captured in a pelagic gill net off southern California near the surface in water between 300 and 400 m deep. This was still alive when discovered in the net and was towed to Dana Point Harbor where it was tethered by a rope to the fishing boat that caught it (Nelson et al., 1997). The shark was extensively photographed by divers and was still alive after being towed and then being tethered for over a day. Observations suggested that the shark could breathe readily by gill pumping and was not dependent on ram-ventilation and constant swimming unlike more active lamnoid sharks. The shark was then towed out to sea, tagged with an acoustic telemetric tag, and released in water about 20 m deep. The shark immediately descended, outswam the accompanying divers, and headed for deep water beyond the continental shelf. It was tracked over a two-day period, which revealed a pattern of vertical, crepuscular migration in the epipelagic zone. The tagged shark ascended at sunset to a depth of 12 to 25 m at night, then descended at sunrise to a depth of 120 to 166 m during the day with greatest depth achieved at midday but stayed well above the bottom at 700 to 850 m. It stayed on a straight southward course at an estimated speed between 1.5 and 2.1 km/hr during day and night. It was thought that the shark was responding to light levels in choosing its depth range, and as light increased it correspondingly sought an optimal level by diving at dawn and conversely responded to decreasing light levels by ascending to near (but not at) the surface at dusk. It has been suggested that the megamouth shark may also follow vertical migrations of euphausiid prey during diel cycles. The telemetric track suggested that the shark was indeed somewhat less active than makos or basking sharks, but that it could sustain a slow rate of swimming for extended periods.

Mode of reproduction is probably aplacental viviparous with uterine cannibalism or cannibal vivipary suspected in the form of oophagy, but no pregnant adult female has been reported to date. A late immature or early adolescent female had two ovaries with many tiny oocytes under 3 mm in diameter, while an adult female had numerous larger oocytes 5 to 10 mm wide. This is similar to the ovaries of several other lamnoids that are oophages. An adult female had numerous bite marks mostly on her flanks and precaudal tail but also on her first dorsal and anal fin and head. These wounds corresponded to the teeth of another megamouth shark (or sharks), and were interpreted as courtship scars inflicted by a male because of the narrow spacing of individual cuts comparable to male rather than female teeth (Yano et al., 1999).

The megamouth shark is the only known selachian victim of the semiparasitic cookiecutter shark, ***Isistius brasiliensis***, and may be especially vulnerable to ***Isistius*** attacks because of its soft skin, epipelagic habitat in warm seas where ***Isistius*** is also found, sluggishness, and relatively slow swimming speed. Three megamouth specimens had 'crater wounds' indicative of cookiecutter attacks. A megamouth shark was seen at the surface off Nain Island, Bunaken Archipelago, North Sulawesi while being possibly harassed or played with by three sperm whales, which left the shark after the observers approached them. The shark was apparently minimally injured by the whales and was photographed at the surface before disappearing.

Size: Maximum total length at least 549 cm. Size at birth unknown. A juvenile free-living male from off Brazil was 190 cm long while a possibly smaller specimen from off Senegal was estimated at about 180 cm long. Adult males were 446 to about 549 cm; a late immature or early adolescent female was 471 cm, another female of uncertain maturity was about 5 m, and an adult female was 544 cm.

Interest to Fisheries and Human Impact: Interest to fisheries minimal at present. Taken as a rare incidental bycatch in pelagic gill nets, purse seines, pelagic longlines, and fixed shore nets, and so far has been mostly utilized by museums and oceanaria, which prize the few specimens landed as display objects. As with certain other large, rare animals it attracts much attention from the general public and shark fans. A few specimens were released alive from fishing gear, while a recent specimen from Philippines was cut up and utilized by fishermen, but details of its utilization were not recorded. Conservation status uncertain, but of concern because of the apparent epipelagic and neritic habitat and possible rarity of this shark, which puts it at risk as unrecorded bycatch of oceanic and offshore littoral fisheries.

Local Names: Megamouth sharks, Big mouth sharks.

Remarks: This giant pelagic filter-feeding shark is perhaps the most spectacular discovery of a new shark in the twentieth century. A recent symposium volume deals primarily with a detailed examination of a single specimen of megamouth shark from Japan, but includes papers on all aspects of megamouth biology (Yano et al., 1997).

Literature: Taylor, Compagno and Struhsaker (1983); Compagno (1984, 1990b); Lavenberg and Seigel (1985); Diamond (1985); Maisey (1985); Nakaya (1989); Berra and Hutchins (1990, 1991); Miya, Hirosawa and Mochizuki (1992); Last and Stevens (1994); Clark and Castro (1995); Carey and Clark (1995); Seret (1995); Nelson et al. (1997); Castro et al. (1997); Berra (1997); Yano et al. (1997); Morrissey, Dunn and Mulé (1997); Martin and Naylor (1997); Nakaya et al. (1997); Yabumoto et al. (1997); Oikawa and Kanda (1997); Tanaka and Yano (1997); Itabashi, Yamaguchi and Nakaya (1997); Yamaguchi and Nakaya (1997); Yano et al. (1999); E.T. Elizaga (pers. comm.); E. Gomes, A. Amorim and B. Hueter (pers. comm.); H. Mollet (pers. comm.); J. Morrissey (pers. comm.); P. Pecchioni (pers. comm.); D. Petersen (pers. comm.).

2.2.5 Family ALOPIIDAE

Family: Subfamily Alopiadini Bonaparte, 1838 (Family Squalidae), *Nuov. Ann. Sci. Nat., Bologna,* ser. 1, 2: 209. Emended to Family Alopiidae Bonaparte, 1838 by Jordan and Gilbert (1883, *Bull. U.S. Nat. Mus.*, 16: 26).

Type Genus: ***Alopias*** Rafinesque, 1810.

Number of Recognized Genera: 1.

Synonyms: Family Alopeciae Müller and Henle, 1839: 74. Type genus: ***Alopecias*** Müller and Henle, 1837. Family Vulpeculidae Garman, 1913: 12, 30. Type genus: ***Vulpecula*** Garman, 1913.

FAO Names: En - Thresher sharks; **Fr** - Renards; **Sp** - Zorros.

Field Marks: Long curving asymmetrical caudal fin with dorsal lobe nearly or quite as long as rest of shark, short ventral caudal lobe, long narrow pectoral fins, large pelvic fins, large first dorsal fins, tiny second dorsal and anal fins, large to huge eyes.

Diagnostic Features: Head much shorter than trunk. Snout moderately long, pointed and conical, niether greatly elongated, nor flattened and blade-like. Eyes moderately large to very large with length 1.8 to 4.3% of precaudal length. Gill openings short, with width of first 3.1 to 5.2% of precaudal length, not extending onto dorsal surface of head; last two pairs of gill openings over pectoral-fin bases; no gill rakers on internal gill slits. Mouth small and arcuate, ventral on head, jaws not strongly protrusable. Teeth small to moderately large, compressed and blade-like, in 22 to 52/20 to 50 (42 to 102 total) rows. Two rows of small to moderately large anterior teeth on each side of upper jaw, the anteriors hardly larger than adjacent laterals and separated from them by a row of small intermediate teeth or a gap; three rows of small lower anterior teeth on each side, these slightly larger than lower laterals and with the third row not reduced in size; small symphysial teeth present or absent in upper and lower jaws. Trunk cylindrical and moderately stout, firm and not flabby. Caudal peduncle slightly compressed, with upper and lower crescentic precaudal pits but no lateral keels. Dermal denticles very small and smooth, with flat crowns, small ridges and cusps and with cusps directed posteriorly on lateral denticles. Pectoral fins very long and narrow, longer than head in adults; pectoral skeletons plesodic with radials extending far into fin webs. Pelvic fins very large, nearly or quite as large as first dorsal fin; fin skeleton plesodic. First dorsal fin large, high, erect and angular; fin skeleton semiplesodic, extending partially into fin web. Second dorsal and anal fins minute, low and with pivoting bases, anal-fin base behind second dorsal-fin base. Caudal fin not lunate, dorsal lobe greatly elongated, about as long as rest of shark, ventral lobe short but strong. Neurocranium high and compressed, with short rostrum, compressed internasal septum and closely adjacent nasal capsules, huge orbits with well-developed supraorbital crests, small stapedial fenestrae, and with hyomandibular facets not extended outward. Vertebral centra strongly calcified, with well-developed double cones and radii but without prominent annuli. Total vertebral count 282 to 477, precaudal count 100 to 125, diplospondylous caudal count 180 to 356. Intestinal valve of ring type with 33 to 45 turns. Size moderately large to very large with adults 2.7 to 5.5+ m long.

Distribution: Threshers occur worldwide in tropical, subtropical, and warm and cold-temperate waters.

Habitat: Threshers are large, active, strong-swimming sharks, ranging in habitat from coastal to epipelagic and deepwater epibenthic.

Biology: Thresher sharks are large, active sharks that are apparently specialized for feeding on small to moderately large schooling fishes and squids. Threshers swim in circles around a school of prey, narrowing the radius and bunching the school with their long, strap-like caudal fins. The caudal fin is also used as a whip to stun and kill prey, and threshers are commonly tail-hooked on longlines after striking the bait with the caudal tip. The three known species of this family broadly overlap in habitat and range, but differences in their structure, feeding habits and spatial distribution suggest that they reduce interspecific competition by partitioning their habitat and available prey to some extent. ***Alopias superciliosus***, with its huge eyes, relatively large teeth, broad caudal fin, and preference for deeper water (including the outer shelves and upper slopes near the bottom), takes somewhat larger pelagic fishes (including small billfishes and lancetfishes) as well as bottom fishes. ***A. vulpinus***, with smaller eyes and teeth, a narrower caudal fin, and preference for the surface and coastal as well as oceanic waters, takes small pelagic fishes (including clupeids, needlefishes and mackerels) and squids, but also bonitos and bluefishes. The oceanic and marginally coastal ***A. pelagicus*** is less well known biologically, but its much smaller teeth and very slender caudal fin suggest that it may take smaller prey than ***A. vulpinus*** or ***A. superciliosus***. Evidence on vascular morphology and from telemetry data suggests that threshers are endothermic (Alexander, 1998), but their behaviour (including activity patterns) is poorly known despite their abundance and wide range.

Interest to Fisheries and Human Impact: Thresher sharks form an important component of oceanic and offshore coastal shark fisheries, particularly because of their high-quality meat which is utilized fresh, frozen, smoked and dried-salted. Their fins are used for shark-fin soup, livers for vitamin extraction, and hides for leather. Sizeable oceanic fisheries for thresher sharks, utilizing floating longlines, have operated in the northwestern Indian Ocean, the central Pacific, the western Pacific, and the western North Atlantic. Threshers are undoubtedly caught as bycatch of longline fisheries targeting scombroid fishes. A pelagic gill net fishery for threshers has operated off the Pacific coast of the USA over the last few decades but declined markedly due to overfishing. Threshers are also captured offshore and near shore with line gear (including rod-and-reel) and fixed bottom gill nets. Sports anglers seek threshers as game fishes, because of their strong fighting qualities and tendency to jump when hooked. Little is available on fisheries statistics for thresher catches worldwide. At present, only New Zealand and the USA report commercial catch statistics of thresher sharks to FAO (***A. vulpinus***) and these amount to only about 100 t or less annually during the last decade. World catches are undoubtedly much larger. Threshers are sometimes seen by divers, but do not, to the writer's knowledge, provide ecotouristic viewing at inshore or offshore dive sites, nor have they been regularly kept in aquaria. The conservation status of threshers is poorly known, but is of concern because of their high value in fisheries, very low fecundity, and their occurrence in areas and habitats subjected to high-intensity oceanic fisheries.

Local Names: Fox sharks, Threshers, Thresher sharks, Thrashers (English); Renards de mer, Chienhai chang, Chienhai chang wei sha k'o; Dlinnokhvostye akuly (Russia); Onagazame-ka (Japan); Zorros (Mozambique).

Remarks: Following Müller and Henle (1839), most authors have recognized the threshers (genus ***Alopias***) as a separate family, Alopiidae or equivalents, which is followed here. However, some authors placed the threshers in the family Lamnidae or Isuridae (Günther, 1870; Hasse, 1879; Woodward, 1889; Regan, 1906a; Goodrich, 1909; Engelhardt, 1913; Berg, 1940; Berg and Svetovidov, 1955; Arambourg and Bertin, 1958; and Norman, 1966). Shirai (1996) recently included the basking sharks (Cetorhinidae) and mackerel sharks (Lamnidae) as subfamilies of the Alopiidae.

The arrangement of genera and species within this family follows Bass, D'Aubrey and Kistnasamy (1975a), Gruber and Compagno (1981), and Compagno (1984) in recognizing a single living genus and three living species, ***Alopias pelagicus***, ***A. superciliosus*** and ***A. vulpinus***. Compagno (1990b), on external and cranial morphology, suggested that threshers were monophyletic, with ***A. vulpinus*** the plesiomorphic sister group of ***A. pelagicus*** and ***A. superciliosus***. Eitner (1995) did electrophoretic analysis of allozymes from muscle samples collected from eastern Pacific threshers. Eitner suggested a similar phyletic relationship as indicated by Compagno (1990b) for the three known species, but indicated that a fourth and possibly undescribed species, initially identified as ***A. superciliosus***, occurred off Baja California, Mexico. Unfortunately the fourth species was not represented by whole-bodied material, parts or even photographs or morphometrics (only muscle samples), so that determination of its status awaits collection and description of additional material from the eastern Pacific. The three known species of threshers are strongly differentiated by external and skeletal morphology (Compagno, 1990b), so that detailed morphological examination of the possible fourth species is highly desirable.

Literature: Garman (1913); Fowler (1941, 1967a); Bigelow and Schroeder (1948); Garrick and Schultz (1963); Lindberg (1971); Shiino (1972, 1976); Compagno (1973, 1984, 1988, 1990a, b, 1999); Bass, D'Aubrey and Kistnasamy (1975a); Gruber and Compagno (1981); Last and Stevens (1994); Eitner (1995); Alexander (1998).

Alopias Rafinesque, 1810

Genus: ***Alopias*** Rafinesque, 1810, *Caratt. gen. sp. anim. piant. Sicilia, Palermo*, pt. 1: 13.

Type Species: ***Alopias macrourus*** Rafinesque, 1810, by monotypy, a junior synonym of ***Squalus vulpinus*** Bonnaterre, 1788, *Tabl. Encyclop. Method. Trois Reg. Nat., Ichthyol.*, Paris: 9.

Number of Recognized Species: 3.

Synonyms: Genus ***Vulpecula*** Jarocki, 1822: 454. Probably based on ***Vulpecula marina*** Valmont, 1768 (work not consistently binomial), equivalent to ***Squalus vulpinus*** Bonnaterre, 1788. Genus ***Alopecias*** Müller and Henle, 1837a: 114. Type species: "***Carcharias vulpes*** Cuv[ier]" by original designation, equals ***Squalus (Carcharias) vulpes*** Cuvier, 1816. Genus ***Alopius*** Swainson, 1838: 91 (unjustified emendation of ***Alopias*** Rafinesque, 1810). Genus ***Vulpecula*** Garman, 1913: 3, 30. Type species: ***Vulpecula marina*** Garman, 1913, by monotypy: "Valmont, 1768, gives a description of ***V. marina*** of earlier authors. His species is ***Squalus vulpinus*** Bonn., 1788, the ***Alopias macrourus*** Raf., 1810, ***A. vulpes*** Bonap. 1841. The genus and the species are adopted from Valmont" (Garman, 1913: 3). Revival of ***Vulpecula*** Valmont (1768: 740). Valmont's names were rejected as being inconsistently binomial by the International Commission on Zoological Nomenclature (1925, Opinion 89: 27-33). Genus ***Alopes*** Vladykov and McKenzie, 1935: 46 (erroneous spelling for ***Alopias***).

Key to Species:

1a. Head nearly flat between eyes, with a deep horizontal groove on nape on each side above gills; eyes very large, with orbits expanded onto dorsal surface of head (Fig. 60); teeth large, in 22 to 27 rows in upper jaw; first dorsal-fin base closer to pelvic bases than to pectoral bases . . . . ***Alopias superciliosus***

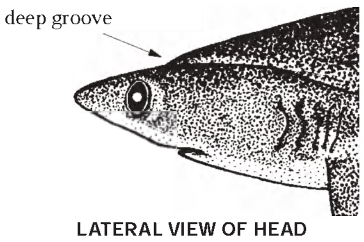


Fig. 60 *Alopias superciliosus*

1b. Head strongly arched between eyes, without a horizontal groove or with an inconspicuous one on nape on each side; eyes smaller, with orbits not expanded onto dorsal surface of head (Fig. 61); teeth smaller, 32 to 52 rows in upper jaw; first dorsal-fin base about equidistant between pectoral and pelvic-fin bases or closer to pectoral-fin bases . . . . → **2**

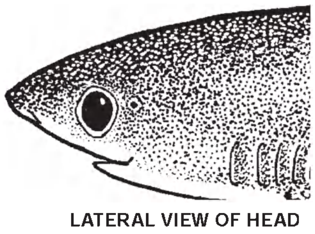


Fig. 61 *Alopias pelagicus*

2a. Head narrow, snout more elongated, forehead nearly straight; labial furrows absent; pectoral fins nearly straight and broad-tipped; sides above pectoral bases dark, without an extension of the white abdominal area (Fig. 62) . . . . . ***Alopias pelagicus***

2b. Head broad, snout shorter, forehead strongly arched; labial furrows present; pectoral fins falcate and narrow-tipped; sides above pectoral-fin bases marked with a white patch extending forward from the abdominal area (Fig. 63) . . . . ***Alopias vulpinus***

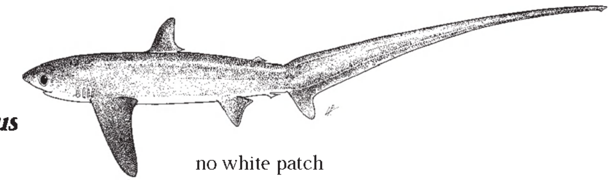


Fig. 62 *Alopias pelagicus*

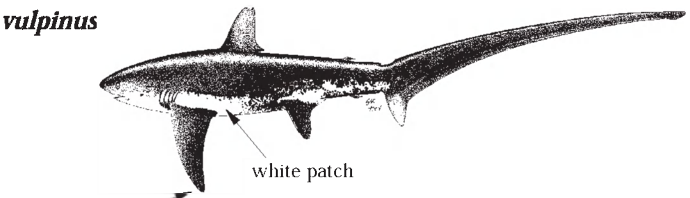


Fig. 63 *Alopias vulpinus*

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Alopias pelagicus Nakamura, 1935

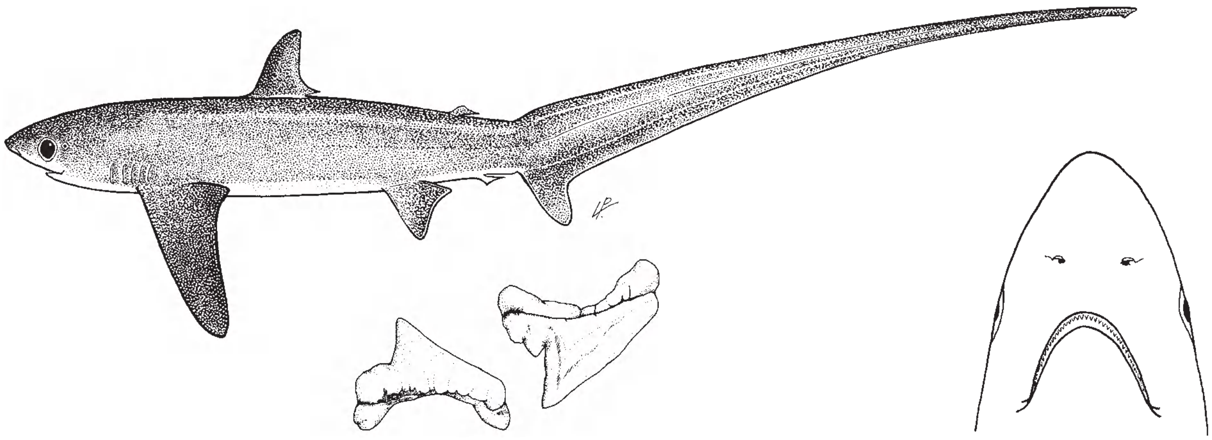
Fig. 64

Alopias pelagicus Nakamura, 1935, *Mem. Fac. Sci. Agric. Taihoku Imp. Univ.* ,14(1): 2, 3, pl. 1, fig. 1. Syntypes: Three large individuals mentioned and measured, these 270, 285, and 330 cm TL, and a large female specimen illustrated but of uncertain size; also foetus 96.5 cm (Nakamura, *ibid.*, 5, pl. 3), probably referable to ***Alopias vulpinus***; all from Suô fish market, Taiwan (Province of China). Whereabouts of syntypes uncertain according to Eschmeyer (1998, *Cat. Fish.*: CD-ROM).

Synonyms: None.

Other Combinations: ***Alopias vulpinus*** (not Bonnaterre, 1788).

FAO Names: En - Pelagic thresher; **Fr** - Renard pélagique; **Sp** - Zorro pelágico.



UPPER AND LOWER TOOTH

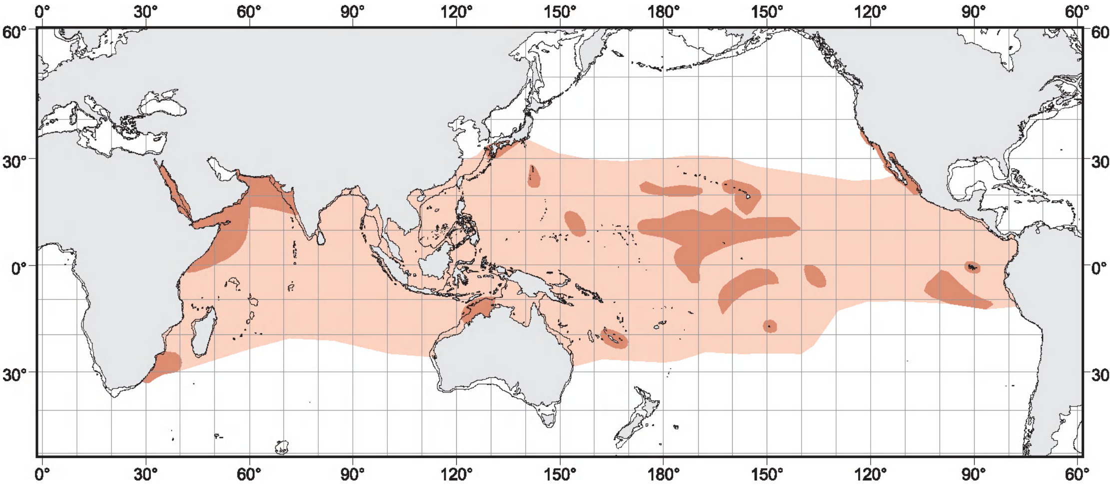
UNDERSIDE OF HEAD

Fig. 64 ***Alopias pelagicus***

Field Marks: Long upper caudal lobe nearly as long as rest of shark, relatively small eyes, very narrow head with arched dorsal profile, straight broad-tipped 'oceanic' pectoral fins, first dorsal fin somewhat closer to pectoral-fin bases than pelvic-fin bases, very slender caudal-fin tip, body colour deep blue or grey above, white below, white colour of abdomen not extending over pectoral-fin bases.

Diagnostic Features: Head narrow in dorsal and ventral views, with a convex, arched dorsolateral profile. Snout moderately long, conical. Eyes moderately large in adults but very large in newborn and foetuses, not expanded onto dorsal surface of head and without a vertical, binocular field of view; interorbital space broadly convex. Labial furrows absent. Teeth very small, in 41 to 45/37 to 38 rows (total for both jaws 75 to 86 rows); posterior tooth rows 5 to 11; symphysial and intermediate tooth rows usually present. Weak nuchal grooves present above branchial region. Pectoral fins of 'macroceanic' type with straight and very broad tips. Claspers moderately slender and not whip-like. First dorsal-fin midbase about equidistant between pectoral and pelvic-fin bases or closer to pectoral-fin bases. Caudal tip very slender with very narrow terminal lobe. Ribs of monospondylous precaudal vertebrae fused ventrally to form a canal extending nearly to the occiput. Total vertebral count 453 to 477. Intestinal valve count 37 to 40. **Colour:** body deep blue to grey on upper surface with sides silvery and underside white, white colour of abdomen not extending over pectoral-fin bases; no white dot on upper pectoral-fin tips.

Distribution: Oceanic and wide-ranging in the Indo-Pacific. Indian Ocean: South Africa (KwaZulu-Natal), Red Sea, Gulf of Aden, Arabian Sea (off Somalia, between Oman and India, and off Pakistan), Australia (northwest Western Australia), Western North Pacific: China, Taiwan (Province of China), Japan (southeastern Honshu). Western South Pacific: New Caledonia, eastern Micronesia, Tahiti. Central Pacific: Hawaiian Islands, equatorial waters north of Howland and Baker, Phoenix and Palmyra Islands. Eastern Pacific: USA (California) and Mexico (Baja California, Gulf of California), equatorial waters northwest of French Polynesia, and off Galapagos Islands.



Habitat: Primarily an oceanic, epipelagic, circumtropical species, but sometimes caught near shore on beaches with a narrow continental shelf, ranging in depth from the surface to at least 152 m. Sometimes seen by divers near coral reefs, near dropoffs and in large lagoons, and on sea mounts.

Biology: A little-known, active, strong-swimming species, probably migratory but with movements little-known. In the eastern North Pacific there is a possible population centre off central Baja California, which tends to shift northward (along with other oceanic sharks) during strong El Niño events. Behaviour and sociobiology is poorly known. Michael (1993) has seen this species repeatedly leap (breach) out of the water.

Ovoviviparous, with uterine cannibalism as in other species of ***Alopias***. Embryos subsist on their yolk-sacs up to about 12 cm, after which they become oophagous, feeding on unfertilized eggs. No evidence of adelphophagy (embryo-eating) was reported by Liu et al. (1999), who examined 233 embryos from 167 pregnant females. Litter size is two, with one foetus per uterus and with sex ratio 1:1. Gestation period uncertain because females give birth all year long without a definite birth season. Liu et al. suggest that the gestation period may be less than a year as with ***A. vulpinus***, but because most adult females were pregnant throughout the year there may be an annual cycle with no resting period between pregnancies. Pupping may also occur in winter in the Gulf of Aden (R. Bonfil, pers. comm.). This species presumably feeds on small fishes and squid but no details are known.

Vertebral growth rings are laid annually in vertebral centra; females mature at about 8 or 9 years old and males at about 6 to 9 years old, with up to 16 growth rings for females and 14 for males for a minimal age of 14 to 16 years old and a maximum age estimated from von Bertalanffy growth curves as 20 years for males and 29 years for females. Assuming birth of two young every year a female might produce about 40 young during her lifetime. This species has unusually large young, with the largest known foetus 43% of the length of the largest adult female. The large size of the young may help to reduce postnatal predation (presumably by other large sharks), but the relatively small size of the adults combined with the low fecundity imposed by large foetal size may in turn require annual breeding.

Size: Maximum total length at least 365 cm. Size at birth uncertain but presumably between about 130 and 160 cm and possibly up to 190 cm. The largest term foetus examined by Liu et al. (1999) off Taiwan (Province of China) was 158 cm and their smallest specimen was 190 cm long and a year old; a freeliving specimen from the western Indian Ocean that was examined by the author was 137 cm long. A term or near-term foetus 96.5 cm long attributed to this species by Nakamura (1935) is probably ***A. vulpinus***. Off Taiwan (Province of China) males were immature at about 174 to 283 cm, adolescent at about 239 to 305 cm, and adult at 259 to 323 cm; onset of maturity was at about 267 cm, with 50% mature at 267 to 276 cm. Females from Taiwan (Province of China) were immature at 176 to 294 cm, adolescent at 253 to 321 cm, and adult at 265 to about 365 cm; onset of maturity was at about 273 cm, with 50% mature at 282 to 292 cm. Elsewhere males were adolescent at 192 to 318 cm and adult at 276 cm, while females were immature or adolescent at 277 to 233 cm, adult at 264 to 330 cm, while pregnant females were 264 to about 300 cm. This is apparently a smaller species than ***A. superciliosus*** or ***A. vulpinus***.

Length-weight equations are given by Liu et al. (1999) for Taiwanese specimens:

Females: $W(kg) = 4.61 \times 10^{-5}\ TL(cm)^{2.494}$ (n = 230)

Males: $W(kg) = 3.98 \times 10^{-5}\ TL(cm)^{2.52}$ (n = 230)

Interest to Fisheries and Human Impact: This species was formerly exploited by the longline fishery in the northwestern Indian Ocean (primarily by the former USSR), but it is also fished in the Central Pacific. It is an important catch off Taiwan (Province of China) with about 222 t landed yearly. It enters the commercial thresher catch off California and is sometimes caught in considerable numbers off the Pacific coast of Mexico and Gulf of California. Also caught by shark fishermen in the Red Sea and Gulf of Aden (R. Bonfil, pers. comm.). Utilized for its meat (for human consumption), liver oil for vitamin-A extraction, hides for leather, and fins for shark-fin soup. Apparently seldom caught by anglers, but listed as a record fish along with other threshers by the International Game Fish Association. It is rarely caught by anti-shark nets off KwaZulu-Natal, South Africa. Harmless to people, seldom encountered by divers and not kept in aquaria as far as is known. Divers have viewed and photographed this shark on coral reefs and seamounts in the Gulf of California and the Red Sea, Indonesia and Micronesia, but it is not a regular subject of ecotouristic diving. According to Michael (1993) it is shy and difficult to approach underwater. The conservation status of this shark is uncertain, but Liu et al. (1999) considered it extremely vulnerable to overexploitation and in need of close monitoring because of its very low fecundity and relatively high age at maturation.

Local Names: Pelagic thresher, Thresher shark, Whiptail shark, Fox shark; Onagazame, Nitara (Japan); Zorro pelagico (Mozambique).

Remarks: Nakamura (1935) described ***A. pelagicus*** from three large specimens 270 to 330 cm TL , for which he presented measurements. He also gave an illustration (pl. 1, fig. 2) of a large female specimen, one-twentieth life size. It is uncertain if the specimen illustrated is one of the three large individuals described, as scaling up the drawing (204 mm long) gives a size of 408 cm. He also included a separate description (p. 5) and illustration (pl. 3) of a foetus 96.5 cm long as ***A. pelagicus***. All of these specimens are apparently syntypes of ***A. pelagicus***. Nakamura did not designate types for ***A. pelagicus*** and did not indicate if one of the three large specimens measured or the large female illustrated was the mother of the illustrated foetus or if the latter was separately obtained.

The large ***A. pelagicus*** specimen illustrated by Nakamura is apparently conspecific with ***A. pelagicus*** of Bass, D'Aubrey and Kistnasamy (1975a), Compagno (1984), and Last and Stevens (1994), as shown by its fin shapes, fin positions, colour pattern (including lacking a white patch over its pectoral base), oblique teeth, and possibly by lacking labial furrows. However, the illustrated foetus is apparently ***A. vulpinus*** and is recognizable by its small eyes, broad head with a strongly convex dorsal profile, short snout, presence of labial furrows, and falcate pectoral fins. Compagno (1984) and Eschmeyer (1998) were unable to provide information on whether or not the syntypes of this species still exist or for that matter if they were even preserved and deposited in a research collection. Nakamura only mentioned that the specimens were drawn by him from life. It may be necessary to designate a neotype for ***A. pelagicus*** based on Taiwan (Province of China) material. The name ***A. pelagicus*** is used here in the sense of Bass, D'Aubrey and Kistnasamy (1975a), Compagno (1984), and Last and Stevens (1994), who served to revise the concept of this species by restricting it to the species represented by Nakamura's illustrated adult.

Alopias pelagicus has commonly been mistaken for ***A. vulpinus***. For example, Gohar and Mazhar (1964, Red Sea), Kato, Springer and Wagner (1967, eastern Pacific), Fourmanoir and Laboute (1976, New Caledonia), Johnson (1978, Tahiti), and Faughnan (1980, Hawaiian Islands) all published illustrations of this species under the name ***A. vulpinus***. This species is probably more wide-ranging than present records show, although it has not been found in the Atlantic Ocean nor Mediterranean Sea and may be absent there.

Literature: Nakamura (1935); Gohar and Mazhar (1964); Kato, Springer and Wagner (1967); Fourmanoir and Laboute (1976); Johnson (1978); Faughnan (1980); Bass, D'Aubrey and Kistnasamy (1975a); Otake and Mizue (1981); Compagno (1984, 1990a, b); Hanan, Holts and Coan (1993); Michael (1993); Last and Stevens (1994); Eitner (1995); Villavicencio-Garaysar, Estrada-Agüero and Downton-Hoffman (1997); Liu et al. (1999); R. Bonfil (pers. comm.); S.P. Applegate (pers. comm.); S. Kato (pers. comm.); J. Crow (pers. comm.).

Alopias superciliosus (Lowe, 1840)

Fig. 65

Alopecias superciliosus Lowe, 1840, *Proc. Zool. Soc. London*, 1840(8): 39 (1841?). Also Lowe, 1849, *Trans. Zool. Soc. London*, 3(1): 18 (sometimes dated 1839). Holotype unknown (Eschmeyer, 1998, *Cat. Fish.*: CD-ROM), type locality Madeira, eastern Atlantic.

Synonyms: ***Alopias profundus*** Nakamura, 1935: 2, pl. 1, fig. 1, pl. 2. Syntypes: Three large specimens, 332, 352 and 366 cm TL, a large female illustrated and of uncertain size (Nakamura, 1935, pl. 1, fig. 1); also a 72 cm foetus, presumably the same as illustrated (Nakamura, 1935., pl. 2); all specimens from Suô fish market, Taiwan (Province of China). Whereabouts of syntypes unknown according to Eschmeyer (1998: CD-ROM), possibly never accessioned in a research collection.

Other Combinations: None.

FAO Names: En - Bigeye thresher; **Fr** - Renard à gros yeux; **Sp** - Zorro ojón.

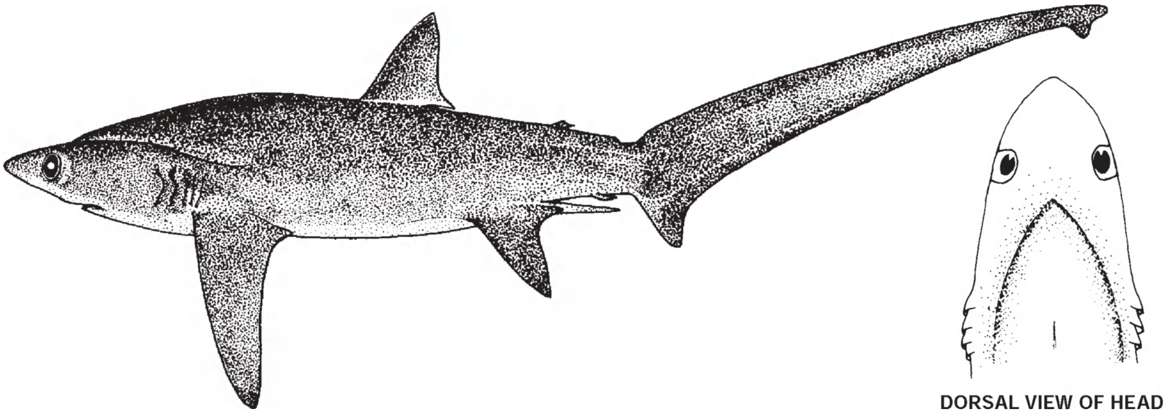
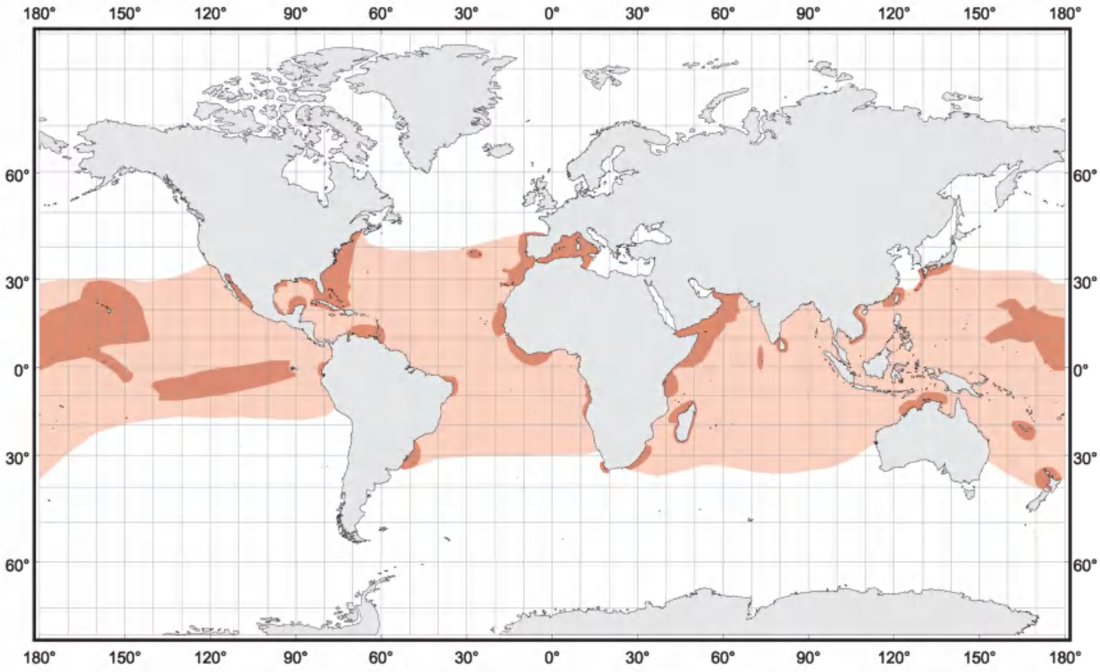


Fig. 65 *Alopias superciliosus*

Field Marks: Long dorsal caudal lobe nearly as long as rest of shark, notched or helmeted contour of head, huge eyes extending onto dorsal surface of head, falcate but rather broad-tipped pectoral fins.

Diagnostic Features: Head broad in dorsal and ventral view, with a notched dorsolateral profile. Snout moderately long, bulbous. Eyes greatly enlarged in young and adults, expanded onto dorsal surface of head and with a vertical, binocular field of view; interorbital space nearly flat. Labial furrows absent. Teeth large and in 22 to 27/20 to 24 rows (total for both jaws 42 to 51 rows); posterior tooth rows 1 to 3; no symphysial or intermediate teeth. Strong nuchal grooves present above branchial region. Pectoral fins falcate with curved and moderately broad tips. Claspers moderately slender and not whip-like. First dorsal midbase closer to pelvic-fin bases than to pectoral-fin bases. Caudal tip broad with wide terminal lobe. Ribs of monospondylous precaudal vertebrae fused ventrally to form a canal extending nearly to the occiput. Total vertebral count 219 to 319. Intestinal valve count 43 to 45. **Colour:** body purplish grey or grey-brown on upper surface and sides with underside grey to white, light colour of abdomen not extending over pectoral-fin bases; no white dot on upper pectoral-fin tips.

Distribution: Oceanic and coastal, virtually circumglobal in tropical and temperate seas. Western Atlantic (including Gulf of Mexico): USA (Atlantic coast from New York to Florida, Gulf of Mexico off Florida, Mississippi and Texas), Mexico (Veracruz to Yucatan), Bahamas, Cuba, Venezuela, central and southern Brazil. Eastern Atlantic: Portugal, Spain, Madeira, near Azores, Morocco, Canary Islands, Senegal, Guinea to Sierra Leone, Angola, South Africa (Western Cape): also western and central Mediterranean Sea. Indian Ocean: South Africa (Eastern Cape and KwaZulu-Natal), Madagascar, Arabian Sea (Somalia), Gulf of Aden, Maldives, Sri Lanka. Western Pacific: Southern Japan (including Okinawa), Taiwan (Province of China), Viet Nam, between northern Mariana Islands and Wake Island, Northwestern Submarine Rise, New Caledonia, Australia (northwestern coast), New Zealand. Central Pacific: Area between Wake, Marshall, Howland and Baker, Palmyra, Johnston, and Hawaiian Islands; north and south of Hawaiian Islands, off east of Line Islands, and between Marquesas and Galapagos Islands. Eastern Pacific: USA (California), Mexico (Gulf of California) and west of Galapagos Islands (Ecuador); possibly off Peru and northern Chile.



Habitat: Found in coastal waters over the continental shelves, sometimes close inshore in shallow waters, and on the high seas in the epipelagic zone far from land; also caught near the bottom in deep water on the continental slopes. Ranges from the surface and in the intertidal to at least 500 m deep, but mostly below 100 m depth.

Biology: An epipelagic, neritic, and epibenthic shark, apparently strong-swimming but little-known behaviourally. Ovoviviparous, with uterine cannibalism (oophagy), number of young usually two per litter, but sometimes with 3 or 4. Sex ratio of foetuses 1:1. Larger females apparently do not have larger term foetuses than smaller females. Birth may occur throughout the year although in the eastern Atlantic more females may give birth in autumn and winter than other times of year. The gestation period may be 12 months long but remains uncertain because of lack of birthing seasonality. In the eastern Atlantic a nursery area occurs off the Straits of Gibraltar, but similar areas no doubt occur elsewhere in the vast range of this species. Bigeye threshers have been aged with annular growth rings in vertebral centra, assuming one ring per year (Liu, Chiang and Chen, 1998). Males mature at about 9 or 10 years old and females at about 12 or 13 years old. Maximum number of growth bands, and maximum known age, about 19 for males and 20 for females.

The bigeye thresher feeds on pelagic fishes, including lancetfishes (Alepisauridae), herring (Clupeidae), mackerel (Scombridae), and small billfishes (Istiophoridae) and bottom fishes including hake (Merluccidae); also squids (Ommastrephidae). Apparently this species stuns its prey with its long caudal fin, as individuals are often tail-hooked on longlines. The arrangement of the eyes, with keyhole-shaped orbits extending onto the dorsal surface of the head, suggest that this species has a dorsal, vertical binocular field of vision (unlike other threshers) which may be related to fixating on prey and striking them with its tail from below. Michael (1993) observed sea lampreys attached near the cloaca of a bigeye thresher.

Size: Maximum total length about 461 cm. Size at birth 100 to 140 cm, with full term foetuses at 105 or 106 cm and free-swimming individuals down to 155 cm. Males immature up to 316 cm, maturing at about 279 to 300 cm; adult males as small as 276 cm and reaching about 410 cm with an estimated maximum of 421 cm. Females immature up to 350 cm, and maturing at about 294 to 355 cm; adult females as short as 341 cm and reaching at least 458 cm. Length-weight equations for this species are given by Kohler, Casey and Turner (1995) for fork length:

$$W\ (kg) = 9.1069 \times 10^{-6} \times FL\ (cm)^{3.0802} \quad (n = 55;\ \text{both sexes})$$

where $FL\ (cm) = 0.5598 \times TL\ (cm) + 17.666 \quad (n = 56)$

Liu, Chiang, and Chen (1998) give equations for total length:

$$\text{Females: } W\ (kg) = 1.02 \times 10^{-5}\ TL\ (cm)^{2.78} \quad (n = 175)$$

$$\text{Males: } W\ (kg) = 3.73 \times 10^{-5}\ TL\ (cm)^{2.57} \quad (n = 65)$$

Interest to Fisheries and Human Impact: Caught or formerly caught in the oceanic longline fisheries operated by the former USSR, Japan, Taiwan (Province of China), Spain, the USA, Brazil, Uruguay, Mexico, and probably other countries. Especially important areas for these fisheries are the northwestern Indian Ocean, western and Central Pacific, eastern North Pacific, and North Atlantic. The bigeye thresher was formerly a very important component of the Cuban longline fishery, and more recently has been taken in considerable numbers by longliners off the northeastern USA and by gill net vessels off southern California (USA) and the eastern Atlantic (by Spanish vessels), and by longliners off Taiwan (Province of China; where about 220 t per year are landed). This species is also taken as incidental bycatch in fixed bottom and pelagic gill nets, in trawls, and as a rare catch of anti-shark nets off KwaZulu-Natal, South Africa. It has been caught by anglers with sportsfishing gear (rod-and-reel) in the USA, South Africa, and New Zealand, in some instances by anglers targeting swordfish at night and using luminous lures. It is listed as a record fish along with other threshers by the International Game Fish Association. Its meat is utilized fresh, smoked and dried-salted for human consumption, its liver oil is processed for vitamin A, its skin for leather, and fins for shark-fin soup. Apparently harmless to people, and not known to have been encountered by divers underwater.

Local Names: Big-eyed thresher, Zorro (Cuba); Zorro ojón (Mexico); Tubarâo raposo, Bigeye thresher (Azores); Deepsea bigeye thresher, Bigeye, Bigeyed thresher shark, Big-eyed thresher, Hachiware (Japan); Grootoog-sambokhaai (South Africa); Zorro olho grande (Mozambique).

Remarks: This account follows Bass, D'Aubrey and Kistnasamy (1975a), Gruber and Compagno (1981), and Compagno (1984) in synonymizing ***Alopias profundus*** with this species. See Gruber and Compagno (1981) for a detailed discussion of the synonymy of ***A. profundus*** and for a general review of the biology of ***A. superciliosus***.

Literature: Nakamura (1935); Springer (1943); Bigelow and Schroeder (1948); Cadenat (1956c); Fitch and Craig (1964); Bass, D'Aubrey and Kistnasamy (1975a); Stillwell and Casey (1976); Blasco and Chapuli (1981); Gruber and Compagno (1981); Cadenat and Blache (1981); Branstetter and McEachran (1983); Gilmore (1983, 1993); Fulgosi (1983); Compagno (1984, 1990b, 1994); Compagno and Smale (1986); Ivanov (1986); Moreno and Morón (1992a); Hanan, Holts and Coan (1993); Michael (1993); Last and Stevens (1994); Eitner (1995); Kohler, Casey and Turner (1995); Bonfil (1997); Santos, Porteiro and Barreiros (1997); Chen, Liu and Chang (1997); Castillo-Geniz et al. (1998); Liu, Chiang and Chen (1998).

Alopias vulpinus (Bonnaterre, 1788) Fig. 66

Squalus vulpinus Bonnaterre, 1788, *Tabl. Encyclop. Method. Trois Reg. Nat., Ichthyol., Paris*: 9. Types unknown according to Eschmeyer (1998, *Cat. Fish.*: CD-ROM), type locality, Mediterranean Sea.

Synonyms: ***Squalus vulpes*** Gmelin, 1788: 1496. Types unknown according to Eschmeyer (1998: CD-ROM). ***Alopias macrourus*** Rafinesque, 1810: 12. Type locality, Sicily. No types. ***Galeus vulpecula*** Rafinesque, 1810: 13, equivalent to "***Squalus vulpecula*** di Linnao", which does not exist. Type locality, Sicily. No types. ***Squalus alopecias*** Gronow, 1854: 7. No types known, according to Eschmeyer (1998: CD-ROM). ***Alopecias barrae*** Perez Canto, 1886: 5. Type locality, Chile. Holotype possibly lost. ***Alopecias chilensis*** Philippi, 1902: 310. Type locality, Chile. No types known, according to Eschmeyer (1998: CD-ROM). ***Alopecias longimana*** Philippi, 1902: 308. Type locality, Chile. Whereabouts of type unknown, according to Eschmeyer (1998: CD-ROM). ***Vulpecula marina*** Garman, 1913: 30, pl. 7, fig. 1. Holotype: Museum of Comparative Zoology, Harvard, MCZ 1166-S (Eschmeyer, 1998:CD-ROM), juvenile 1 321/1 346 mm long (52 or 53 in) or 546 mm PCL, from Massachusetts Bay. Revival of ***Vulpecula marina*** Valmont, 1768: 740, rather than a description of a new species. Valmont's names were rejected as being not consistently binomial by the International Commission on Zoological Nomenclature (1925, Opinion 89: 27-33). ***Alopias caudatus*** Phillipps, 1932: 226. Based on specimen in Melbourne Museum figured by McCoy (1885: pl. 88) from Victoria, Australia. Holotype possibly NMV 58434 or 58437 according to Eschmeyer (1998: CD-ROM). ***Alopias greyi*** Whitley, 1937: 5. Holotype? ca. 305 cm, type locality, Bermagui, New South Wales; jaws only, whereabouts unknown according to Eschmeyer (1998: CD-ROM).

Other Combinations: ***Alopias vulpes*** (Gmelin, 1788), ***Alopecias vulpes*** (Gmelin, 1788), ***Carcharias vulpes*** (Gmelin, 1788).

FAO Names: **En** - Thresher shark; **Fr** - Renard; **Sp** - Zorro.

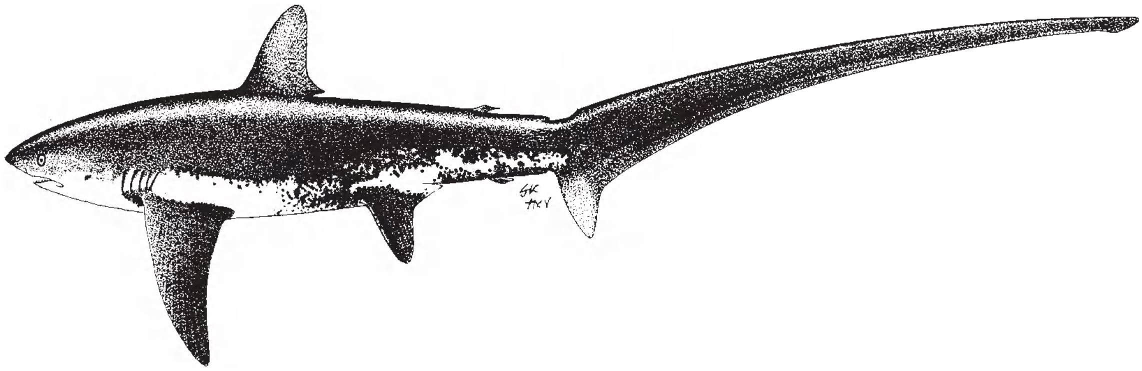
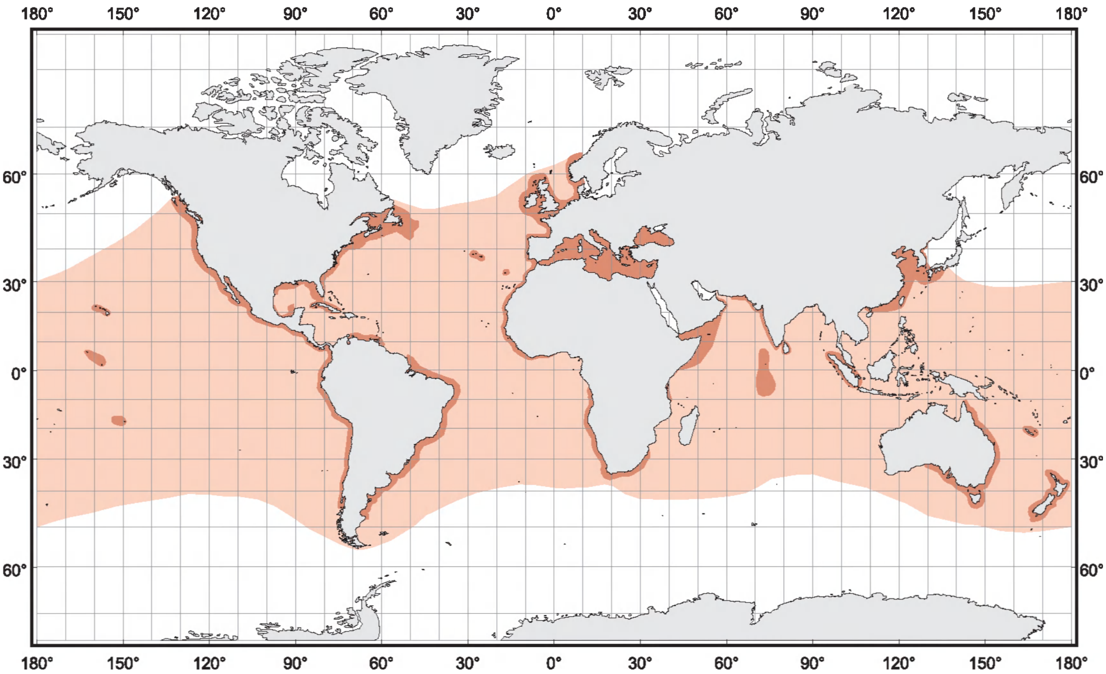


Fig. 66 *Alopias vulpinus*

Field Marks: Long curving dorsal caudal lobe about as long as rest of shark, relatively small eyes, falcate pointed pectoral fins, white colour of abdomen extending over pectoral-fin bases.

Diagnostic Features: Head broad in dorsal and ventral view, with a strongly convex dorsolateral profile. Snout relatively short, conical and pointed. Eyes moderately large at all sizes, not expanded onto dorsal surface of head and without a vertical, binocular field of view; interorbital space broadly convex. Labial furrows present. Teeth smaller with 32 to 52/25 to 50 rows (total for both jaws 58 to 102 rows); posterior tooth rows 2 to 10; symphysial and intermediate tooth rows usually present. No nuchal grooves present above branchial region. Pectoral fins falcate and with curved and narrow tips. Claspers extremely slender and whip-like. First dorsal-fin midbase closer to pectoral-fin bases than to pelvic fin bases. Caudal tip moderately slender with moderately broad terminal lobe. Ribs of monospondylous precaudal vertebrae lateral and not fused ventrally as a canal. Total vertebral count 339 to 364. Intestinal valve count 33 to 34. **Colour:** body blue-grey to dark grey or blackish above with sides silvery or coppery and underside white, white colour of abdomen extending dorsally and anteriorly over pectoral-fin bases as a conspicuous patch; white dot often present on upper pectoral-fin tips.

Distribution: Oceanic and coastal, virtually circumglobal in tropical to cold-temperate seas but commonest in temperate waters. Western Atlantic (including Gulf of Mexico): Canada (Newfoundland, Nova Scotia, New Brunswick, and Quebec, north to the Bay of Chaleur, Gulf of St. Lawrence), USA (entire Atlantic Coast but rare south of New England; Gulf Coast off Florida, Mississippi and Texas), Cuba, Mexico (Veracruz to Campeche), Venezuela, Brazil to Argentina. Eastern Atlantic: Norway and British Isles to Mediterranean and Black Seas, Morocco, Madeira, the Azores, Ghana, Côte d'Ivoire, Angola, Namibia, and South Africa (Western Cape and probably Northern Cape). Indo-West Pacific: South Africa (Eastern Cape and KwaZulu-Natal), Tanzania, Somalia, Maldives, Chagos Archipelago, Gulf of Aden, possibly Oman, Pakistan, India, Sri Lanka, Sumatra, Japan, Republic of Korea, China, Taiwan (Province of China), Australia (Queensland, New South Wales, Victoria, Tasmania, South Australia), New Zealand, New Caledonia. Central Pacific: Society Islands, Fanning Islands, Hawaiian Islands. Eastern Pacific: Canada (British Columbia), the USA (Washington, Oregon and California) and Mexico (Baja California), south to Panama and Chile.



Habitat: Coastal over the continental and insular shelves and epipelagic far from land in temperate to tropical waters, most abundant near land; young often close inshore and in shallow bays. Depth range from the surface and the intertidal to at least 366 m, often near the surface.

Biology: An active, strong-swimming shark, sometimes leaping out of the water. Thresher sharks in the northwestern Indian Ocean and off the west coast of North America show spatial and depth segregation by sex. Off the west coast of North America (and probably elsewhere) the species is seasonally migratory, and moves northward from Baja California into California waters during the spring, with adult males tending to travel farther northward than females and reaching the coast of British Columbia. Juveniles are mostly found in shallow warm-temperate inshore waters, particularly off southern California where an important nursery area occurs. Juveniles may be less cold-tolerant than adults, and seldom range north of central California. Both adults and juveniles congregate in inshore waters of southern California, primarily during spring and summer. Behaviour is otherwise poorly known, and little is known of sociobiology and behaviour patterns.

Transoceanic migrations have not been demonstrated, and there may be separate populations with slightly different fecundity and size at maturity in the eastern Pacific and western Indian Ocean, and possibly elsewhere, but this remains to be determined.

Ovoviviparous and apparently a uterine cannibal (oophagous), number of young 2 to 4 and rarely 6 in a litter off California (usually 2 to 4, commonly 4), and 3 to 7 in the eastern Atlantic. This species apparently uses inshore nursery areas in temperate waters (east coast of the United States, California, South Africa, the northeastern Atlantic and western Mediterranean, and probably elsewhere), with young sharks occurring in shallow bays (California, South Africa). In the eastern North Pacific (California) the species mates in summer, has a gestation period of nine months and gives birth during the spring. This shark matures between 3 and 8 years old, with a maximum age estimated at 45 to 50 years (Cailliet et al., 1983).

Feeds mostly on small schooling fishes but also bottom fishes, including herring, sardines, shad, pilchards and menhaden (Clupeidae), anchovies (Engraulidae), lanternfishes (Myctophidae), lancetfishes (Alepisauridae), needlefishes (Belonidae), scad (***Trachurus***, Carangidae), mackerels (Scombridae), bluefishes (Pomatomidae), plaice and flounder (Pleuronectidae) and sole (Soleidae); also squids, octopi and pelagic crustaceans, and rarely seabirds. Herds and stuns its prey with its long, whip-like caudal fin, and is often caught on longlines by being tailhooked. It swims in narrowing circles around schools of small fishes, splashing water with its caudal fin and compressing the school, then strikes and injures fishes with the caudal. Two threshers may cooperate on bunching and killing small fish.

Size: The largest thresher. Maximum total length at least 573 cm and possibly to over 610 cm, with an estimated maximum at 651 cm from growth curves and older unconfirmed records up to 760 cm. Size at birth 114 to 160 cm, with term foetuses up to 139 to 156 cm and small freeliving specimens down to 117 to 145 cm. Immature males up to at least 252 cm, while an adolescent male examined was 288 cm and adult males are 314 to at least 420 cm. Females maturing at about 315 to 400 cm, with immature or adolescent females up to 395 cm and adult females 376 to at least 549 cm. A length-weight equation is given by Kohler, Casey and Turner (1995) for fork length:

$$W(kg) = 1.8821 \times 10^{-4}\ FL(cm)^{2.5188} \quad (n = 88;\ both\ sexes)$$

where: $FL(cm) = 0.5474 \times TL(cm) + 7.0262$ (n = 13)

Interest to Fisheries and Human Impact: Widely caught or formerly caught in offshore longline and pelagic gill net fisheries including those of the former USSR, Japan, Taiwan (Province of China), Spain, the USA, Brazil, Uruguay, Mexico, and other countries. Especially important areas for these fisheries are the northwestern Indian Ocean, the western, central, and eastern Pacific, and the North Atlantic. Also fished with anchored bottom and surface gill nets, and accidentally caught in other gear including bottom trawls and fish traps. The species became the object of an important targeted pelagic gill net fishery off the west coast of the United States (particularly California but also Washington and Oregon) in the late 1970s, peaking at about 1 000 t in 1982 and declining due to overfishing to less than 300 t by the late 1980s. The targeted fishery was ended by 1990 but the species was still caught as bycatch of the swordfish gill net fishery and may be sold for higher prices in the market than swordfish. The meat is highly prized fresh for human consumption (cooked) but is also eaten smoked and dried-salted; the fins are valuable for shark-fin soup; the hide is usable for leather and the liver oil can be processed for vitamins.

Sports anglers seek these sharks in the USA, South Africa, and elsewhere with rod and reel. These sharks fight strongly when hooked and may jump out of the water. This and other threshers are listed as record fishes by the International Game Fish Association.

Apparently harmless to people, though the size of adults of this species should invite respect. There is an unconfirmed anecdotal account of a fisherman on the western North Atlantic coast of the USA that was decapitated by a tailstroke from a big adult thresher (Mundus and Wisner, 1971). A few assaults on boats are doubtfully attributed to this species. Small specimens have been seen underwater by divers, at the surface or close to the bottom, and have circled them at the limit of visibility without acting aggressively. Michael (1993) notes that this species is shy and difficult to approach underwater, but mentions an incident where a thresher of this species was aggressive toward a spearfishing diver off New Zealand. To the writer's knowledge, this species has seldom if ever been kept in captivity and is not currently the subject of ecotouristic shark-diving.

The conservation status of this shark is little known but is of some concern despite its midrange intrinsic rebound potential (a measure of the capacity to recover from fishing pressure; Smith, Au and Show, 1998) because of the history of the eastern Pacific thresher fishery (which declined quickly despite a relatively small and localized catch), and its exposure to high-intensity offshore fisheries virtually wherever it occurs.

Local Names: Common thresher, Fox shark, Thrasher shark, Long-tailed shark, Sea fox, Sea ape, Slasher (England); Whiptail shark, Thintail thresher, Fynstert-sambokhaai (South Africa); Lluynog mor (Wales); Renard, Singe de mer, La faux, Poisson épée, Péi aspasu ratou, Touille à l'épée (France); Rabosa, Peix espasa, Zorra de mar, Pez zorro, Zorro blanco (Spain); Arequim, Peixe alecrim, Peixe raposo, Peixe zorra (Portugal); Peixe rato, Peixe cavallo (Madeira); Tubarâo raposo, Romano, Româo, Thresher shark (Azores); Pesce volpe, Pesce sorcio or Pavone, Pesce bandiera, Pesce pavone, Pesce bannera, Volpe di mare, Pescio ratto, Allopia coda lunga, Allopia volpe marina, Pavone di mare, Pisce surci, Pisci cuda longa, Pisci cuduto, Pisci sciabula turca (Italy); Pas sabljas (Adriatic); Raefhajen (Sweden); Onagazame, Nadebuka, Nezumezame, Ma-onaga (Japan); Zorro (Cuba); Lisitska morskayia (Russia); Zorro cauda longa (Mozambique).

Remarks: This account follows Bass, D'Aubrey and Kistnasamy (1975a) and Compagno (1984) in combining several regional species of threshers from Chile, New Zealand and Australia into one wide-ranging species, ***A. vulpinus***. Threshers examined by the writer from the west coast of the USA and South Africa agree closely in morphology and meristics.

Literature: Garman (1913); Bigelow and Schroeder (1948); Gubanov (1972, 1978); Bass, D'Aubrey and Kistnasamy (1975a); Hixon (1979); Gruber and Compagno (1981); Cailliet et al. (1983); Cailliet and Bedford (1983); Compagno (1984, 1990b); Cailliet, Radtke and Welden (1986); Pascoe (1986); Bedford (1987); Cailliet and Radtke (1987); Moreno, Parajua and Morón (1989); Cailliet, Holts and Bedford (1993); Hanan, Holts and Coan (1993); Michael (1993); Last and Stevens (1994); Kohler, Casey and Turner (1995); Eitner (1995); Smith, Au and Show (1998).

2.2.6 Family CETORHINIDAE

Family: Subfamily Cetorhininae Gill, 1862b, *Ann. Lyceum Nat. Hist. New York*, 7(32): 397-398 (Family Lamnoidae). Emended to Family Cetorhinidae Gill, 1862, by Gill (1872, *Smiths. Misc. Coll.*, [247]: 24).

Type Genus: Subgenus ***Cetorhinus*** Blainville, 1816 (Genus ***Squalus*** Linnaeus, 1758).

Number of Recognized Genera: 1.

Synonyms: Group ***Selachina*** Günther, 1870 (Family Lamnidae): 389, 394. Emended to Family Selachidae Günther, 1870, by Poey, 1875: 85. Also Subfamily Selache (Family Lamna) Hasse, 1879: tab. 2. Type genus: Subgenus ***Selache*** Cuvier, 1816 (Genus ***Squalus*** Linnaeus, 1758). Family Halsydridae Whitley, 1934: 196. Type genus: ***Halsydrus*** Neill, 1809.

FAO Names: En - Basking sharks; **Fr** - Requins pélerin; **Sp** - Peregrinos.

Diagnostic Features: Head moderately long but much shorter than trunk. Snout moderately long, pointed and conical, not depressed, flattened or blade-like. Eyes small with length 0.8 to 1.3% of precaudal length. Gill openings extremely large, width of first 17.7 to 29.2% of precaudal length, extending onto dorsal and ventral surfaces of head; all gill openings anterior to pectoral-fin bases; gill rakers present on internal gill slits, in the form of hair-like modified dermal denticles with extremely elongated crowns. Mouth large and arcuate, ventral on head; jaws hardly protrusable but greatly distensible laterally. Teeth very small, hook-like, not blade-shaped, and in 203 to 255/225 to 230 (432 to 480 total) rows. Several rows of small anterior teeth in upper jaw, separated from the similar-sized laterals by a broad gap but without intermediate teeth; no symphysial teeth. Trunk fusiform and moderately stout, firm and not flabby. Caudal peduncle depressed and with strong lateral keels and upper and lower crescentic precaudal pits. Dermal denticles large and rough, with erect hooked crowns, strong cusps and ridges, with cusps of lateral denticles pointing in several directions. Pectoral fins long and moderately broad, much shorter than head in adults; pectoral skeleton plesodic with radials extending far into fin webs. Pelvic fins smaller than first dorsal fin but larger than second; fin skeleton aplesodic, not extending into fin web. First dorsal fin large, high, erect and angular; fin skeleton semiplesodic, extending partways into fin web. Second dorsal and anal fins moderately large but less than half size of first dorsal, with broad, non-pivotable bases. Caudal fin lunate, dorsal lobe moderately long but less than one-third length of rest of shark, ventral lobe nearly as long as dorsal lobe. Neurocranium with a high cranial roof but otherwise low, not compressed, with long rostrum, depressed internasal septum and widespread nasal capsules, small orbits with strong supraorbital crests, small stapedial fenestrae, and with hyomandibular facets not extended outward. Vertebral centra strongly calcified, with well-developed double cones and radii and prominent annuli. Total vertebral count 109 to 116, precaudal count 50 to 54, diplospondylous caudal count 55 to 62. Intestinal valve of ring type with 47 to 51 turns. Size gigantic with adults 5 to about 10 m and possibly to 12 to 15 m long.

Remarks: This family includes the single living genus ***Cetorhinus*** Blainville, 1816, and possibly a single living species, the basking shark, ***C. maximus*** (Gunnerus, 1765) as well as several fossil species (Woodward, 1889; Cappetta, 1987). Publication of ***Cetorhinus*** Blainville and its synonym ***Selache*** Cuvier in the same year caused confusion, with several prominent nineteenth century authors using ***Selache*** or the emended ***Selachus*** instead of ***Cetorhinus*** (Bonaparte, 1838; Müller and Henle, 1839; Swainson, 1838; Bleeker, 1859; Dumeril, 1865; Günther, 1870). ***Cetorhinus*** was used by several nineteenth century authors (Gray, 1851; Gill, 1862b, 1872, 1893; Jordan and Gilbert, 1883; Jordan and Evermann, 1896) and was in general use by most twentieth century authors. Whitley (1934), followed by Fowler (1941) and Smith (1949), proposed that the genus ***Cetorhinus*** should be replaced by ***Halsydrus***, which was based on the carcass of a 'sea monster' washed ashore in the Orkney Islands and eventually identified as a basking shark. According to Bland and Swinney (1978), ***Halsydrus*** as originally proposed by Neill, 1809, was apparently a *nomen nudum*, separately proposed from descriptions of the Orkney 'monster', and does not comprise a senior synonym of ***Cetorhinus***. Rafinesque's (1810) genus ***Tetroras*** (and its variant ***Tetnoras***) is hard to identify from its generic description, with Rafinesque's claim that ***Tetroras*** has four gill openings being probably erroneous (unless the specimen examined was abnormal). Rafinesque's description of ***Tetroras angiova***, the only species in the genus, does indeed suggest a basking shark in certain details ("denti in forma di raspa... ha gli occhi piccolissimi, e le aperture delle branchie bastantemente larghe."). However, even if more evidence was available to prove that ***T. angiova*** actually was a basking shark, the substitution of ***Tetroras*** for ***Cetorhinus*** would not serve the stability of zoological nomenclature due to universal usage of ***Cetorhinus*** for the basking shark at present.

Couch (1862) proposed the genus ***Polyprosopus*** as separate from ***Cetorhinus*** and including two species apparently based on aberrant basking sharks. ***Polyprosopus*** was recognized by Gill (1862b) but was synonymized with ***Cetorhinus*** or ***Selache*** by Dumeril (1865), Günther (1870) and subsequent authors.

Following Müller and Henle (1839) and Bonaparte (1838, 1839), ***Cetorhinus*** or ***Selache*** were often placed in the family Lamnidae or Isuridae (Gray, 1851; Bleeker, 1859; Dumeril, 1865; Woodward, 1889; Regan, 1906a; Goodrich, 1909; Garman, 1913; Engelhardt, 1913; Berg, 1940; Norman, 1966; Bailey et al., 1970; Nelson, 1976, 1984). Gill (1862b) proposed a subfamily Cetorhininae within the Lamnidae for ***Cetorhinus***; the Cetorhininae as a subfamily of Lamnidae was recognized by Berg and Svidovidov (1955). Günther (1870) proposed a group Selachina within Lamnidae for ***Selache***, which was followed by Hasse (1879). Gill (1872) elevated Cetorhininae to the family Cetorhinidae, which has been recognized by most modern authors (Jordan and Gilbert, 1883; Gill, 1893; Jordan and Evermann, 1896; Bridge, 1910; Jordan, 1923; Lozano y Rey, 1928; White, 1936, 1937; Bertin, 1939a; Romer, 1945, 1966; Bigelow and Schroeder, 1948; Matsubara, 1955; Arambourg and Bertin, 1958; Glikman, 1964, 1967; Fowler, 1967a; Patterson, 1967; Blot, 1969; Budker and Whitehead, 1971; Lindberg, 1971; Rass and Lindberg, 1971; Pinchuk, 1972; Compagno, 1973, 1981b, 1982, 1984, 1990b, 1999; Applegate et al., 1979; Chu and Meng, 1979; Gubanov, Kondyurin and Myagkov, 1986; Cappetta, 1987; Carroll, 1988; Eschmeyer, 1990, 1998; Robins et al., 1991a; Nelson, 1994; Helfman, Collette and Facey, 1997). Shirai (1996) in contrast placed ***Cetorhinus*** in a subfamily Cetorhininae of the family Alopiidae. Whitley (1940), Fowler (1941), and Smith (1949) substituted the family Halsydridae for Cetorhinidae after synonymizing ***Cetorhinus*** with ***Halsydrus*** (see above). Maisey (1985) synonymized the megamouth family Megachasmidae with Cetorhinidae, which was followed by Robins et al. (1991a). As noted by Springer and Gilbert (1976) and Compagno (1990b), ***Cetorhinus*** is very distinct. It may be the sister group of the family Lamnidae (Compagno, 1990b) but is apparently not closely related to Megachasmidae on its anatomy. Martin and Naylor (1997) suggested that Lamnidae and ***Cetorhinus*** are sister groups on gene similarities from cytochrome b DNA, while Long and Waggoner (1996) suggested that ***Megachasma*** and ***Cetorhinus*** are sister groups on dental morphology.

Most authors recognize only one species of living basking shark (summarized in Garman, 1913; Bigelow and Schroeder, 1948; Springer and Gilbert, 1976; and Compagno, 1984), but Siccardi (1960, 1961) suggested that there are four species (or subspecies) of ***Cetorhinus***, two from the North Atlantic and Mediterranean (***C. maximus*** and ***C. rostratus***), one from southern Australia (***C. maccoyi***) and one from the western South Atlantic (***C. normani***), based on morphometric, morphological and meristic differences. Characters included differences in head length, numbers of functional-tooth rows, gill opening width, body height, prepectoral length, trunk shape, interdorsal space, position of the dorsal and anal fins, vertebral numbers, and size. Apart from Argentinean material of ***C. normani*** which she examined, Siccardi's morphometrics were based on available literature accounts of basking sharks from other areas. More recently Tomés and Gomes (1989) suggested that two specimens of Brazilian basking sharks they had examined differed morphologically from those from the North Atlantic.

Springer and Gilbert (1976) suggested that there was insufficient evidence at present to separate the four ***Cetorhinus*** species on the basis suggested by Siccardi, with which Compagno (1984) concurred. The 'small' species ***C. rostratus*** seems to represent juveniles of ***C. maximus,*** and ***C. maximus***, ***C. maccoyi***, and ***C. normani*** as defined by Siccardi differed in characters that need more detailed analysis and consistent collection of data from basking sharks from various parts of the world to factor out individual variation, allometry, sexual dimorphism, and data idiosyncrasies. The question of allopatric species, subspecies, or populations within ***Cetorhinus*** needs further study. A problem with conventional morphological studies is the lack of sufficient data for adequate comparisons, as well as the existence of data sets (including morphometrics and illustrations) that are difficult to compare. This stems in part from the great size of the basking shark, which makes data-collecting (particularly of morphometrics, as the writer can attest) and illustration difficult and prone to error, as well as low and sporadic interest in basking shark variation, limited opportunities to collect data, and lack of agreement on data protocols for morphometrics, meristics and descriptive morphology.

Even if the basking shark comprises a single species, its known distribution suggests that there may be isolated populations in temperate and boreal waters with potentially limited genetic interchange. Records of occasional basking sharks from warm-temperate to tropical inshore waters suggest, however, that interchange by crossing the tropics in deep water is possible if infrequent. Populations or subpopulations of basking sharks could include a North Pacific population (with possible eastern and western North Pacific subpopulations?), a North Atlantic population (with possible western North Atlantic, eastern North Atlantic and Mediterranean subpopulations?), a temperate South American population (with possible eastern South Pacific and western South Atlantic subpopulations?), a southern African (Namibia and South Africa) population ('Cape basking shark'), and an Australian-New Zealand population (if not forming separate New Zealand and Australian subpopulations?). Some efforts are being made to collect tissue samples from Northern Hemisphere basking sharks for DNA comparisons (UK CITES proposal, 1999), which should be extended to Southern Hemisphere sharks. Lack of recovery of basking shark numbers following intensive localized fisheries suggests isolated, geographically limited populations or subpopulations that are not readily replaced through immigration. Some of these populations may be very small; basking sharks occurring off southern Africa and possibly Brazil and Argentina are apparently present in very small numbers compared to northern hemisphere localities.

Cetorhinus Blainville, 1816

Genus: Subgenus ***Cetorhinus*** Blainville, 1816 (Genus ***Squalus*** Linnaeus, 1758), *Bull. Sci. Soc. Philomat. Paris*, (8): 121.

Type Species: not designated; Blainville included the species "***Gunneri***; ***Peregrinus***; ***Shavianus***; ***Homianus***?" in ***Cetorhinus*** without further comment. Gill (1862b, *Ann. Lyceum Nat. Hist. New York*, 7(32): 398), designated ***Squalus maximus*** "Linnaeus" (= Gmelin, 1788) as type of ***Cetorhinus***, but this was not an included species. Jordan and Gilbert (1883, *Bull. U. S. Nat. Mus.*, 16: 31) designated "***Cetorhinus gunneri*** Blainv. = ***S. maximus*** L." (a junior synonym of ***Squalus maximus*** Gunnerus, 1765) as type of ***Cetorhinus***, which may be the earliest valid type designation. Eschmeyer (1998, *Cat. Fish.*: CD-ROM) cited Jordan and Evermann (1896, *Bull. U.S. Natn. Mus.*, (47), pt. 1: 51) as a later, similar type designation.

Number of Recognized Species: 1.

Synonyms: Genus ***Halsydrus*** Neill, 1809a: 5-6; also Neill, 1809b: 90-91 (*nomina nuda*, not seen; Bland and Swinney, 1978: 134; Eschmeyer, 1998: CD-ROM). ?Genus ***Tetroras*** Rafinesque, 1810a: 11. Type species, ***Tetroras angiova*** Rafinesque, 1810, by monotypy. Also Rafinesque, 1810b: 46; Rafinesque, 1815: 93. Subgenus ***Selache*** Cuvier, 1816 (Genus ***Squalus*** Linnaeus, 1758): 129. Type species, "***Sq. maximus*** L." by monotypy (***Squalus maximus*** Gmelin, 1788, a junior synonym of ***Squalus maximus*** Gunnerus, 1765). Genus ***Halsydrus*** Fleming, 1817: 713; Fleming, 1822: 380. Type species: ***Halsydrus pontoppidani*** Fleming, 1817, by monotypy? (Bland and Swinney, 1978: 134). ?Genus ***Scoliophis*** Anonymous, 1817: 44, cited by Sherborn (1930: 5809) and Neave (1940: 150). Listed in synonymy of ***Halsydrus maximus*** by Whitley (1939: 241) without explanation; possibly a 'sea serpent' based on a basking shark carcass? Genus ***Selanche*** Jarocki, 1822: 452 (error for ***Selache*** Cuvier, 1816?). Genus ***Selachus*** Minding, 1832: 52 (unjustified emendation of ***Selache*** Cuvier, 1816?). Genus ***Ceteorhinus*** Agassiz, 1846: 75 (error or emendation for ***Cetorhinus*** Blainville, 1816?). Genus ***Polyprosopus*** Couch, 1862: 67. Two species, ***P. rashleighanus*** (Couch, 1832) and ***P. macer*** Couch, 1862 included in the genus without a type designation. Type species, "***Polyprosopus Rashleighanus*** Couch", by subsequent designation of Gill (1862b: 398) and according to Eschmeyer (1998: CD-ROM). Genus ***Hannovera*** van Beneden, 1871: 504. Type species: ***Hannovera aurata*** van Beneden, 1871, possibly by original designation. Based on fossil basking shark gill rakers from the Pliocene of Belgium (Woodward, 1889), possibly the same species as the living basking shark (Cappetta, 1987). Genus ***Cethorhinus*** Escribano, 1909: 340 (error or emendation for ***Cetorhinus*** Blainville, 1816?). Genus ***Scapasaurus*** Marwick, 1942: 1. *Nomen nudum,* no species name, apparently proposed for a 'sea monster', based on the carcass of a basking shark washed up in Scapa Flow. The vertebrae of this shark are in the British Museum (Natural History), BMNH 1946.8.3.1 (citation from Bland and Swinney, 1978: 134). Genus ***Tetnoras*** Fowler, 1941: 112. Based on ***Tetroras*** Rafinesque, 1815: 93, the printing of which resembles ***Tetnoras*** in the original but seems to be a poorly printed "r" rather than an "n". ?Genus ***Tetraoras*** Bigelow and Schroeder, 1948: 146. Variant spelling on ***Tetroras*** Rafinesque, 1810? Genus ***Hannoveria*** Capetta, 1987: 107. Variant spelling on ***Hannovera*** van Beneden, 1871.

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Cetorhinus maximus (Gunnerus, 1765) Fig. 67

Squalus maximus Gunnerus, 1765, *K. Norske Vidensk-selsk.Scr. Trondh.*: 33, pl. 2. Holotype, apparently none. Type Locality: Trondhjem, Norway.

Synonyms: ***Halsydrus pontoppidani*** Neill, 1809: 5-6; also Neill, 1809: 90-91 (*nomina nuda*; Bland and Swinney, 1978: 134). ?***Tetroras angiova*** Rafinesque, 1810a: 11. No types?, *species dubium*. Also Rafinesque, 1810b: 46; Rafinesque, 1815: 93. ***Squalus gunnerianus*** Blainville, 1810: 256, pl. 2, fig. 3; also Blainville, 1810b: 170. Types? (Eschmeyer, 1998: CD-ROM). ***Squalus homianus*** Blainville, 1810: 257, pl. 2, fig. 1. Also Blainville, 1816: 121. Types? (Eschmeyer, 1998: CD-ROM). ***Squalus pelegrinus*** Blainville, 1810a: 256, pl. 2, fig. 2. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN 9853 (Eschmeyer, 1998: CD-ROM). ***Squalus peregrinus*** Blainville, 1811: 365. Also Blainville, 1816: 121. Variant and possibly emended spelling of ***Squalus pelegrinus*** Blainville, 1810. ***Squalus (Cetorhinus) Gunneri*** Blainville, 1816: 121 (*nomen nudum*). ***Squalus (Cetorhinus) Shavianus*** Blainville, 1816: 121 (*nomen nudum*). ?***Scoliophis atlanticus*** Anon., 1817: 44, cited by Sherborn (1923: 535). Listed in synonymy of ***Halsydrus maximus*** by Whitley (1939: 241) without explanation, possibly a 'sea serpent' based on a basking shark carcass? ***Halsydrus pontoppidani*** Fleming, 1817: 713. Stronsa, Orkney Islands. Holotype: National Museum of Scotland, NMSZ-1979.012, three vertebrae in alcohol and dried ceratotrichia, *fide* Herman, McGowan and Swinney (1990: 1). ***Squalus isodus*** Macri, 1819: 76, pl. 1, fig. 2. Mediterranean. No types (Eschmeyer, 1998: CD-ROM). ***Squalus rostratus*** Macri, 1819: 76, pl. 1, fig. 1, pl. 2. Mediterranean. No types known (Eschmeyer, 1998: CD-ROM). ***Squalus elephas*** Le Sueur, 1822: 350, pl. Types: Based on a large adult male specimen, about 10 m (32 ft 10 in) TL from the New Jersey coast, possibly not saved. Types? (Eschmeyer, 1998: CD-ROM). ***Squalus rashleighanus*** Couch, 1838: 51. Type locality, Cornwall. Types? (Eschmeyer, 1998: CD-ROM). ***Squalus rhinoceros*** Mitchell, *in* DeKay, 1842: 358 (reference to name in newspaper article by Mitchell, 1828 citation unknown). Name only, not available, Maine Coast (Eschmeyer, 1998: CD-ROM). ***Squalus cetaceus*** Gronow, 1854: 6. Type locality, Norway. No types known (Eschmeyer, 1998: CD-ROM). ***Polyprosopus macer*** Couch, 1862: 68, pl. 15, fig. 2. Type locality, Startpoint, Cornwall, England. No types known (Eschmeyer, 1998: CD-ROM). ***Cetorhinus blainvillei*** Capello, 1870: 233, 1 pl. Type locality, Portugal. Types? (Eschmeyer, 1998: CD-ROM). ***Selachus pennantii*** Cornish, 1885: 351. Type locality: Cornwall. No types known (Eschmeyer, 1998: CD-ROM). ***Tetroras maccoyi*** Barrett, 1933: 13. Types? Australia. Reference from Whitley (1934: 197) and Eschmeyer (1998: CD-ROM). ?***Tetraoras angiona*** Bigelow and Schroeder, 1948: 146. Error for ***Tetroras angiova*** Rafinesque, 1810. ***Cetorhinus maximus*** forma infanuncula van Deinse and Adriani, 1953: 309. Holland, for specimens without gill rakers. Types? Not available, according to Eschmeyer (1998: CD-ROM). ***Cetorhinus maximus normani*** Siccardi, 1960: 255, pl. 1. Syntypes (4): Museo Argentino de Ciencias Naturales, Bernardino Rivadavia, Capital Federal, Argentina, MACN (Eschmeyer, 1998: CD-ROM). Also Siccardi, 1961: 96-97 (as species, ***C. normani***).

Other Combinations: ***Halsydrus maximus*** (Gunnerus, 1765), ***Selache maxima***, ***Selache maximus*** or ***Selache maximum*** (Gunnerus, 1765), ***Selache elephas*** (Le Sueur, 1822).

FAO Names: En - Basking shark; **Fr** - Pélerin; **Sp** - Peregrino.

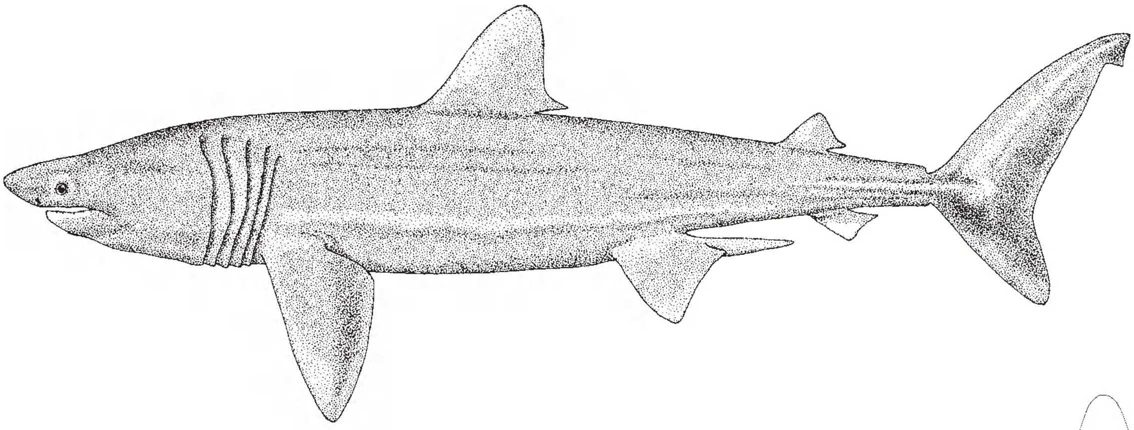
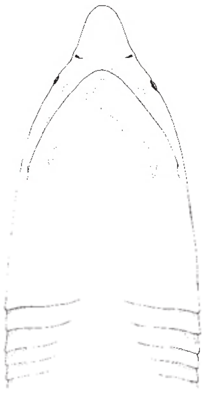


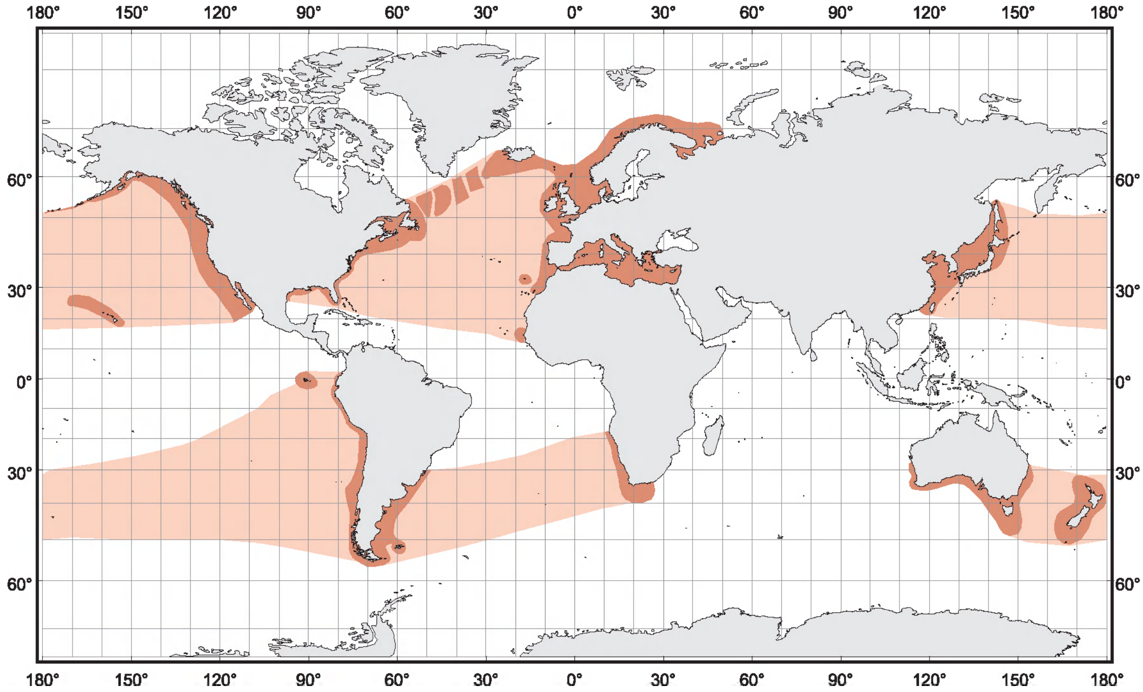
Fig. 67 *Cetorhinus maximus*



Field Marks: The great size, enormous gill slits that virtually encircle the head, dermal denticle gill rakers, pointed snout, huge, subterminal mouth with minute hooked teeth, caudal peduncle with strong lateral keels, and lunate caudal fin distinguish this shark from all others. **Colour:** blackish to grey-brown, grey or blue-grey above and below on body and fins, undersurface sometimes lighter, often with irregular white blotches on the underside of the head and abdomen; flanks sometimes with lighter linear striping and spots.

Diagnostic Features: See family Cetorhinidae above.

Distribution: Circumglobal with a wide but possibly disjunct distribution: Western North Atlantic: Canada (Newfoundland, Nova Scotia, New Brunswick) and the United States (Maine, New Hampshire, Massachusetts, Connecticut, Rhode Island, New York, New Jersey, Delaware, Maryland, Virginia, North Carolina, Georgia and Florida, also northern Gulf of Mexico), with most records in the Gulf of Maine and in the Mid-Atlantic Bight. Western South Atlantic: Southern Brazil, Uruguay and northern Argentina, Falkland (Malvinas) Islands. Eastern North Atlantic, Arctic Ocean, and Mediterranean Sea: Iceland (south and west coast), Faeroe Islands, Norway and Russia (western Barents Sea and White Sea), south to Sweden, Scotland, Ireland, England, France, Spain, and Portugal, the entire Mediterranean Sea (including Italy, Greece and Turkey), Morocco, and Senegal. Eastern South Atlantic and southwestern Indian Ocean: Namibia and South Africa (Northern and Western Cape Provinces). Western North Pacific: Japan, Korean Peninsula, Taiwan (Province of China), China. Western South Pacific: Australia (New South Wales, Victoria, Tasmania, South Australia and Western Australia), New Zealand. North-central Pacific: Hawaiian Islands (USA). Eastern North Pacific: Gulf of Alaska and Aleutian Islands to Gulf of California, including Canada (British Columbia), the United States (Alaska, Washington, Oregon, and California), and Mexico (Baja California and northern Gulf of California). Eastern South Pacific: Ecuador, Peru and Chile, Galapagos Islands.



Habitat: A coastal-pelagic and semioceanic or oceanic shark found in boreal to warm-temperate waters of the continental and insular shelves, occurring well offshore and often very close to land, just off the surf zone, and entering enclosed bays. Most individuals are observed in shallow coastal waters, but records from aerial cetacean and sea turtle surveys in the western North Atlantic, a stranding at an oceanic island chain (Hawaiian Islands), and pelagic driftnet records in the temperate North Pacific suggests that it readily ventures into the epipelagic zone. It has been sighted at the surface over the slopes from 200 to 2 000 m, and with a few sighted in the oceanic basins at 2 000 to 4 000 m. The basking shark is thought to overwinter in deep offshore waters, possibly near the bottom, and has occasionally been caught in deep bottom trawls in the Gulf of St. Lawrence and off Scotland. Off the United Kingdom, Japan and Newfoundland most records are in waters of 8 to 14°C, though off the Atlantic coast of New England sightings were in waters of 11 to 24°C with most at 16 to 24°C. Basking sharks seem to prefer ocean fronts, where differing water masses meet, and close inshore off headlands, around islands and in bays with strong fluctuation of water masses from tidal flow and where aggregations of zooplankton occur.

Biology: The sociobiology, behaviour and population biology of the basking shark are sketchily known and need further investigation. Although basking sharks are huge impressive animals that are readily accessible to underwater observation and are conspicuous to surface observers, a limited amount is known of displays, courtship, and social structure, though this is changing with intensive behavioural observation of basking sharks off the UK (Earll et al., 1992). A problem is that the basking shark is traditionally studied and viewed as a fisheries object, so that many details of its behaviour and general biology remain to be elucidated.

Basking sharks are apparently social animals as in some other lamnoids, and show some behaviours that may be intraspecific displays. This shark is often seen at or near the surface, singly, in pairs or triads or in schools up to a hundred or more individuals, basking with dorsal fins out of the water or even with bellies upward. Adults have been seen together, as have pairs with young individuals and adult females (the former assumed to be offspring). These sharks are often seen moving slowly forward or in short arcs with their mouths distended like hoops and pharynx expanded while feeding, sometimes with snouts out of the water. They also *cruise* when not feeding, with mouth partly closed and pharynx not expanded. The open-mouthed feeding posture of basking sharks is analogous to *gaping* in certain other lamnoids, although it is not established if the basking shark uses gaping in a social context apart from feeding. Surface-basking in this shark is thought to be correlated with surface concentrations of zooplankton and also with courtship and mating. Two, three or more individuals may engage in *tandem-swimming*, in a straight line or in circles, which suggests to some writers that a row of these sharks swimming together may have been mistaken for a single huge 'sea serpent' in the past. They also show *parallel-swimming* or *stalling* (stopping, sometimes for protracted periods), with sharks alongside one another, and sometimes make a *wedge-formation* of three individuals while feeding. Nose to tail *circling* has been described with a male and female and even a pair of males. The sharks direct their feeding along tidal lines, may circle zooplankton patches, and may swim in one direction, do a *U-turn*, then parallel their previous track. They can also stop and gulp down plankton concentrations, may stall and keep in one position, may swim very slowly, and show relatively fast dashes at the surface. They may dive suddenly when disturbed, and may flick their tails sharply before doing so. Individuals may *droop* their dorsal fins nearly 45° to one side; they also may lift their tails out of the water and do a *tail-sweep*, wagging the tail from side to side at a 45° angle in an exaggerated movement. Under provocation (particularly when harpooned) this species may defend itself by *tail-swatting*. Basking sharks may approach divers and boats quite closely, possibly out of curiosity, and swim around them or follow them.

Recent observations and photographs confirm that basking sharks *breach* or jump partway or entirely out of the water, and it has been suggested that they do so to dislodge parasites or commensals such as lampreys or remoras. In addition to the ectoparasitic copepods found on other sharks, basking sharks often have sea lampreys (***Petromyzon marinus***) attached to their skin in the North Atlantic, and although lampreys apparently are unable to cut through the formidable denticle-armoured skin of the shark, they may be enough of an irritant to evoke a reaction like breaching or rubbing on objects or the bottom (*chafing*) to dislodge them. Basking sharks may breach alone or while in groups, and breaching may also have a social significance in intraspecific communication.

Dead basking sharks are often stranded on the beach, in a state of advanced decay and damaged and partly dismembered from rolling in the surf, and they have been also occasionally lifted from the bottom by trawls on fishing boats. Several times such carcasses have been misidentified as 'sea serpents', plesiosaurs or other fabulous monsters, some of which have been given specific and even generic names.

Numbers of basking sharks sighted may fluctuate greatly in given areas each year, with irregular increases ('invasions') and decreases that are of uncertain cause. Estimates of world population numbers are unavailable, as with most other sharks, but aerial surveys suggest that numbers of basking sharks in localized areas (e.g., New England coast and Monterey Bay) may not exceed 2 000 to 6 000, nor have catches in the eastern North Atlantic much exceeded 3 000 per year when catches were highest.

The massive liver of the basking shark, contained in a long body cavity, apparently serves as a 'hepatic float' to adjust it to approximately neutral buoyancy.

Basking sharks are highly migratory, and noteworthy for their seasonal appearance in numbers in given localities and subsequent disappearance. Off the Atlantic seaboard of North America they appear in the southern part of their range in spring (North Carolina to New York), apparently shift northward in summer (New England and Canada), and disappear in autumn and winter. Off the eastern North Pacific basking sharks occur in greatest numbers during autumn and winter in the southernmost part of their range there (California), but shift at least in part to more northern latitudes in spring and summer (up to Washington and British Columbia). Off the United Kingdom the bulk of the population there appears in the springtime and disappears by autumn, but individuals may be present at all seasons of the year. Aerial surveys off New England suggests that basking sharks move into shallow coastal waters from deeper water in springtime as zooplankton blooms develop; sightings there indicate that basking sharks occur at the surface in the epipelagic zone in deep water, above the slopes and even in the ocean basins. Research is currently in progress in the eastern North Atlantic using satellite radio tags to resolve some of the problems of migration in this species. Priede (1984) details an early successful short-term satellite tracking effort on a radio-tagged basking shark, and plans for satellite tagging using more modern equipment are underway in the United Kingdom (Dunbar, Fowler and Denham, 1995). This space-age methodology may unravel some of the secrets of the basking shark's seasonal migrations and movements. Adult individuals found off the United Kingdom in summertime are apparently engaged in courtship activity and copulation, as indicated by behavioural observations and courtship and mating scars found on captured individuals.

Pronounced spatial and seasonal populational segregation may be a characteristic of this species, as suggested by fisheries catches off the United Kingdom. Most individuals caught there in the summer were subadult or nonpregnant adult females, outnumbering the males by 40:1, but in the winter the few individuals caught were mostly males. Off Japan most basking sharks taken in fisheries are or were females.

Pregnant females are almost entirely unknown for the species, suggesting that such females are spatially and bathymetrically separated from those members of the population that are regularly seen basking at the surface. It is also possible that the number of pregnant females is very low relative to the number of non-pregnant adult females, with correspondingly few being taken and with extremely low fecundity for the species. Juveniles below 3 m long have been extremely rare in the literature, with a single record of a freeliving individual about 1.7 m long reported from the British Isles. More recently, field observers from the UK Marine Conservation Society have reported larger numbers of sightings of individuals between 2 and 4 m long (34%), 4 to 6 m (about 38%), and 6 to 8 m (about 18%), but with few young below 2 m (3%) or large adults above 8 m (8%) of over 3 300 individuals sized (Pollard, 1996). This suggests low local recruitment of young, but large numbers of juveniles (2 to 6 m) and smaller numbers of adults (6 to 8+ m).

A pregnant female has been reported with a litter of six young. Adult, nonpregnant female basking sharks have immense numbers of small eggs in their ovaries, which suggests that this shark has uterine cannibalism as in many other lamnoids, with embryos feeding on the small eggs (oophagy). Feeding on smaller siblings (adelphophagy) has not been demonstrated. Young below 2 m appear in waters of the United Kingdom in springtime, suggesting spring pupping.

Age of this shark has been estimated by counting vertebral rings and attempting to correlate them with supposed changes in size of individuals within a population, but this has met with limited success. It has been suggested that birth occurs after a 3.5 year gestation period, and that two calcified rings per year are laid down until maturity at between 6 and 8 years for males (Parker and Stott, 1965). The correlation of the rings with time is uncertain and controversial. Pauly (1978) initially suggested a yearly rate of ring deposition, but Pauly (in press) recently suggested that vertebral rings were unreliable for estimates of age in basking sharks due to variation in numbers of rings along the vertebral column and apparent lack of correlation of vertebral ring numbers to yearly cycles. Pauly (in press) used size frequency data to develop a von Bertalanffy growth curve for the basking shark, assuming a size at birth of 1.5 m (see below), a gestation period of about 2.6 years, and an age at greatest length (10 m) of about 50 years. There may be a possible cycle of two to three years between litters, and a possible age at maturity for males at 12 to 16 or more years and up to 20 years for females (UK CITES Authority, 1999).

The basking shark is one of the four types of large, filter-feeding elasmobranchs, the others being the megamouth and whale sharks, and the manta rays (Mobulidae). The basking shark may be unique in relying entirely on the passive flow of water through its pharynx generated by swimming for filtration; the other filter-feeders may assist the process of food ingestion by actively pumping or gulping water and food organisms into their pharynxes. The basking shark feeds on small planktonic organisms trapped on its unique gill rakers, apparently with the help of mucus secreted in its pharynx. Food items include small copepods (including calanids), barnacle, decapod, stomatopod larvae and fish eggs. On the average a half tonne of material may be present in the stomach of these sharks. While feeding the basking shark usually cruises with mouth widely open and gills distended, occasionally closing its mouth to ingest its prey. An average adult has been estimated to be capable of filtering over 2 000 t of water per hour assuming a constant cruising speed of about 2 knots. They seem to feed almost at random in low plankton densities, but are highly selective and actively search in restricted areas for high densities of zooplankton above a minimum concentration before feeding. Off southwestern England they actively seek plankton concentrations at the surface along boundaries of tidally influenced water masses or tidal fronts over bottom about 20 to 50 m deep.

The facts that the basking shark periodically sheds its gill rakers and that plankton densities seasonally fall below levels thought essential to maintain ordinary swimming and metabolic activity in this shark have spawned a controversy over whether or not the species remains active when deprived of gill rakers and high plankton densities. It has been suggested that the basking shark may hibernate on the bottom, perhaps at the edges of continental shelves or on the slopes, until its rakers are replaced and plankton blooms reoccur. Proof of hibernation has never been forthcoming, and an alternate hypothesis has been suggested that the basking shark may turn to benthic feeding when it loses its gill rakers. A possible additional factor is that the massive, oil-filled liver of this species may serve as a metabolic store to supply energy to support a reduced rate of activity (slower swimming in colder, deep water) while gill rakers regenerate and plankton supplies eventually recuperate. Estimates have been proposed that, in north European waters, the basking shark drops its gill rakers in early winter and takes about 4 or 5 months to fully replace them. An anecdotal report suggests that basking sharks may feed on small schooling fishes such as herring as a possible alternative to plankton-sieving, but this remains to be confirmed.

By far the most important enemy of this shark is humanity, primarily from fisheries but also from collisions with boats. A dead basking shark with wounds was once seen near a pod of killer whales (***Orcinus orca***), with the implication that the whales killed the shark. White sharks (***Carcharodon carcharias***) will readily consume meat from dead basking sharks, but have not been recorded as attacking living ones. A large white shark or a group of white sharks are sufficiently formidable to kill a basking shark. Lampreys, copepods and cookiecutter sharks (***Isistius***) may produce external wounds, but it is not known if they contribute to mortality.

Size: Basking sharks have been credited as reaching a maximum total length of 12.2 to 15.2 m, but even if this is correct most specimens do not exceed approximately 9.8 m. Pauly (in press), analyzing the largest North Atlantic records of basking sharks in an 'extreme value theory plot', suggested that individuals over 10 m long were unlikely to exist. This is supported by observational data off the UK (Pollard, 1996), in which few basking sharks (8% of over 3 300) over 8 m long were seen. Size at birth is uncertain with few pregnant females examined. An unconfirmed record of a foetus about 1.7 m long, another foetus 1.5 m long, and a 165 cm freeliving individual suggests that size at birth may be about 1.5 to 1.7 m, and hence is slightly greater than any other known ovoviviparous or viviparous shark except perhaps the common thresher and white shark. Males mature between 4 and 7 m and reach about 9 m; a late adolescent male 6.85 m long from Cape Town, South Africa (dissected by the writer) had almost fully calcified claspers; six adult males examined by Matthews and Parker (1950), Springer and Gilbert (1976), and the writer were 7.01 to 8.46 m long (average 7.83 m). Females are immature at 3.19 and 3.59 m (Springer and Gilbert, 1976, L.J.V. Compagno, unpub. data), females are mature at 8.0 to 9.8 m; six adult females examined by Matthews and Parker (1950) and Springer and Gilbert (1976) were 8.03 to 8.48 m long (average 8.27 m), suggesting that females slightly exceed males in size as with many other sharks. Pauly (in press) suggested a maximum weight of 7.5 t at 10 m using an isometric weight curve, $W(t) = 0.0075 * TL(m)^3$. The basking shark is apparently the second largest shark, neoselachian elasmobranch, and living fish-like vertebrate after the whale shark (***Rhincodon typus***), although it may be rivalled in size by the manta (***Manta birostris***).

Interest to Fisheries and Human Impact: The basking shark has been the object of small-scale targeted harpoon fisheries from small boats and small ships (some built and equipped like whale-catchers) during the eighteenth, nineteenth and twentieth centuries. In the twentieth century such fisheries operated primarily off the Norwegian coast, Ireland, Scotland, Iceland, Spain, United States (California), Peru, Ecuador, China and Japan. It has been sporadically if heavily fished due to periodic depletion of basking shark stocks or intrinsic factors of the fisheries such as falling demand for this shark. During the eighteenth and nineteenth centuries basking sharks were also harpooned from large whaling vessels in the Gulf of Maine (United States and Canada) and probably elsewhere; basking sharks in the western North Atlantic were apparently decimated by such activities. The basking shark has also been taken as discarded and utilized bycatch in net gear, including bottom anchored gill nets, floating gill nets, pelagic gill nets, bottom trawls, pelagic trawls, and even anchored fish weirs. It is caught as a rare bycatch of gill netters targeting thresher sharks and swordfish off California and was taken by squid gill netters as an uncommon bycatch in the epipelagic zone of the temperate North Pacific. It was formerly perceived as a problem to salmon gill netters off British Columbia and elsewhere in the Pacific Northwest by fouling and damaging gill nets, and was formerly subjected to a localized eradication programme in British Columbia using a modified fisheries vessel with a knife-like ram on its bow to impale and kill sharks at the surface. The activities of this vessel in the 1950s apparently decimated the basking shark locally, which has not shown signs of recovery almost fifty years later.

Meat from the basking shark is used fresh or dried-salted for human consumption. The fins of the basking shark are used for shark-fin soup and currently are extremely valuable, with the huge pectoral and dorsal fins recently (1999) sold for US$10 000 to 20 000 each. The basking shark was traditionally targeted for its liver, which is rich in oil and very large. The liver oil of the basking shark was formerly used for tanning leather and for lamp oil; it also yields vitamin A, and in modern times has been extracted for its high level of squalene which is used for medicinals and cosmetics. The hide of the basking shark is processed for leather, the cartilage for medicinals, and the carcass is sometimes rendered into fishmeal. Basking shark fisheries have not been monitored in detail except in the eastern North Atlantic and New Zealand, and catch statistics for basking sharks have been reported to FAO from New Zealand, Portugal, France and Norway. Norwegian catches were the highest reported for any nation, with catches of 2 200 to 18 700 t reported to FAO in the 1960s and 1970s, but have declined to less than 500 t in 1997 and have been caught under a quota from 1978 onward. Slightly more than 12 000 sharks were caught off the west coast of Ireland over a 29 year period, with peak catches in the 1950s and apparently no recovery in recent years. New Zealand, Portugal and France report tiny catches of 1 to 14 t at present, with the New Zealand catch strictly regulated as utilized bycatch only and with targeted fisheries not allowed.

The basking shark is usually quite tolerant of boats approaching it, which makes it easy to hunt with harpoons from small boats. Divers have been able to swim up to individuals and photograph them without invoking flight reaction. Basking sharks may approach divers quite closely, possibly out of curiosity, and swim around them. This species is regarded as ordinarily harmless and inoffensive when not provoked or molested. The immense size and power of the basking shark should invite respect by ecotouristic divers who swim with these sharks. Divers should take care in contacting the skin of basking sharks, which has large dermal denticles with sharp, hooked crowns that point forward and sideways as well as backward. As the writer can attest from dissecting large basking sharks, these denticles can inflict irritating lacerations on unprotected skin.

There is considerable and growing concern over the conservation status of the basking shark because of declining numbers caught over the last five decades, with total catches dropping from 0.5 to 0.2 of their peaks during the 1970s and with some localized fisheries depressed to less than 0.1 of their peaks in 10 to 25 years (UK CITES , 1999). Localized basking shark fisheries have a short-term boom and bust nature, and apparently are not sustainable at even moderate levels for very long due to the biological limitations of the basking shark as a fisheries species. The basking shark has proved to be extremely vulnerable to overfishing, perhaps more so than most sharks, and this can be ascribed to its slow growth rate, late maturity, long gestation period, probably low fecundity, long life, few predators when adult, probable small size of existing populations (belied by the immense size of individuals in their small schools), ready access to small fishing vessels inshore and off built-up areas, and possibly little interchange between populations or stocks. A recent and major problem is the extraordinarily high value of basking shark fins, which promotes finning of sharks caught as bycatch of other fisheries rather than the release of captured individuals alive. The fin trade also supports small-scale targeted fisheries beyond the commercial limits imposed by the lesser value of other basking shark products such as liver oil, and by the depleted stocks of basking sharks in most parts of the world. High fin prices can also promote illicit poaching and illegal trade despite local, national and international protective measures.

The basking shark has been placed on the IUCN Red List as a vulnerable species, and has received protection from exploitation in the territorial waters of the United Kingdom, Malta, New Zealand and the United States (East Coast, including separate protection by the State of Florida in its territorial waters). It was sponsored for CITES listing on Appendix II by the United Kingdom (for the 2000 CITES meeting), to promote regulation of basking shark catches and limits to international trade in fins and other products. However the CITES proposal was very narrowly defeated and the UK is going on to propose the basking shark for CITES Appendix III listing, effective from 2000 onward. The basking shark will be fully protected in the entire Mediterranean Sea once the Barcelona Convention for the Protection of the Mediterranean Sea is ratified by its Member Nations. It is listed as a strictly protected species of the Bern Convention on Conservation of European Wildlife. It is under consideration for total protection off South Africa (2000).

The basking shark has become a 'supershark', with a high-profile and fortunately positive public image, and has a strong and highly motivated conservationist following in the United Kingdom. This is somewhat similar to, albeit better organized than conservationists promoting the whale shark in the western Atlantic and the Indo-Pacific, which ensures public awareness of the conservation problems and interest in protecting both 'gentle giants'. The basking shark is being monitored by three different conservation groups in the United Kingdom, with sightings by volunteers reported on standard data-cards.

Local Names: Basking shark, Giant basking shark, Elephant shark, Capidolo, Oilfish, Pelerin, Sun fish or Sunfish, Sail fish or Sailfish, Hoe mother or Homer, Bone shark, Gurry shark (English); Hoe mother, Homer (Orkneys); Heulgi (Wales); Cearban (Scotland); Sun fish, Liabhán mór, Liabhán chor gréine (Ireland); Haar moer (Scandinavia); Brugde, Brygde, Ry brigde (Norway); Brugden (Sweden); Rymer, Beinhaakal (Iceland); Brugde (Denmark); Mandelhai, Riesenhai (Germany); Reusenhaai (Belgium); Reuzenhaai (Holland); Le pélerin, Le très grand, Le squale a fanons, Poisson à volies, Elephant de mer (France); Squalo massimo, Cagnea, Selachio gigante, Cagnia, Imbestinu, Caniscu, Squalo elefante (Italy); Pixi tunnu (Malta); Carago, Peixe carago, Peixe frade (Portugal); Peregrino (Spain); Peixe frade, Tubarâo frade, Basking shark (Azores); Psina golema (Adriatic); Ubazame or Old woman shark, Teguzame [Tenguzame?] or Long-nosed shark, Bakazame or Foolish shark, Zozame or Elephant shark (Japan); Elefante (Cuba); Peje-vaca or Cow-fish (Chile); Akula gigantakaia, Akuloobraznye, Bol'shezhabernye akuly, Gigantskie akuly, Akuly nastoiaschie, Lao sha k'o (Russia); Southern basking shark (Australia); Cape basking shark, Koesterhaai (South Africa).

Literature: Garman (1913); Barnard (1925, 1937, 1947); Lahille (1928); Fang and Wang (1932); Whitley (1934, 1939, 1940, 1967); Norman (1937); Fowler (1941, 1967a); Hildebrand (1946); Bigelow and Schroeder (1948); Matthews (1950, 1956); Matthews and Parker (1950a, b); Van Deinse and Adriani (1953); Parker and Boeseman (1954); Lindberg and Legeza (1959); Siccardi (1960, 1961); Baldwin (1961); Larkins (1964); Parker and Stott (1965); Kato, Springer and Wagner (1967); Squire (1967, 1990); Lindberg (1971); Shiino (1972, 1976); Miller and Lea (1972); Hart (1973); Sadowsky (1973); Antezana (1977); Bass, D'Aubrey and Kistnasamy (1975a); Springer and Gilbert (1976); Pauly (1978, in press); Applegate et al. (1979); Konstantinov and Nizovtsev (1979); Davis (1983); Silva-Santos, Gomes and Ferreira (1983); Compagno (1984, 1990a, b); Nakaya (1984); Quero (1984); Kenney, Owen and Winn (1985); Horsman (1987); Paulin et al. (1989); Tomas and Gomes (1989); Herman, McGowan and Swinney (1990); Springer (1990); Earll et al. (1992); Hanan, Holts and Coan (1993); Izawa and Shibata (1993); Michael (1993); Bonfil (1994); Darling and Keogh (1994); Last and Stevens (1994); Dunbar, Fowler and Denham (1995); Taylor (1995); Uchida (1995); Pollard (1996); Fowler (1996); Santos, Porteiro and Barreiros (1997); Fairfax (1998); McEachran and Fechhelm (1998); Sims and Quayle (1998); Castro, Woodley and Brudek (1999); UK CITES Authority (1999); D. Ebert (pers. comm., on Namibian records); S. Fowler (pers. comm.); J. Naughton (pers. comm., on Hawaiian record); L.J.V. Compagno (unpub. data from South Africa).

2.2.7 Family LAMNIDAE

Family: Lamnoidea Müller and Henle, 1838a, *Mag. Nat. Hist., new ser.*, 2: 36. Also Subfamily Lamnini Bonaparte, 1838, *Nuov. Ann. Sci. Nat., Bologna*, ser., 1, 2: 209 (Family Squalidae); Family Lamna Hasse, 1879, *Nat. Syst. Elasmobr.*, (1): 52. Emended to Family Lamnidae Müller and Henle, 1838 by Richardson, 1846, *Ichthyol. China Japan*: 195.

Type Genus: ***Lamna*** Cuvier, 1816.

Number of Recognized Genera: 3.

Synonyms: Tribe Isurina Gray, 1851 (Family Squalidae): 58. Emended and raised in rank to Family Isuridae Gray, 1851 by Gill, 1893: 130. Type genus: ***Isurus*** Rafinesque, 1810. Subfamily Carcharodontinae Gill, 1893 (Family Isuridae): 130. Type genus: ***Carcharodon*** Smith, 1838. Family Carcharodontidae Whitley, 1940: 68. Independently proposed from Gill, 1893. Type genus ***Carcharodon*** Smith, 1838. Family Lamiostomatidae Glikman, 1964: 11, 105. Type genus ***Lamiostoma*** Glikman, 1964: 105.

FAO Names: En - Mackerel sharks, Porbeagles, White sharks; **Fr** - Requins taupe; **Sp** - Jaquetones, Marrajos.

Field Marks: Large sharks with pointed snouts and spindle-shaped bodies, long mouths with large blade-like teeth, long gill slits, long pectoral fins and high first dorsal fins, small pivoting second dorsal and anal fins, large lateral keels and prominent precaudal pits on the caudal peduncle, and lunate caudal fins.

Diagnostic Features: Head moderately long but shorter than trunk. Snout moderately long pointed and conical not greatly elongated flattened or blade-like. Eyes small to moderately large, length 0.9 to 3.4% of precaudal length. Gill openings large, width of first 7.6 to 10.8% of precaudal length, extending onto dorsal surface of head; all gill openings anterior to pectoral fin bases; no gill rakers on internal gill slits. Mouth large and parabolic, ventral on head; jaws moderately protrusable but not greatly distensible laterally. Teeth large, anteriors and laterals narrow and awl-shaped or blade-like to broad, compressed and triangular, in 22 to 31/20 to 29 (43 to 60 total) rows; two rows of large anterior teeth on each side in upper jaw, separated from the smaller upper lateral teeth by one row of small intermediate teeth on each side; three rows of lower anterior teeth on each side, the first two variably enlarged but the third about as large as laterals; no symphysial teeth. Trunk fusiform and moderately slender to very stout, firm and not flabby. Caudal peduncle strongly depressed and with strong, high keels and both upper and lower crescentic precaudal pits. Dermal denticles very small and smooth, with flat crowns, small ridges and cusps and with cusps directed posteriorly on lateral denticles. Pectoral fins very long and narrow, shorter to somewhat longer than head in adults; pectoral-fin skeletons plesodic with radials extending far into fin webs. Pelvic fins small, much smaller than first dorsal fin but larger than second dorsal and anal fins; pelvic-fin skeleton aplesodic, not extending into fin web. First dorsal fin large, high, erect and angular or somewhat rounded; fin skeleton semiplesodic, extending partway into fin web. Second dorsal and anal fins minute, much smaller than first dorsal fin, with narrow pivoting bases. Caudal fin lunate, dorsal lobe moderately long, less than one third as long as rest of shark, ventral lobe long and strong, nearly as long as upper lobe. Neurocranium moderately high, not compressed, with moderately long rostrum, depressed internasal septum and widespread nasal capsules, large orbits with strong supraorbital crests, greatly enlarged stapedial fenestrae, and posteriorly expanded hyomandibular facets. Vertebral centra strongly calcified, with well-developed double cones and radii but without prominent annuli. Total vertebral count 153 to 197, precaudal count 85 to 114, diplospondylous caudal count 66 to 86. Intestinal valve of ring type with 38 to 55 turns. Size moderately large to very large with adults 1.8 to about 6 m long.

Distribution: Lamnids have a broad geographic distribution in virtually all seas except where the ice pack covers the Arctic and Antarctic Oceans. One of them, the white shark (***Carcharodon carcharias***) has one of the widest ranges of any cartilaginous fish. The salmon shark (***Lamna ditropis***) has the most limited distribution in the family, the temperate and boreal North Pacific and Arctic fringe, but lives in an enormous area.

Habitat: Lamnids are tropical to boreal or notal, littoral to epipelagic sharks in continental and insular waters from the surf line and intertidal of shallow bays to the outer shelves and open ocean and rarely down the slopes to at least 1 280 m. Lamnids are apparently intolerant of fresh water and do not ascend rivers. Salmon sharks and porbeagles (***Lamna***) are tolerant of cold and moderate water temperatures but avoid the tropics, while makos (***Isurus***) are restricted to tropical and temperate seas. ***Carcharodon*** broadly overlaps the habitats of ***Lamna*** and ***Isurus.***

Biology: The mackerel sharks are fast-swimming, active pelagic and epibenthic swimmers, some of which are capable of swift dashes and spectacular jumps when chasing their prey. Mackerel sharks are partially warm-blooded, and have a modified circulatory system that enables them to retain a body temperature warmer than the surrounding water. This permits a higher level of activity and may increase the power of their muscles as well as allow some of them to be active in cold temperatures. They feed on a wide variety of bony fishes, other sharks, rays, chimaeras, marine birds and reptiles, seals and sea lions, whales and dolphins, squid, bottom crustaceans and molluscs, carrion, and occasionally terrestrial vertebrates (rarely including humans). Development is ovoviviparous, without a yolk-sac placenta. Like other lamnoids these sharks have uterine cannibalism, in which developing foetuses feed on fertilized eggs (oophagy) for most of their gestation period. More than one foetus survives in each uterus in most species, and it is not known if intrauterine siblings will attack and devour one another as in ***Carcharias taurus***. All the living species of lamnids are of large size, with a maximum length of 3.0 to perhaps 6 m or more. A giant, rather recently extinct (late Pliocene) member of the white shark genus (the megatooth shark, ***Carcharodon megalodon***, often placed in other genera or even families by some modern palaeontologists) attained an estimated length when adult of about 11 to 20 m (Gottfried, Compagno and Bowman, 1996). It was one of the largest and most powerful predatory vertebrates ever to live, rivalled only by certain cetaceans (sperm whales, orcas and giant archaeocetes), the largest pliosaurs and mosasaurs, giant Mesozoic and Cenozoic crocodiles, and the largest terrestrial theropod dinosaurs.

Interest to Fisheries and Human Impact: These sharks are important objects of oceanic and offshore continental fisheries because of their fine meat, but are also utilized for their oil, fins, hides, fishmeal, jaws and teeth. Some species are oceanic in whole or part, and are mainly taken with pelagic longlines and gill nets. Anchored gill nets and trammel nets, fish traps, hook-and-line, harpoons, and pelagic and bottom trawls can capture these sharks.

Porbeagles and salmon sharks (***Lamna***) are apparently inoffensive and have not bitten people in the water. The shortfin mako (***Isurus oxyrinchus***) has bitten swimmers and divers on a few occasions but may often display and stage mock-charges while confronted by divers. More often shortfin makos have bitten boats, especially after being provoked by hooking. The longfin mako has never been known to bite people or boats. However, this family contains what is generally considered the most 'dangerous' shark, the white shark (***Carcharodon carcharias***), because of its regular if infrequent habit of biting swimmers, divers, surfers and boats.

Local Names: Mackerel sharks, Man-eater sharks, Man-eating sharks, Man-eaters, Great white sharks, Mako-sharks, Porbeagles (English); Lamie, Requin-bleu, Taupe, (France); Heringshai, T'u sha k'o; Akuly sel devye or Sel devye akuly (Russia); Nezumizame-ka (Japan); Anequins (Mozambique).

Remarks: This account follows Compagno (1984, 1990b, 1999) in recognizing a single family for the genera ***Carcharodon***, ***Isurus*** and ***Lamna***, which is termed Lamnidae or Isuridae by most authors. Lamnidae has priority, stemming from Müller and Henle's (1838a, 1839) family Lamnoidea or Lamnae, and being recognized by numerous authors including Bonaparte (1838, 1839, subfamily Lamnini), Müller (1845), Bleeker (1859), Gill (1862b, 1872), Owen (1866), Günther (1870), Hasse (1879), Jordan and Gilbert (1883), Woodward (1889), Jordan and Evermann (1896), Regan (1906a), Goodrich (1909), Bridge (1910), Engelhardt (1913), Jordan (1923), Bertin (1939a), Berg (1940), Fowler (1947, 1967a), Berg and Svetovidov (1955), Matsubara (1955), Patterson (1967), Blot (1969), Bailey et al. (1970), Lindberg (1971), Pinchuk (1972), Compagno (1973, 1981b, 1982, 1984, 1999), Nelson (1976, 1984, 1994), Applegate et al. (1979), Gubanov, Kondyurin and Myagkov (1986), Cappetta (1987), Carroll (1988), Eschmeyer (1990, 1998), Robins et al. (1991a), and Helfman, Collette and Facey (1997). Isuridae was apparently not used until Gill (1893) essentially revived Gray's (1851) Isurini as a family. Although an unjustified replacement of Lamnidae the family Isuridae was used by a number of influential authors, including Garman (1913), Lozano y Rey (1928), White (1936, 1937), Whitley (1940), Fowler (1941), Romer (1945, 1963), Bigelow and Schroeder (1948), Schultz and Stern (1948), Smith (1949), Arambourg and Bertin (1958), Garrick and Schultz (1963), Budker and Whitehead (1971), Bass, D'Aubrey and Kistnasamy (1975a), and Chu and Meng (1979).

Whitley (1940) separated the white shark (***Carcharodon***) in its own family Carcharodontidae as distinct from Isuridae (***Isurus*** and ***Lamna***). This was independently proposed by the innovative Soviet palaeontologist L.S. Glikman (1964, 1967), who also placed ***Lamna*** in a subfamily Lamninae of the family Odontaspididae. In addition, Glikman separated living fossil species of ***Isurus*** into two genera, ***Isurus*** and ***Lamiostoma***, and placed these respectively in the families Isuridae and Lamiostomatidae. Glikman's arrangement was followed by Rass and Lindberg (1971), while Lindberg (1971) recognized Lamiostomatidae as distinct from Lamnidae. Glikman (1964) suggested that the living lamnid genera were independently derived from the basal family Odontaspididae, and so required separate families. However, phyletic studies utilizing morphology (Maisey, 1985; Compagno, 1990b; Long and Waggoner, 1996) and DNA sequencing (Martin and Naylor, 1997; Naylor et al., 1997) suggest that the Lamnidae is a monophyletic group for the living ***Carcharodon***, ***Isurus*** and ***Lamna***, which is followed here.

Günther (1870), Regan (1906a) and Engelhardt (1913) included ***Isurus*** or its synonym ***Oxyrhina*** as a synonym of ***Lamna*** while Garman (1913), White (1936, 1937), and Fowler (1941) synonymized ***Lamna*** with ***Isurus***. Most modern authors follow Müller and Henle (1839) and more recently Bigelow and Schroeder (1948) in considering ***Isurus*** and ***Lamna*** as separate genera, which is supported by external morphology, dentition and anatomical studies (Compagno, 1990b; Long and Waggoner, 1996). Gray (1851) recognized both genera but used ***Isurus*** as a synonym of ***Lamna*** and ***Oxyrhina*** in place of ***Isurus***.

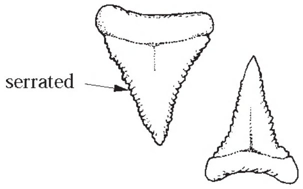
Many earlier authors included the basking shark (***Cetorhinus***) and the threshers (***Alopias***) in the family Lamnidae. Modern authors generally recognize Lamnidae (or Isuridae), Cetorhinidae and Alopiidae as distinct families, although Shirai (1996) recently demoted the Lamnidae as a subfamily Lamninae of the Alopiidae along with the subfamilies Cetorhininae and Alopiinae.

Literature: Garman (1913); Fowler (1941, 1967a); Bigelow and Schroeder (1948); Garrick and Schultz (1963); Farquhar (1963); Shiino (1972, 1976); Bass, D'Aubrey and Kistnasamy (1975a); Compagno (1984, 1990b); Alexander (1998).

Key to Genera:

1a. Teeth serrated, uppers flat and with broadly triangular cusps (Fig. 68) . . . . ***Carcharodon***

1b. Teeth smooth-edged, uppers not greatly flattened and with narrowly triangular cusps (Fig. 69a) . . . . → **2**

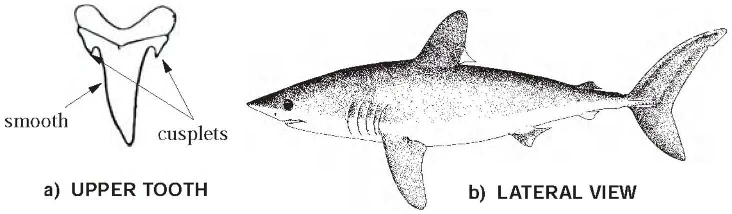


UPPER AND LOWER TOOTH

Fig. 68 ***Carcharodon***

2a. Lateral cusplets present on most teeth (sometimes absent in young) (Fig. 69a); origin of first dorsal fin over or anterior to inner margins of pectoral fins; origin of second dorsal fin over origin of anal fin; a secondary keel present below main keel on caudal fin (Fig. 69b) . . . . ***Lamna***

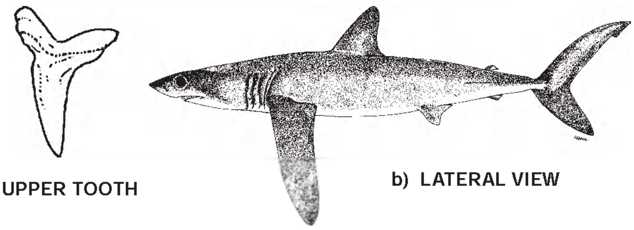
2b. No cusplets on teeth (Fig. 70a); origin of first dorsal fin over or behind rear tips of pectoral fins; origin of second dorsal fin well in front of anal-fin origin; no secondary keel on caudal fin (Fig. 70b) . . . . ***Isurus***



a) UPPER TOOTH

b) LATERAL VIEW

Fig. 69 ***Lamna***



a) UPPER TOOTH

b) LATERAL VIEW

Fig. 70 ***Isurus***

Carcharodon Smith, 1838

Genus: ***Carcharodon*** Smith, *in* Müller and Henle, 1838a, *Mag. Nat. Hist., new ser.*, 2: 37. Placed on the Official List of Generic Names in Zoology (Name no. 1658) by the International Commission on Zoological Nomenclature (1965, Opinion 723.3b, *Bull. Zool. Nomencl.*, 22(1): 32).

Type Species: ***Squalus carcharias*** Linnaeus, 1758, by subsequent monotypy through ***Carcharias lamia*** Rafinesque, 1810 (*International Commission on Zoological Nomenclature*, 1965, *loc. cit.*).

Number of Recognized Species: 1.

Synonyms: Subgenus ***Carcharias*** Cuvier, 1816 (Genus ***Squalus*** Linnaeus, 1758): 125, in part. Placed on the List of Rejected and Invalid Generic Names in Zoology (Name no. 811) by the International Commission on Zoological Nomenclature (1965, Opinion 723.5c: 33). Cuvier's ***Carcharias*** had only three species, ***Squalus carcharias***, ***S. vulpes*** (= ***Alopias vulpinus***), and ***S. glaucus*** (= ***Prionace glauca***). ***S. carcharias*** is the type of ***Carcharias*** Cuvier by absolute tautonymy, but is a junior homonym of ***Carcharias*** Rafinesque, 1810 (***Carcharias taurus***, type species by monotypy). ***Carcharias*** Cuvier was used extensively for carcharhinids following Müller and Henle (1839: 27). Genus ***Carcharoden*** Bleeker, 1860: 58, in combination ***Carcharoden rondeletii***. Apparent misspelling for ***Carcharodon***, as it is spelled correctly in that paper on p. 57 (***Carcharodon capensis***).

Diagnostic Features: Snout bluntly conical. Eyes small, 0.7 to 1.8% of total length. Nostrils situated adjacent to head rim in ventral view. Mouth width 1.1 to 2.3 times its length. Anterior teeth enlarged; anterior, intermediate and lateral teeth compressed and forming a continuous cutting edge; intermediate teeth enlarged and over two-thirds height of adjacent anteriors, with reversed cusps that are directed anteromesially; second lower anterior teeth moderately enlarged and about as high or usually lower than second upper anterior tooth; total tooth count 44 to 52; roots of anterior teeth broadly arched, with root lobes broad and not elongated; lateral cusplets present only on teeth of smaller sharks below about 3 m long but lost in adults; teeth with serrated edges; cusps of anterior teeth not strongly flexed. Body usually stout. First dorsal-fin origin usually over the pectoral inner margins. Anal-fin origin under or slightly posterior to second dorsal-fin insertion. Secondary caudal keels absent. Total vertebral count 170 to 187. Cranium with rostral cartilages not swollen and hypercalcified. Intestinal valve count 47 to 55. Length of adults 3.8 to almost 6 m and possibly longer. Usually a black axillary spot at pectoral fin insertions; pectoral fin tips usually abruptly black on their ventral surfaces.

Remarks: The white shark (***Carcharodon carcharias***) is apparently the sole living species of this genus although many fossil species are also recognized. The white shark was often confused with requiem sharks (Carcharhinidae) and other sharks by eighteenth and early nineteenth century writers, and was often placed in the genus ***Carcharias*** along with other large lamnoid and carcharhinoid sharks. Smith (1838a) proposed ***Carcharodon*** as a unique genus for the white shark, but without allocating any species. Müller and Henle (1839) recognized a single species, ***Carcharodon rondeletii*** Müller and Henle, 1839. The genus was accorded essentially universal recognition by subsequent authors, but the type species was questionable and was eventually stabilized by a ruling of the International Commission on Zoological Nomenclature (1965). Bigelow and Schroeder (1948), White, Tucker and Marshall (1961), and the International Commission on Zoological Nomenclature (1965) give further details of the complex nomenclatural history requiring this ruling.

There have been a few attempts to name regional species of white sharks and distinguish separate regional populations. Smith (1849) proposed a new species, ***C. capensis***, from South Africa, while Whitley (1939) separated Australian white sharks as ***C. albimors***. Neither of these were especially characterized, and are generally synonymized with ***C. carcharias***. More recently Bass, D'Aubrey and Kistnasamy (1975a) distinguished South African white sharks from those from the Northern Hemisphere by coloration and vertebral count. These authors noted that the axillary spots reported on western Atlantic white sharks (Garman, 1913; Bigelow and Schroeder, 1948) were absent in specimens they examined. At least one of the specimens examined by Bass, D'Aubrey, and Kistnasamy (1975a, fig. 10) lacked axillary spots, but Smith (1849), Smith (1951), and D'Aubrey (1964) illustrated South African white sharks with axillary spots. The writer has examined many white sharks specimens with axillary spots from South Africa and California, United States, while axillary spots were present on several live white sharks filmed at Dyer Island and Struis Bay, South Africa. Axillary spots may be absent in white sharks from Argentina (Siccardi, Gosztonyi and Menni, 1981) and were poorly defined on one examined by the writer from California. Apparently the absence of axillary spots cannot be used to distinguish South African white sharks.

Bass, D'Aubrey and Kistnasamy (1975a) suggested that lower counts of precaudal vertebral centra (100 to 108, mean = 103.2, n = 24) might distinguish white sharks from Natal as a separate population from California white sharks (103 to 108, mean = 105.2, n = 14; California data from Springer and Garrick, 1964). Further comparison of precaudal vertebrae counts for Californian and South African specimens by the author (Compagno unpub. data; n = 56) verified a small but statistically significant difference in means between the samples, but the small sample sizes, broad overlap in ranges and standard deviations in the vertebral count samples, do not rule out the differences as being a result of sampling error. Siccardi, Gosztonyi and Menni (1981) presented precaudal counts for two Argentinean white sharks (a female with 104 centra and a male with 105), which fall within the range of the South African and Californian samples.

It is not obvious from available data on morphometry, meristics, coloration and skeletal anatomy that white sharks from different 'centres of abundance' are recognizably separable. The wide distribution and habitat of the white shark suggests a single species, but discrete centres of abundance and concentration of breeding areas in warm-temperate coastal seas suggest discrete populations or subpopulations with potential genetic interchange via wide-ranging adults. There are several projects underway to compare DNA of white sharks from various areas to determine possible populational differences.

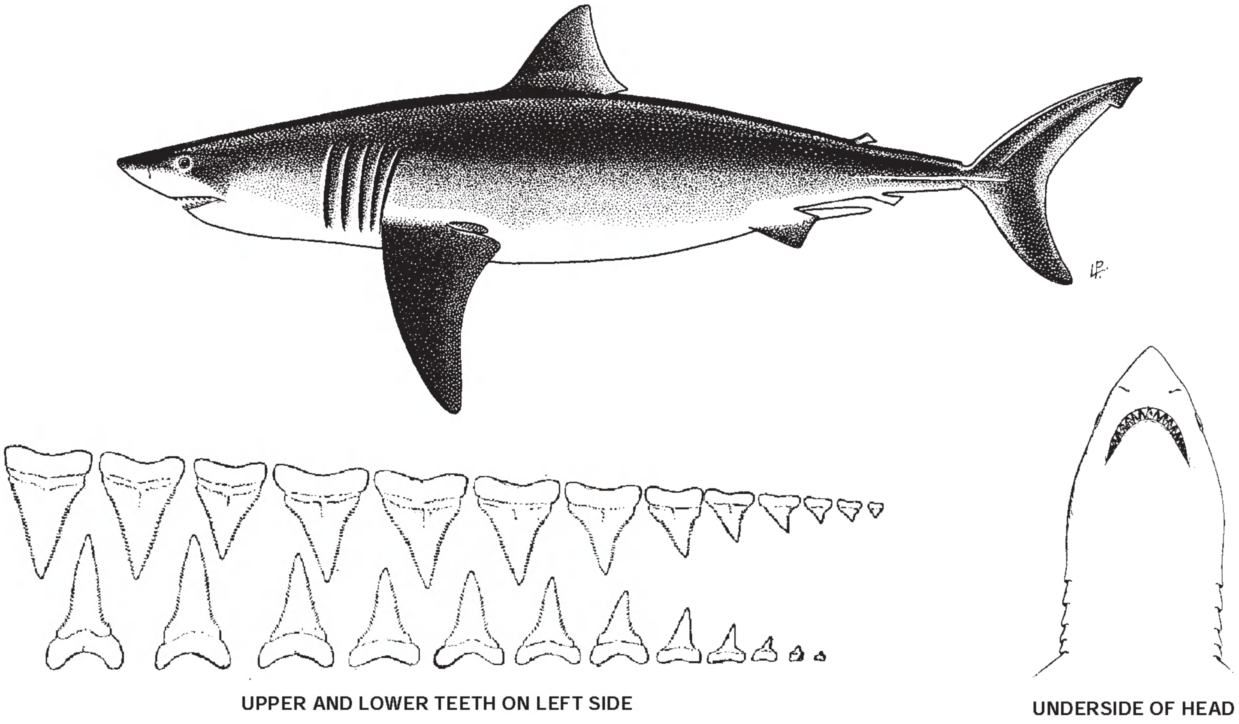
Carcharodon carcharias (Linnaeus, 1758) Fig. 71

Squalus carcharias Linnaeus, 1758, *Syst. Nat.*, ed. 10, 1: 235. Placed on the Official List of Specific Names in Zoology (Name no. 2056) by the International Commission on Zoological Nomenclature, (1965, Opinion 723.4b, *Bull. Zool. Nomencl.*, 22(1): 32). Holotype unknown, type locality "Europa". Also no types known according to Eschmeyer (1998, *Cat. Fish.*: CD-ROM).

Synonyms: ***Carcharias lamia*** Rafinesque, 1810b: 44. Type locality: Sicily. No types? Placed on the List of Rejected and Invalid Species Names in Zoology (Name no. 811) by the International Commission on Zoological Nomenclature, (1965, Opinion 723.6: 33). ?***Squalus (Carcharhinus) lamia*** Blainville, 1816: 121 (in part?). Name only. ***Carcharias verus*** Cloquet, 1817: 69. Europe. No types? ?***Squalus (Carcharhinus) lamia*** Blainville, 1825: 88, pl. 22, fig. 2 (in part?). No types? ***Carcharias rondeletti*** Bory de Saint-Vincent, 1829: 596. Europe. Types? ***Squalus (Carcharias) vulgaris*** Richardson, 1836: 288. All seas. An unexplained new name, without types, according to Eschmeyer (1998: CD-ROM). ***Carcharodon smithii*** Müller and Henle, *in* Agassiz, 1838: 91. Name only, attributed to teeth from two jaws in pl. F, fig. 3; dentition pictured shows some overlap and no intermediate, quite possibly a ***Carcharhinus***. Type locality: Possibly South Africa, presumably named after Andrew Smith and perhaps a *nomen nudum*. ***Carcharodon smithii*** was not mentioned *in* Müller and Henle (1838a, 1839, 1841) though these authors (1839: 70) note dentitional differences between a specimen collected by A. Smith and other material and suggest that there may be two species. ***Carcharodon smithii*** Müller and Henle, 1839: 9 (in synopsis, name only). Type locality: Probably South Africa, and presumably named after Andrew Smith. Apparently a *nomen nudum*. Note difference in spelling from Agassiz, 1838: 91. ***Carcharodon rondeletii*** Müller and Henle, 1839: 70. Type locality: "Mittelmeer, atlantischer Ocean, Kap, stilles Meer.". This appears to be an original description and not merely a reallocation of ***Carcharias rondeletti*** Bory de Saint-Vincent, 1829, to ***Carcharodon***. Syntypes: A stuffed specimen (holotype of ***Carcharodon capensis***) belonging to Andrew Smith and now in the British Museum (Natural History), a specimen in the Senkenberg Museum from the Adriatic Sea, a jaw in the Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin, and two specimens in the "United Services Museum" (US National Museum of Natural History, Eschmeyer, 1998: CD-ROM), from the Pacific Ocean. ***Carcharias atwoodi*** Storer, 1848: 72. Type locality, Provincetown, Massachusetts. Holotype: Museum of Comparative Zoology, Harvard, MCZ 89505 (missing), jaws may be MCZ 775-S (Eschmeyer, 1998: CD-ROM). ***Carcharodon capensis*** Smith, 1849: pl. 4 and accompanying text, pages not numbered. Holotype and only specimen: 2.135 m (7 ft) TL stuffed female, from Cape Seas, South Africa, deposited in the Museum of the Zoological Society of London, but according to Gray (1851: 61), subsequently donated to the British Museum (Natural History). The holotype, BMNH 1850.9.5:3, is still extant and in good condition and was located and examined on 10 June 1994 in the BMNH collections; current TOT (extended TL) is about 2 035 mm. ***Carcharias vorax*** Owen, 1853: 94. Holotype? No locality, identity uncertain, based on vertebrae and teeth of a 7.65 m (23 ft) specimen. ***Carcharias maso*** Morris, 1898: 412. Australia. Possible *nomen nudum* according to Eschmeyer (1998: CD-ROM). Not ***Squalus (Carcharias) maou*** Lesson, 1830 = ***Carcharhinus longimanus*** (Poey, 1861). ***Carcharodon albimors*** Whitley, 1939: 240. Holotype: Australian Museum, Sydney, AMS I.1723 (Paxton et al., 1989: 67; Eschmeyer, 1998: CD-ROM), New South Wales, Australia.

Other Combinations: None.

FAO Names: En - Great white shark; **Fr** - Grand requin blanc; **Sp** - Jaquetón blanco.



UPPER AND LOWER TEETH ON LEFT SIDE

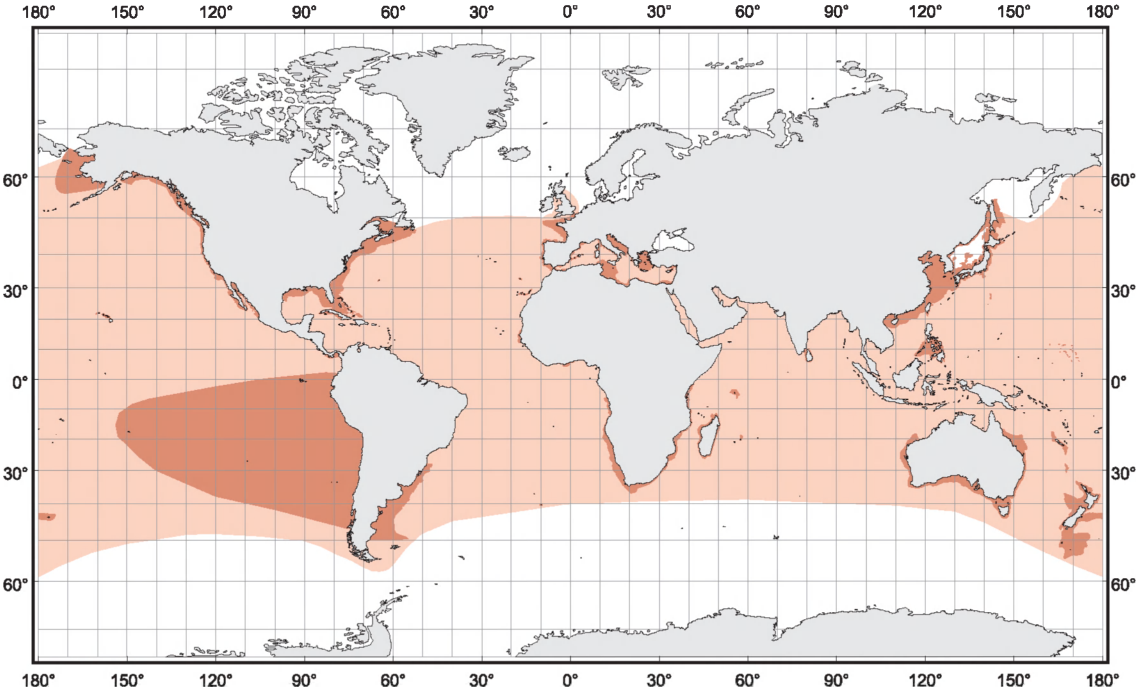
UNDERSIDE OF HEAD

Fig. 71 ***Carcharodon carcharias***

Field Marks: Heavy spindle-shaped body, moderately long conical snout, huge, flat, triangular, serrated blade-like teeth, long gill slits, large first dorsal fin with dark free rear tip, minute, pivoting second dorsal and anal fins, strong keels on caudal peduncle, no secondary keels on caudal base, crescentic caudal fin. **Colour:** dorsal surface lead grey or brownish grey to blackish above, ventral surface of body white, iris of eye conspicuously black, margin between dorsal dark and ventral white surfaces sharply delimited.

Diagnostic Features: See genus ***Carcharodon*** above.

Distribution: Wide-ranging in most seas. Western Atlantic: Newfoundland to Florida, Bahamas, Bermuda, Cuba, northern Gulf of Mexico; also Brazil and Argentina. Eastern Atlantic: Possibly England, also France and Bay of Biscay, to Gibraltar, the entire Mediterranean Sea (absent from Black Sea), Madeira, Canary Islands, Senegal, Gambia, Ghana, possibly Zaire, Angola, Namibia, South Africa (Northern and Western Cape Provinces); also Gough Island. Indo-West Pacific: South Africa (Eastern Cape and KwaZulu-Natal Provinces), Mozambique, Tanzania (Zanzibar), Kenya, Seychelles, Madagascar, Mauritius, possibly Red Sea and Persian Gulf (Kuwait?), Sri Lanka, possibly Indonesia, Australia (Queensland, New South Wales, Victoria, Tasmania, South and Western Australia), New Zealand (including Norfolk, Stewart, and Chatham Islands), New Caledonia, Philippines (Mindanao, Palawan), China, Taiwan (Province of China), Japan, North Korea, South Korea, Russia (Siberia, possibly Sea of Okhotsk and Bering Sea), Bonin Islands (Tanna Island). Central Pacific: Marshall Islands, Hawaiian Islands, open ocean between Polynesia and South America. Eastern Pacific: Bering Sea and Gulf of Alaska to Gulf of California, including Canada (British Columbia) and the entire Pacific coast of the USA (Washington, Oregon, California, Alaska), and much of Mexico, also Panama, Ecuador, Peru, Chile, and Galapagos Islands.



Habitat: This huge and formidable shark is best known as a coastal and offshore inhabitant of the continental and insular shelves in temperate seas, but it readily penetrates the epipelagic zone and occurs in the inshore equatorial tropics and at high latitudes. The presence of large individuals off oceanic islands far from land and where breeding does not occur (e.g., Hawaiian Islands, Gough Island, Mauritius, Seychelles) as well as recent open-ocean gill net records in the North Pacific suggest that it regularly occurs in the epipelagic zone although less commonly than smaller, more abundant species of ***Isurus*** and ***Lamna***. It is seldom recorded from pelagic longline catches unlike other lamnids. This may be a function of relative rarity in the epipelagic zone and gear selectivity, with larger animals breaking off gangions and the species seldom being caught or reported in the past.

The white shark often occurs close inshore to the surfline and even penetrates shallow bays, estuaries and the intertidal zone in continental coastal waters, but also frequents offshore continental and oceanic islands (especially those with pinniped colonies) and inshore and offshore fish banks. The white shark can be found at the surface down to the bottom in epicontinental waters but rarely ranges down the continental slope, where it was once caught on a bottom longline at 1 280 m along with the large sixgill shark (***Hexanchus griseus***). More recently it has been taken in bottom trawls on the outer shelf down to 130 m off South Africa. It is often seen by divers off rocky reefs and near shipwrecks but in the tropics it is occasionally sighted on coral reefs. The white shark has one of the widest habitat and geographic ranges of any fish-like vertebrate, and readily tolerates temperature extremes from the Bering Sea and sub-Antarctic islands to the inshore tropics. It apparently does not occur in fresh water, but can be expected to occur in most marine environments if only sporadically.

Biology: This species is a very active, nomadic, social shark with a fluid, powerful, scombroid-like mode of cruising that allows it to efficiently cruise and manoeuvre for long periods at a relatively slow speed. Tracking of white sharks off the east coast of the United States and south Australia with sonic tags indicated an average cruising speed of about 3.2 kph, with one shark covering 190 km in 2.5 days. The white shark is capable of sudden high-speed dashes and drastic manoeuvres. It sometimes jumps (*breaches*) right out of the water in pursuit of prey, and jumps to attack prey at the surface, in midair, or even on rocks above the water. It can shoot straight out of the water like a dolphin for no obvious reason.

The white shark is most commonly reported from cold and warm temperate 'centres of abundance', though there are enough tropical continental and oceanic records to suggest that at least larger individuals have a wide temperature range and readily penetrate the tropics. Smaller individuals, below 3 m long, may be mostly restricted to temperate continental seas, and the distribution of presumably newborn individuals in the 100 to 160 cm size range suggest that pupping and nursery grounds for the species are also in temperate to subtropical coastal and mostly continental waters. Known centres of abundance, including nursery and probably breeding areas, include the west coast of the United States (California), Mexico (Baja California, possibly Gulf of California), the Mid-Atlantic Bight off the USA (New England and Mid-Atlantic States), the Mediterranean Sea, the east coast of South Africa (from False Bay to KwaZulu-Natal), southern Australia, New Zealand, and Japan.

White sharks are endothermic and by development of countercurrent vascular heat exchangers maintain higher temperatures in their body musculature, brains, eyes and viscera than the surrounding water (Carey and Teal, 1969; Carey et al., 1982, 1985; Carey, 1982, 1990; Tricas and McCosker, 1984; Block and Carey, 1985; McCosker, 1987; Goldman et al., 1996; Goldman, 1997). Body muscle may run 3 to 5°C higher than ambient (with few sharks measured and possible problems with measuring gear), but stomach temperatures can be 10 to 14°C above ambient and relatively constant in cold water. The heat retention system of the white shark (and possibly its large size) may be particularly advantageous in allowing it to function efficiently as a fast, agile predator in cold water, and to hunt active large prey.

Relatively little is known of the abundance of this species, except that it is uncommon to rare compared to most other sharks where it lives, even in temperate coastal waters. Catches in some areas have been as many as 50 to 100 per year (South Africa and South Australia) in the past but mostly less in others. There have been unsubstantiated claims that the species is increasing in numbers in some areas (off central California and South Africa), as a result of increasing numbers of pinnipeds. There is no hard evidence to prove this, and increasing fishing pressure and injuries from targeted and bycatch fisheries in such areas may be very well having the reverse effect. Declines in shark-meshing catches of white sharks have occurred off Queensland and New South Wales, and reductions in sightings of white sharks in Spencer Gulf, South Australia may have been related to commercial and sports fishing mortality.

Pronounced periodicity in white shark abundance may occur in some areas, apparently correlated with temperature and to some extent with life stage, or by movements of individuals or groups in response to prey concentrations or other stimuli. Also, shifts may occur in size and gender composition of white sharks off 'white shark sites' such as fish banks or seal colonies where the sharks congregate. In colder, higher latitudes at the periphery of its range in North America, the white shark moves into more northern areas when water masses warm up in the summertime. Off KwaZulu-Natal, South Africa, it was believed that individuals below 2.8 m long segregated themselves from larger individuals and moved out of the area when temperatures rose above 22°C, but this was proven wrong by more extensive data presented by Cliff, Dudley and Davis (1989). Essentially both size classes are present all year round in the area, although numbers of both fluctuated by time of year and area. In central California (Monterey Bay) white sharks are present year round but are slightly commoner when water temperatures rise to 14 to 15°C than when it is below 11°C.

Observation of white sharks at 'white shark sites' suggest that they are nomadic and may spend relatively short periods of less than a day at a given site, but at least some individuals revisit these sites periodically, from a few days to over several years. Recognizable individuals have been photographed and resighted for several years off the Farallon Islands, California. Streamer and plate tagging off Australia and South Africa, and sonic tagging off Australia also revealed short to moderately long-term site specificity of some individuals. Tagging of white sharks and photographing of dorsal fins and body patterns ('bodyprinting') have shown fairly long-range movements, including between northern and southern California (over 700 km, Anderson and Goldman, 1996) and between Dyer Island and Mossel Bay (about 300 km) or from Dyer Island to KwaZulu-Natal, South Africa (over 1 100 km, M. Marks and L.J.V. Compagno, unpub. data). So far there have been no intercontinental resightings or recaptures of tagged or photographed sharks, but given the size and strong swimming abilities of this shark and scattered records in the tropics and off oceanic islands these are to be expected and may be revealed by usage of improved tracking technologies and by development of 'bodyprint' libraries that could be made widely available via the Internet.

The white shark occurs singly or in pairs but is apparently a social animal that can be found in aggregations or congregations of 10 or more; polarized schooling possibly does not occur (apart from parallel swimming of two individuals) but sharks in a group may mill about and interact socially while showing various behaviours, often one-on-one but sometimes with more individuals involved. White sharks are 'inquisitive' animals, and often closely and repeatedly investigate human activities (including divers). Behaviour and sociobiology of this species is sketchily known at present but it is apparently at least as complex as the better-known bonnethead shark (***Sphyrna tiburo***), with most of the noncourtship, social and asocial behaviours reported by Myrberg and Gruber (1974) being present in the white shark along with several additional behaviours not observed in the bonnethead. A detailed account of these behaviours will be published elsewhere. A possibly agonistic behaviour commonly directed at people underwater or above the surface is *gape*, a graded distension and protrusion of jaws also seen in the shortfin mako (Strong, 1996). *Spy-hopping*, in which the shark raises its head out of the water (often alongside a boat), and *tail-slap*, in which the shark raises its tail and caudal fin out of the water and smashes it against the surface, are common behaviours. Klimley, Pyle and Anderson (1996) suggest the latter is a social signal between contesting sharks over a prey item, which is plausible from their evidence although tail-slapping also occurs in situations of ambiguity as when a shark has a bait pulled out of its grasp and may also be directed toward inanimate objects or even people. White sharks will *hunch*, arching their backs and depressing their pectoral fins in a possibly agonistic display as in bonnetheads and grey reef sharks (***Carcharhinus amblyrhynchos***). One white shark may closely *follow another*, and two approaching white sharks on a collision course may *give-way*, with one shark avoiding the other, or both may give-way almost simultaneously (*stand-back*). *Follow give-way* is sometimes seen at baits, where a shark approaching a bait is followed by a second (sometimes larger); the first shark suddenly aborts its approach and the second eats the bait, or a third shark may follow and displaces the second. Courtship behaviour is poorly known in the white shark but rows of limited tooth marks on the pectoral fins of large adult female sharks suggests that complex courtship behaviour may be present as in the sand tiger shark (***Carcharias taurus***; Gordon, 1993).

Territoriality in the white shark (as contrasted with site specificity) cannot be demonstrated at present, but there is some evidence for sorting of individuals into a partly size-related hierarchy around food sources such as dead whales, pinniped colonies or feeding stations provided by people. White shark tooth scratches and inhibited bite marks are seen on individuals of all sizes, both sexes, and all postnatal maturity stages. They have been interpreted as evidence of intraspecific conflict, possibly in competition for food resources, but they probably have a broader context of social interactions. In certain areas (southern Australia, the south coast of South Africa, and central California), white sharks may have habituated to human-provided food sources and may have learned to seek out fishing boats to exploit hooked fish or the baits provided by shark cage-dive operators and film-makers.

The white shark is ovoviviparous (aplacental viviparous) and practices uterine cannibalism as do many other lamnoids, apparently in the form of embryos and foetuses eating large numbers of nutritive eggs (oophagy). The gestation period is not known at present but could be a year or more, and may or may not include taking a year off to recuperate. There are few records of pregnant females and litter size, which varies from 2 to possibly 14 young. Females mature between 4 and 5 m long and 12 to 14 years old and reach at least 23 years old, while males mature between 3.5 and 4.1 m long and 9 or 10 years old (ageing from growth rings on vertebral centra, assumed to be annual); the maximum age of either sex is unknown but has been roughly estimated at about 27 years from a von Bertalanffy growth model (Cailliet et al., 1985) assuming a maximum size of 7.6 m and indeterminate growth to that size.

The rarity of pregnant female white sharks could be explained in part by spatial separation from other white sharks during pregnancy (without evidence, however) and their sheer size that precludes capture by most fishing gear. However, it is possible that adult female white sharks are uncommon (more so than adult males), and possible also that they may have very low fecundity, with only a few adult females being pregnant at any one time and with an interval of a few years between pregnancies.

The white shark readily scavenges on available carrion, garbage, and fish caught on lines. This species probably obtains most of its prey by killing it, but is highly opportunistic as with terrestrial apex predators. Its diet in different areas may vary according to the availability (including abundance) and vulnerability of suitable prey, as well as by motivation of the predator. Live prey of individual white sharks is mostly marine vertebrates and invertebrates smaller than itself, ranging in size from small schooling fishes and squid to elephant seals and grey whale calves. The chief prey categories of the white shark are ray-finned bony fishes (Actinopterygii), cartilaginous fishes, marine mammals, marine birds, cephalopods, and crustaceans, with marine reptiles (sea turtles) and gastropods being relatively unimportant.

Bony fish prey of the white shark includes a wide range of large and small, demersal and pelagic forms, such as sturgeon (Acipenseridae), menhaden and pilchards (Clupeidae), salmon (Salmonidae), sea catfish (Ariidae), lings (Gadidae), hake (Merluccidae), flounders and halibut (Paralichthyidae), rockfish (***Sebastes* spp.**, Scorpaenidae), cabezon (***Scorpaenichthys marmoratus***, Cottidae), lingcod (***Ophiodon elongatus***, Hexagrammidae), barracuda (Sphyraenidae), striped bass (***Morone saxatilis,*** Percichthyidae), bluefish (Pomatomidae), butterfish (Stromateidae), grunters (Pomadasyidae), croakers (Sciaenidae), garrick and maasbanker (***Lichia*** and ***Trachurus***, Carangidae), porgies or sea bream (Sparidae), mackerels and tuna including bluefin tuna (***Thunnus thunnus***, Scombridae), swordfish (***Xiphias gladius***, Xiphiidae), and ocean sunfish (***Mola mola***, Molidae). White sharks are known to congregate at concentrations of schooling bony fishes such as pilchards and bluefish, and follow the KwaZulu-Natal sardine (***Sardinops***) run off South Africa.

Chondrichthyan prey of the white shark includes other sharks such as shortfin mako (***Isurus oxyrinchus***, Lamnidae), sand tiger sharks (***Carcharias taurus***, Odontaspididae), catsharks (Scyliorhinidae), houndsharks (***Galeorhinus***, ***Mustelus***, Triakidae), requiem sharks (***Carcharhinus***, ***Prionace***, ***Rhizoprionodon***, Carcharhinidae), hammerheads (***Sphyrna***, Sphyrnidae), and spiny dogfish (***Squalus***, Squalidae). Basking shark (***Cetorhinus***) meat has been found in several white sharks, apparently taken as carrion from harpooned sharks. Whale shark (***Rhincodon***) remains were found in one shark taken in a beach meshing net. It is presently unknown if the white shark ever attacks adult basking or whale sharks though smaller juveniles of both might be readily killed and eaten. Batoid prey includes giant guitarfish (***Rhynchobatus***, Rhynchobatidae), guitarfish (***Rhinobatos***, Rhinobatidae), skate egg cases (Rajidae), stingrays (Dasyatidae), and eagle rays (***Myliobatis*** and ***Pteromylaeus***, Myliobatidae). Chimaeras (Chimaeriformes) are eaten and include shortnose chimaeras (Chimaeridae), and elephantfish (Callorhinchidae). No small white sharks have been found in white shark stomachs, although large white sharks will eat shortfin makos and other very fast prey, will attack hooked, injured conspecifics, and will deliver inhibited bites to other white sharks. The writer suspects that white sharks have behavioural inhibitions on cannibalization under ordinary circumstances, as reflected by known prey records and from social interactions of small and large white sharks within aggregations.

Sea turtles are occasionally eaten by the white shark, including loggerhead and green turtles (Carettidae) and leatherback turtles (Dermochelyidae) but apparently not to the degree that the tiger shark (***Galeocerdo***) preys on them (Fergusson, Marks and Compagno, 2000).

Marine birds fall prey to white sharks and include cormorants (Phalacrocoracidae), gannets (Sulidae), gulls (Laridae), giant petrels (***Macronectes***, Procellariidae), pelicans (Pelicanidae), and penguins (Spheniscidae). Jackass penguins (***Spheniscus demersus***) are commonly grabbed, cut or slashed by white sharks off South Africa and are often killed but seldom eaten. White sharks also use their snouts to flip or bounce seabirds on the surface without eating them, and victims have included gulls (Laridae) and shearwaters and fulmars (Procellariidae).

Marine mammals can be an important food source for white sharks in some areas, and these include a number of cetaceans and pinnipeds. Those cetaceans killed and eaten include harbor porpoises (***Phocaena phocaena***, Phocaenidae), common dolphins (***Delphinus delphis***) and bottlenose dolphins (***Tursiops*** sp., Delphinidae), and even a grey whale calf (***Estrichtius robustus***). White shark inhibited bite marks have been seen on striped dolphins (***Stenella caerulalba***) from South Africa and on a pygmy sperm whale from California (Long, 1991). White shark predation on odontocetes is more difficult to study than pinniped predation, though careful study of stranded cetaceans can reveal greater diversity of cetacean predation, scavenging, and non-predatory biting by white sharks. Dead baleen whales and other large cetaceans may contribute a significant amount to the white shark's diet in some areas (Long and Jones, 1996), but such food is sporadically available at best.

True, earless or 'hair' seals (Phocidae) taken by white sharks include harbor seals (***Phoca vitulina***), grey seals (***Halichoerus grypus***) and northern elephant seals (***Mirounga angustirostris***), with predation suspected for leopard seals (***Hydrurga leptonyx***), Hawaiian and Mediterranean monk seals (***Monachus***), and southern elephant seals (***Mirounga leonina***). Eared seals (Otariidae) taken include Steller's sea lion (***Eumetopias jubata***), California sea lions (***Zalophus californianus***), South African fur seals (***Arctocephalus pusillus pusillus***), Australian fur seals (***A. p. doriferus***), South American fur seals (***A. australis***), northern fur seals (***Callorhinus ursinus***), and probably several other species. Sea otters (***Enhydra lutris***, Mustelidae) are commonly killed by white sharks off California, but have yet to be found as stomach contents. Mammalian carrion from slaughterhouses and other sources, including mutton, pig, horse, dog, cattle, and rarely human, has been found in the white shark's stomach also. Terrestrial mammals probably do not figure as a significant part of the white shark's diet.

Larger white sharks above 3 m long tend to prey more readily on marine mammals than smaller sharks below 2 m long which feed more readily on bony fishes and sharks (although the young of smaller pinnipeds can be taken by small white sharks). This and other observations have lead to the belief that large white sharks are virtually dependent on pinnipeds for prey. However, large white sharks are not restricted to pinniped prey (even in areas with pinniped colonies and abundant seals), but also catch large teleost fishes, sharks and rays, birds, dolphins and marine reptiles, and are presumably capable of subsisting on such other small to large prey, in areas where seals are uncommon or absent (Mediterranean Sea, Spencer Gulf in South Australia, Brazil). One 4.4 m specimen from the USA (Washington State) had 150 crabs (Cancridae) as well as salmon, hake, rockfish and seal hides in its stomach (LeMier, 1951). Pinnipeds may be especially important prey for white sharks where they occur together, especially at seal colonies where pinnipeds are highly vulnerable. An observational problem is that seal predation by white sharks at concentrated seal colonies can be more easily studied than their interactions with other prey items. Rather than comprising a simple growth-related switch from fish to mammal prey as some authors have assumed, the prey spectrum of the white shark is more likely to increase with growth in maximum prey size and in diversity. Only larger white sharks are apparently able or motivated to kill large pinnipeds, dolphins, bony fish, sharks, rays and turtles while retaining the ability to capture smaller prey.

Recent observations and filming of white sharks at Dyer Island, South Africa, suggest that larger animals are anything but inept, clumsy predators. The slow cruise speed and deliberate investigation of boats and baits by large white sharks belies their high dash speed and ability to chase, overhaul, and kill fast, agile prey such as Cape fur seals, sometimes after multiple jumps. Large, live, active prey may be taken by a sudden, swift rush at high speed, sometimes from below but also at the surface or even after jumping into the air. The white shark is inconspicuously coloured when viewed from above and below, and may take advantage of its cryptic coloration to stalk potential prey (as with apical terrestrial predators), but it also will cruise through Cape fur seal rafts and suddenly attack a selected victim. If the shark misses its prey, a fast chase (including jumping) may ensue. Attachment of sonic tags (Strong et al, 1992) and self-contained remote cameras ('crittercams', I. Fergusson and G. Marshall, pers. comm., and supplied footage) to white sharks show slow patrolling just below the surface and near the bottom, punctuated by occasional fast dashes (apparently after prey), with little time spent in midwater.

Invertebrate prey includes squid (Loliginidae), abalone (***Haliotis***) and other gastropods, bivalves, and crabs (Cancridae). Inedible garbage is occasionally taken from the stomachs of white sharks, but apparently this species is not fond of swallowing oddities as does the tiger shark.

Much speculation has occurred on the predatory behaviour of white sharks, particularly in the context of biting people. The white shark is clearly capable of inflicting mortal wounds on a human with a single bite, but often merely clamps lightly onto a diver or swimmer without completing its bite and releases them after a short time. Such inhibited biting behaviour has been interpreted as a predation tactic ('bite and spit') of an inept, ambush predator to avoid injury from prey, but is unlikely because of the nature of full-fledged white shark predation bouts on large active, potentially injurious prey such as seals. A white shark generally delivers a powerful bite (or bites) to immobilise, incapacitate or kill the prey item outright, then may continue biting while feeding, may resume biting after a short to long interval, or may leave without consuming more of the victim. The presence of other white sharks near a kill may influence the predator's activities via social interactions. An 'exsanguination' predation tactic has been suggested for white sharks (Klimley, 1994), in which the shark bites to kill a victim by bleeding it to death. However, white shark bites often cause severe or mortal injury (including decapitation and removal of limbs) apart from blood loss. The predation tactic used by white sharks on large, active prey is more likely the rapid infliction of 'massive trauma' to halt and kill its victim, which also begins the feeding process (somewhat as in pack-hunting terrestrial carnivores that run down their ungulate prey and eat them to death). Smaller prey items including neonate Cape fur seals may be swallowed whole by large white sharks without powerful biting or chasing (sometimes after slowly following them at the surface), and this may be likewise with large sharks eating small bony fish, crabs, and other small, defenceless prey.

Non-feeding, inhibited bites on people may be agonistic, such as possibly happens in contact encounters among white sharks, or alternatively exploration, displacement (displaced aggression), or even play. Inhibited bites have been explained as 'mistaken identity' predation bouts, in which the shark bites its victim after mistaking it for a seal or turtle and then aborts its activity after biting. Observation on free-ranging white sharks suggests that white sharks are highly selective visual predators and may be readily able to distinguish prey from divers or surfers and will react accordingly. Mistakes are possible, however, when visibility is impaired. Full-fledged predation bouts in which the white shark repeatedly bites and dismembers a human victim have been reported, but fortunately these are extremely rare compared to inhibited bites, and are very rare compared to episodes of human predation by large terrestrial carnivores, particularly tigers and the largest macropredatory crocodilians.

Ironically, ***Homo sapiens*** is the chief *known* predator and cause of mortality to white sharks, through targeted and bycatch fisheries. A large orca (***Orcinus orca***) was recently seen to kill a white shark off the Farallon Islands, California, United States, but little is otherwise known of the interactions between these apical predators. Orcas and white sharks broadly overlap in distribution and take much the same prey (except for large baleen whales occasionally killed by orcas), but complement each other ecologically and possibly displace each other in different areas. Colder seas near the poles tend to have more killer whales, cool to warm-temperate seas more white sharks, while both can occur in the tropics. The behavioural and ecological relationships of killer whales and white sharks are little understood. Large pinnipeds and other species of large, macropredatory sharks are potential predators or sources of injuries to white sharks, but without much evidence except occasional seal bite-marks on sharks. White sharks will also cut and bite one another in possible dominance-related aggressive interactions, and adult male white sharks may bite females during courtship. The injuries are often minimal and apparently inhibited and it is not known what the contribution of such injuries are to white shark mortality. Nothing is known of white shark bacterial or viral diseases, or if common parasites such as the large copepods on the maxillary valve of white sharks or the intestinal cestode fauna are a source of problems for them. Sometimes large white sharks are found dead on beaches with no obvious external or internal injuries.

Size: Maximum total length to about 6 m, and possibly to 640 cm or more; the largest free-swimming individuals commonly captured are between 500 and 580 cm (mostly adult females). Records of white sharks 6.4 to 7 or even 9 m long are difficult or impossible to verify. A much quoted record of an 11 m (36 ft) shark from Australia is erroneous and based on a jaw from a shark 4.9 to 5.5 m long in the British Museum of Natural History (Natural History Museum). Size at birth is assumed as being between 109 and about 165 cm, with term foetuses at 100 to 165 cm and free-living young down to 109 to 129 cm. Male white sharks mature at a smaller size than females and reach a smaller maximum size. Size at maturity for males is about 350 to 410 cm, with adolescence roughly between 250 and 400+ cm, and with small but fully adult males at 356, 368 and 380 cm; maximum length for males is between 501 and at least 517 cm and possibly 550 cm. Females mature somewhere between 400 and 500 cm, with females 441, 470 and 490 cm being immature or early adolescent (Florida, United States, and South Africa) and adults reported at 420 to 580 cm; maximum size of females possibly about 6 m.

Several length-weight equations are available for the white shark. See Mollet and Cailliet (1996) for a detailed review of length-weight methodology.

Compagno (1984): $W(kg) = 4.34 \times 10^{-6}\, TL(cm)^{3.14}$ (n = 98, TL = 127 to 554 cm, mostly from California)

Tricas and McCosker (1984): $W(kg) = 3.8 \times 10^{-6} \times TL(cm)^{3.15}$ (n = 127)

Casey and Pratt (1985): $W(kg) = 4.804 \times 10^{-6} \times TL\,(cm)^{3.095}$ (n = 200, from the western North Atlantic)

Cliff, Dudley and Davis (1989): $W(kg) = 1.84 \times 10^{-5} \times PCL(cm)^{2.97}$ (n = 309, from South Africa)

Cliff, Dudley and Jury (1996): $W(kg) = 2.14 \times 10^{-5} \times PCL(cm)^{2.944}$ (n = 383, from South Africa)

Kohler, Casey and Turner (1995): $W(kg) = 7.5763 \times 10^{-6} \times FL(cm)^{3.0848}$ (n = 125)
where $FL(cm) = 0.9442 \times TL - 5.7441$ (n = 112, from the western North Atlantic)

Compagno (update from 1984): $W(kg) = 3.026 \times 10^{-6} \times TL(cm)^{3.188}$ (n = 156, from California and South Africa).

Interest to Fisheries and Human Impact: The importance of the white shark as a fisheries species is limited because of its low abundance wherever it occurs, which restricts targeted commercial fisheries for conventional bulk fisheries products such as meat or liver oil. However, the high value of its jaws, teeth and fins makes it a viable target of small-scale targeted commercial fisheries as well as an added value to bycatch. It is mostly caught as a bycatch of fisheries for other sharks and other marine organisms (including bony fishes and cephalopods), by many forms of gear utilized by modern marine fisheries including longlines, specialized heavy line gear, rod-and-reel, fixed bottom gill nets, floating inshore gill nets, pelagic gill nets, fish traps, herring weirs, trammel nets, harpoons, bottom and pelagic trawls, and purse seines. Its tendency to investigate human activities (including fishing operations) and to scavenge from fishing gear, as well as the value of its jaws and fins, makes it very vulnerable to being killed and captured despite its size and strength. It is subject to targeted sports fisheries for game-fishing records and trophy jaws because of its great size, notoriety, and powerful resistance to capture. It is also targeted by small-scale and erratic commercial fisheries in several countries.

The meat of the white shark is or has been utilized fresh, fresh-frozen, dried-salted, and smoked for human consumption, although the extremely high mercury content of the meat limits its utility. The flesh has been used in traditional medicine in South Africa. White shark meat has been sold as 'shark' in California, but in the 1980s at least one market got higher values by marketing it as white shark meat. The liver of the white shark has been extracted for vitamin oil. Presumably white shark cartilage is processed for medicinals but the writer has no evidence of it. White shark carcasses have been processed for fishmeal, but also frozen or preserved whole for exhibit in oceanaria and museums. White shark specimens are also cast and modelled whole for oceanarium and museum exhibits and for trophies. The skin of the white shark has been utilized for leather, although rarely at present.

White shark teeth and jaws are used for trophies, decorations and collectibles. Properly prepared white shark jaws may bring an inflated price, essentially what the upscale international private collector's market will bear, with greatest value for the jaws and teeth of large sharks over 5 m long. In South Africa, offers of US$20 000 to 50 000 have been made for white shark jaws, and US$600 to 800 for individual teeth.

Apart from their size, white shark fins are boosted in value because of notoriety. A fin set from a large white shark may be valued at over US$1 000. Unfortunately, as with rhino horns and elephant tusks the high value of white shark products encourages poaching, clandestine trade, and flouting of protective laws.

Live white sharks have been avidly sought by public aquaria and oceanaria for exhibits, but capture trauma usually insures that the sharks perish after a day or a few days in captivity. White sharks were mostly caught for display during the 1970s and 1980s, but seldom are taken at present.

The white shark has for the last few decades been the subject of commercial underwater cage-diving operations in South Australia allowing sport SCUBA and snorkel divers to view and film white sharks, as well as intensive and sometimes oral-obsessive filming of these sharks by professional film crews. This activity also started in South Africa in the early 1990s, continues unabated at present, and has engendered some problems for the sharks and for researchers trying to study them. Regulation of capture and ecotouristic access to white sharks was seriously debated in Australia and South Africa, and licensing and guidelines have been imposed to limit access to white shark sites and methods of attracting white sharks to boats. A flurry of shark-bite incidents off South Africa in the late 1990s spawned a high-profile media-hyped controversy on the assumption that exposure of white sharks to cage diving in the Western Cape somehow caused them to bite people elsewhere.

The white shark is feared by many people as the most 'dangerous' living shark; more instances of white sharks biting swimmers, divers, surfers, and boats have been reported than for any other shark. Although much has been made of white shark encounters with people and boats in the popular news and entertainment media, including the JAWS motion pictures that established the white shark as a Hollywood science-fiction monster, the white shark is not very 'dangerous' when compared to other causes of injuries and fatalities to people. Most white shark bites are nonfatal and may not be predatory (see above). The rate of white shark bite incidents averaged about three per year worldwide between 1952 and 1992 (range 0 to 8, with an 18% fatality rate) and a slowly increasing trend from about 1.5 per year between 1952 and 1962 to 5.3 per year between 1983 and 1992 (data in part from Ellis and McCosker, 1992; see also Burgess and Callahan, 1996). During the last decade (1990 through 1999) unprovoked incidents averaged 6.9 per year (69, range 0 to 12 per year, with a 16% fatality rate), with most occurring off the United States and South Africa (G. Burgess, International Shark Attack File, pers. comm.). This is far less than drownings, diving accidents, automobile accidents, deaths from lightning strokes, injuries or deaths from terrestrial animals including tigers, large crocodilians, and even domestic livestock, or other calamities that afflicted humans in the countries where white shark incidents occurred.

Most injuries and fatalities from white shark encounters have occurred off California (United States), southern Australia, New Zealand, South Africa, and Japan, but about 80% of reported shark biting incidents have occurred in the tropics, where white sharks are rare or uncommon but where large carcharhinid sharks predominate. There might very well be tropical and warm-temperate carcharhinoids, particularly the tiger and bull sharks, that may be responsible for more shark bite incidents than the white shark, but this remains to be verified.

Several surfers and paddleboarders have been bitten by white sharks or knocked off their boards. The sharks have sometimes destroyed the boards or held, shook, and released the boards without harming the surfers. Boats may be bitten, particularly if boaters provoke the sharks by landing fish out of their grasp or try to ram the sharks. For some reason False Bay, South Africa, was the site of more boat incidents involving white sharks than all other places combined between 1940 and 1980, although hardly since then. White sharks have on a few occasions persistently bitten at boats until they sank, and in a few instances leapt into a boat or punched through the hull like a torpedo.

Despite the frightful, JAWS-inflated reputation of the white shark there is accumulating evidence that the presence of a white shark near people (especially divers) does not necessarily mean that the shark will automatically bite (much less kill and eat) them. Numerous incidents have been reported where these sharks swim up to divers as close as a few feet and depart without biting or without displaying possible agonistic behaviours such as *gape* or *hunch*, and these have been followed up by deliberate encounters by film-makers with white sharks outside shark cages without adverse affects. Numerous close, deliberate, and systematic encounters involving divers without a cage in proximity to numerous white sharks ranging in size from about 2 to over 5 m long have shown very little agonistic behaviour by the sharks, although they were inquisitive, were sometimes present in groups, and often came very close to the diver (M. Marks pers. comm. and videos). This is definitely not recommended for ordinary divers seeking recreational thrills, and should be seen as deliberate and calculated risk in support of science comparable to behavioural observation of large, potentially harmful terrestrial carnivores and large ungulates.

World catches of white sharks from all causes are difficult to estimate. Compagno (1984) noted that off California 10 to 20 or more white sharks were killed each year as a bycatch of various fisheries, vs. 0.13 humans per year killed by white sharks. These figures were over a period of about three decades up to the early 1980s, and protection of the white shark in the 1990s may have reduced the catch since then.

Conservationists have been concerned with the vulnerability of the white shark to possible extinction, and it is currently considered a *vulnerable* species in the IUCN Red List. This seems warranted given that this species has a relatively low intrinsic rebound potential (a relative measure of the ability to recover from fishing; Smith, Au and Show, 1998). Threats to the white shark include: 1. Targeted commercial and sports fisheries for jaws, fins and game fish records. 2. Anti-shark measures to protect beaches. 3. Ad-hoc media-fanned campaigns to kill white sharks after a biting incident occurs. 4. Long-term increases in use and efficiency of commercial and artisanal fishing gear that have an impact on white sharks. 5. Degradation of inshore habitats used by white sharks for pupping and nurseries. 6. Increased demand for shark products in general, including vastly inflated values of white shark jaws, fins and teeth. 7. The tendency of white sharks to investigate human activities, which can be fatal to them. 8. Lack of knowledge on many crucial aspects of white shark biology, and limited interest on investigating them. 9. The negative JAWS image, which invites neglect, killing of sharks, and disregard of conservation measures. 10. Slow maturation and low fecundity. 11. Proximity of concentrations of white sharks to highly-developed coastal areas such as those of California, the Mid-Atlantic Bight, and the Mediterranean Sea. 12. Inadequate catch data in most places where the white shark occurs.

Numbers of white sharks have been thought to be declining off Australia due to sports and commercial fisheries and anti-shark nets. The white shark is currently protected in Australia (nationally and statewise), South Africa, Namibia, Israel, Malta and the United States (statewise off California and Florida and with directed fisheries prohibited off all coasts). Protective laws are strict, but loopholes and inadequate enforcement may cause problems including promoting a black market for high-value white shark products. The United States and Australia proposed the white shark for CITES I and II listing at the 2000 CITES Conference to ban trading in white shark parts, but the proposals were not approved. These countries are currently proposing the white shark for a CITES III listing while Australia has developed a comprehensive and multidisciplinary recovery plan for white sharks in its waters (Environment Australia, 2000b).

Local Names: Sarda (Canary Islands); Jaquetón de ley (Cuba); Uptail, Tommy, White death shark, White death, Great white death, Death shark, White pointer (Australia); Great white shark, White shark (AFS), Maneater or man-eater shark, (England and USA); Ami, Lamea, Lamie, Lameo, Le Carcharodonte lamie, Le grand requin, Pei can, Requin blanc (France); Menschen fresser, Menchenhai, Merviel fras, Weisshai (Germany); Ca mari, Marraco, Salroig, Salproig, Salproix, Taburo, Tiburo, Tiburón blanco, Tauró blanc (Spain); Tubarâo branco, White shark (Azores); Carcarodonte, Cagnia, Cagnesca grande, Cagnia, Caniscu, Carcarodonte lamia, Carcarodonte di rondelet, Damiano [sic] or Demon shark, Imbestinu, Lamia, Mastinu feru, Mangia alice or Anchovy-eater, Pesce cane, Pesca can, Pescecane, Pesce can grande, Pesciu can, Pici bistinu, Pisci cani or Can grossu, Pisci mastinu, Squalo bianco, Tunnu palamitu di funnu or Tuna shark (Italy); Hohojirozame, Hitokiuzame, Oshirozame (Japan); Psina ljudozdera (Yugoslavia); Gab doll, Kelb Il-bahar, Kelb-il-bahar abjad, Huta tax-xmara (Malta); Taniwha, Mango-tuatini, Hare hongi (New Zealand); Haa skieding (Norway); Tabarao (Portugal); Gench, Kersch (Red Sea); Blue pointer, White shark, Great white shark, Springhaai or Jumping shark, Witdoodshaai, Withaai, Cowshark, Mudshark, Sarda (South Africa); Niuhi (Hawaiian Islands); Tanifa (Samoa).

Literature: Linnaeus (1758); Müller and Henle (1839); Smith (1849); Garman (1913); Barnard (1925, 1937); Fowler (1936, 1941); Springer (1939); Whitley (1940); Bonham (1942); Bigelow and Schroeder (1948); Smith (1949, 1951); LeMier (1951); Herre (1953); Schultz et al. (1954); Strasburg (1958); Farquhar (1963); Smith and Smith (1963); Garrick and Schultz (1963); Limbaugh (1963); Stead (1963); Follett (1966); Squire (1967); Case (1968); Carey and Teal (1969); Mundus and Wisner (1971); Arnold (1972); Randall (1973, 1987); Springer (1973); Bass, D'Aubrey and Kistnasamy (1975a); Ellis (1976); Allen and Allen (1978); Wallett (1978); Penrith (1978); Ames and Morejohn (1980); Ainley et al. (1981, 1985); Miller and Collier (1981); Carey (1982, 1990); Carey et al. (1982, 1985); le Boeuf, Riedman, and Keyes (1982); Pratt, Casey and Conklin (1982); Brodie and Beck (1983); Compagno (1984, 1990a, b, d, 1991); Engaña and McCosker (1984); Quero (1984); Tricas and McCosker (1984); Block and Carey (1985); Cailliet et al. (1985); Pratt and Casey (1985); Klimley (1985); Taylor (1985); Tricas (1985); Tricas and McCosker (1985); McCosker (1985); Bass (1986); deSilva (1986); Corkeron, Morris and Bryden (1987); Nakano and Nakaya (1987); Stafford-Deitsch (1987); Randall, Randall and Compagno (1988); Uchida et al. (1988); Paxton et al. (1989); Cliff, Dudley and Davis (1989); Cockcroft, Cliff and Ross (1989); Paulin et al. (1989); Fulgosi (1990); Strong (1990, 1996); Springer (1990); Cousteau and Richards (1991); Ellis and McCosker (1991); Long (1991, 1996); Bruce (1992, 1995); Klimley et al. (1992); Strong et al. (1992, 1996); Francis and Randall (1993): Hanan, Holts and Coan (1993); Michael (1993); Compagno and Fergusson (1994); Klimley (1994); Seret (1994); Last and Stevens (1994); Bonfil (1994); Fergusson (1994, 1996); Nakaya (1994, 1996); Anderson and Goldman (1996); Burgess and Callahan (1996); Cliff, Dudley and Jury (1996); Collier, Marks and Warner (1996); Goldman et al. (1996); Francis (1996); Gadig and Rosa (1996); Klimley, Pyle and Anderson (1996); Long and Jones (1996); Long and Waggoner (1996); Long et al. (1996); Mollet and Cailliet

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(1996); Mollet et al. (1996); Pratt (1996); Strong (1996); Uchida et al. (1996); Goldman (1997); Smale and Heemstra (1997); Compagno, Marks and Fergusson (1997); Santos, Porteiro and Barreiros (1997); McEachran and Fechhelm (1998); Smith, Au and Show (1998); Cliff et al. (2000); Environment Australia (2000b); Fergusson, Marks and Compagno (2000); D. Ainley (pers. comm.); R. Alexander (pers. comm.); D. Allen (pers. comm.); G. Burgess (pers. comm.); G. Cailliet (pers. comm.); S. Cook (pers. comm.); D. Ebert (pers. comm.); A.P. Klimley (pers. comm.); R. Lea (pers. comm.); M. Marks (pers. comm.); S. Smith (pers. comm.); I. Fergusson (pers. comm.); G. Zorzi (pers. comm.).

Isurus **Rafinesque, 1810**

Genus: ***Isurus*** Rafinesque, 1810a, *Caratt. gen. sp. anim. piant. Sicilia, Palermo*, pt. 1: 11.

Type Species: ***Isurus oxyrinchus*** Rafinesque, 1810, by monotypy.

Number of Recognized Species: 2.

Synonyms: Genus ***Oxyrhina*** Agassiz, 1838: 86, pls. 33-34. Type species: “***Lamna oxyrhina*** Cuvier and Valenciennes, MS.” by absolute tautonymy, a junior synonym of ***Isurus oxyrinchus*** Rafinesque, 1810. Genus ***Oxyrrhina*** Bonaparte, 1846: 17. Type species: ***Oxyrhina gomphodon*** Müller and Henle, 1839, a junior synonym of ***Isurus oxyrinchus*** Rafinesque, 1810. Genus ***Plectrostoma*** Gistel, 1848: 10. Replacement name for ***Oxyrhina*** Agassiz, 1835, and thereby taking the same type species, ***Lamna oxyrhina*** Cuvier and Valenciennes, 1838, a junior synonym of ***Isurus oxyrinchus*** Rafinesque, 1810. Genus ***Isuropsis*** Gill, 1862b: 397. Type species: ***Oxyrhina glauca*** Müller and Henle, 1839, by original designation. Genus ***Plectrosoma*** Bigelow and Schroeder, 1948: 123 (error for ***Plectrostoma*** Gistel, 1848). Genus ***Lamiostoma*** Glikman, 1964: 105. Type species: ***Lamiostoma belyaevi*** Glikman, 1964, by original designation.

Diagnostic Features: Snout bluntly to acutely conical. Eyes large, 1.3 to 3.1% of total length. Nostrils situated adjacent to head rim in ventral view. Mouth width 0.9 to 1.5 times its length. Anterior teeth enlarged; anterior and intermediate teeth not compressed but upper lateral teeth more or less compressed, teeth not forming a continuous cutting edge; intermediate teeth very small and less than half height of adjacent anteriors, with normal cusps directed posterodistally or nearly vertical; second lower anterior teeth greatly enlarged and taller than second upper anterior tooth; total tooth count 43 to 54; roots of anterior teeth deeply arched, with root lobes narrow and elongated; lateral cusplets absent from teeth at all stages; teeth smooth-edged; cusps of anterior teeth weakly to strongly flexed. Body usually fairly slender. First dorsal-fin origin usually behind the pectoral-fin free rear tips. Anal-fin origin under second dorsal-fin midbase or slightly posterior to second dorsal-fin insertion. Secondary caudal keels absent or present and weak. Total vertebral count 182 to 197. Cranium with rostral cartilages neither swollen nor hypercalcified. Intestinal valve count 47 to 54. Length of adults 2.0 to 4.2 m. Usually a black axillary spot at pectoral-fin insertions; pectoral-fin tips usually abruptly black on their ventral surfaces.

Local Names: Makos, Mako sharks, Mackerel sharks, Awozame-zoku (Japan).

Remarks: The systematics of makos (genus ***Isurus***) was formerly chaotic, with a few regional species recognized on growth changes within a single species, ***Isurus oxyrinchus*** (Garman, 1913; Fowler, 1941; Bigelow and Schroeder, 1948; Smith, 1957). Guitart (1966) described a second, highly distinctive macroceanic mako, ***I. paucus*** from Cuba, which Garrick (1967) independently described as ***I. alatus*** from the central Pacific. Garrick (1967) sorted out the growth change problems and his arrangement and synonymy for ***I. oxyrinchus*** were followed by Bass, D’Aubrey and Kistnasamy (1975a), Pinchuk (1983), Compagno (1984), and Moreno and Morón (1992b), who recognized two living species, ***I. oxyrinchus*** and ***I. paucus***. Moreno and Morón presented detailed comparisons of eastern Atlantic makos from extensive fisheries samples and confirmed the differentiation of ***I. oxyrinchus*** and ***I. paucus*** on morphometry, external morphology including coloration, and dentitional characters. They noted, however, that ***I. oxyrinchus*** specimens caught around the Azores closely agreed with other eastern Atlantic specimens in morphometrics, morphology and dentition, but had a dusky snout and mottled or all-dark underside as in ***I. paucus***. They suggested that the Azores mako represented a distinct, localized population or ‘population variant’ of ***I. oxyrinchus***. This is plausible but needs further research, including molecular studies, and is of some urgency as the Azores mako is possibly declining due to overfishing. The Azores mako may have an analogy within the genus ***Lamna***, in which the North Pacific ***L. ditropis*** differs from the North Atlantic ***L. nasus*** in having a dusky or mottled underside, but Southern Hemisphere ‘black-faced’ ***L. nasus*** have similar dark undersides and have been mistaken for ***L. ditropis***. Compagno (1990b) noted chondrocranial differences between ***Isurus oxyrinchus*** and ***I. paucus***.

Key to Species:

1a. Snout usually acutely pointed; cusps of upper and lower anterior teeth flexed, with tips reversed; pectoral fins considerably shorter than head, relatively narrow-tipped in young and acutely pointed in adults (Fig. 72); underside of snout and mouth white in adults (dusky in Azores' 'marrajo criollo') . . . . ***Isurus oxyrinchus***

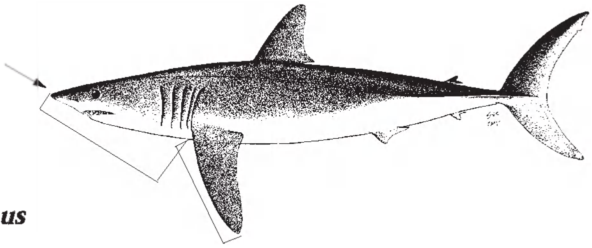


Fig. 72 *Isurus oxyrinchus*

1b. Snout narrowly to bluntly pointed, usually not acute; cusps of upper and lower anterior teeth straighter, with tips not reversed; pectoral fins about as long as head or longer (Fig. 73), relatively broad-tipped in young and adults; underside of snout and mouth dusky in adults . . . . ***Isurus paucus***

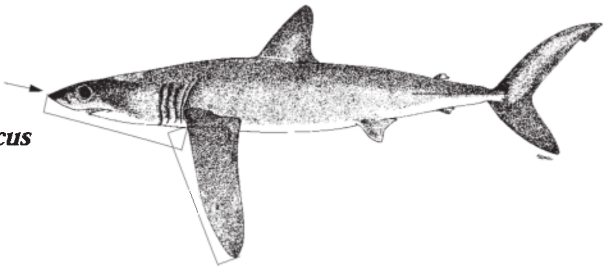


Fig. 73 *Isurus paucus*

Isurus oxyrinchus Rafinesque, 1810

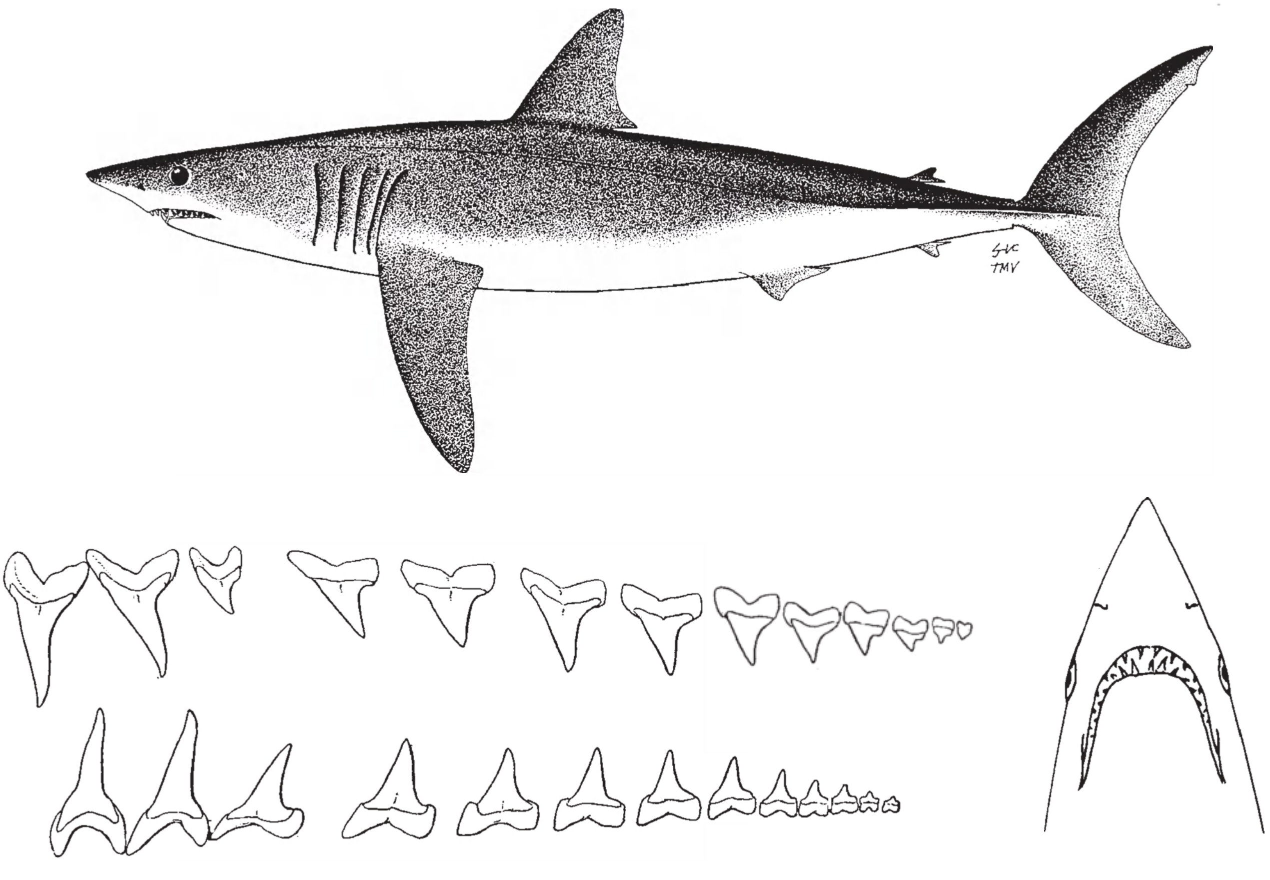
Fig. 74

Isurus oxyrinchus Rafinesque, 1810a, *Caratt. gen. sp. anim. piant. Sicilia, Palermo*, pt. 1: 12, pl. 13, fig. 1. Also Rafinesque, 1810b, *Indice Ittiol. Sicil.*: 45. Holotype unknown, type locality Sicily, Mediterranean Sea. Variant spellings include ***Lamia oxyrhincus*** Bory de St. Vincent, 1829, and ***Isurus oxyrhynchus*** Jordan and Evermann, 1896.

Synonyms: ***Isurus spallanzanii*** Rafinesque, 1810b: 45, 60. Type locality: Sicily. No types known according to Eschmeyer (1998: CD-ROM). ***Squalus (Lamna) cepedii*** Lesson, 1830: 93. Holotype: 1.83 m individual, Equatorial Atlantic, 6°S, 27°W; according to Eschmeyer (1998: CD-ROM) the whereabouts of this specimen is unknown. ***Lamna oxyrhina*** Cuvier and Valenciennes, *in* Agassiz, 1838: 86. Manuscript name only cited by Agassiz, but without a species description. Types uncertain: Agassiz mentioned a set of jaws in the collection of the Museum National d'Histoire Naturelle, Paris, without specific data. A tooth set from a mako was illustrated by him (Agassiz, 1835, pl. G, fig. 2, as ***Lamna***) and may be from the Paris specimen. ***Oxyrhina gomphodon*** Müller and Henle, 1839: 68, pl. 28. Holotype, Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin, ZMB 4528, a stuffed adult male 1 650 mm +, without head, jaws separate according to Paepke and Schmidt (1988: 163), from "Ocean". ***Oxyrhina glauca*** Müller and Henle, 1839: 69, pl. 29. Syntypes, three stuffed specimens, Rijksmuseum van Natuurlijke Historie, Leiden, RMNH 2529, 1 020 mm TL male (a lectotype, designated by Garrick, 1967: 675), RMNH 2533, 750 mm TL male, RMNH 2587, 660 mm TL male, and two jaws of uncertain deposition, possibly Berlin (not mentioned in Paepke and Schmidt, 1988). Type locality originally stated as Java, but actually Japan according to Garrick (1967). ***Lamna latro*** Owen, 1853: 96. Locality unknown. Types? ***Isuropsis dekayi*** Gill, 1862: 409. Based on ***Lamna punctata*** DeKay, 1839, not ***Oxyrhina daekayi*** Gill, 1862b, (= ***Lamna nasus***). ***Carcharias tigris*** Atwood, 1865: 81. No distinguishing features; also Atwood, 1869: 268. Types: None, according to Eschmeyer (1998: CD-ROM), from Gulf of Mexico and Massachusetts, Provincetown, Cape Cod. ***Lamna guentheri*** Murray, 1884: 349. Type locality, Kurrachee (= Karachi), Pakistan. Original spelling ***Lamna güntheri***. Holotype: a 2 580 mm specimen according to Garrick (1967: 665-667). Disposition of holotype uncertain, presumably in the British Museum (Natural History); Garrick (*loc. cit.*) and Eschmeyer (1998: CD-ROM) had no information. ***Lamna huidobrii*** Philippi, 1887: 548, pl. 3, fig. 1. Holotype: 2.90 m female (possibly stuffed) in collection of Universidad de Chile, Departamento de Biología Celular y Genética, Santiago, Chile (Eschmeyer, 1998: CD-ROM), possibly lost (S. Kato, pers. comm.), type locality, Santiago Province, Chile. ***Isurus mako*** Whitley, 1929: 101. A new name based on the account of ***I. glaucus*** by Phillipps, 1932: 268, off Manaukau Bar, Auckland, New Zealand. No types according to Eschmeyer (1998: CD-ROM). ***Isurus bideni*** Phillipps, 1932: 227, fig. 2. According to Phillipps (loc. cit.) and Eschmeyer (1998: CD-ROM), the holotype is a South African specimen in the Australian Museum, Sydney, AMS IA.4311 (jaws and photographs) sent to Mr G.P. Whitley by Mr C. Leo Biden of Cape Town and possibly from the Western Cape Province, South Africa. ***Isurus tigris africanus*** Smith, 1957: 96, pl. 1, fig. 1. Holotype: J.L.B. Smith Institute of Ichthyology, RUSI 426, jaws from 2 540 mm TL adult male. Type locality, Algoa Bay, South Africa.

Other Combinations: ***Isurus*** or ***Isuropsis glaucus*** (Müller and Henle, 1839), ***Isurus guentheri*** (Murray, 1884).

FAO Names: En - Shortfin mako; **Fr** - Taupe bleu; **Sp** - Marrajo dientuso.



UPPER AND LOWER TEETH OF LEFT SIDE

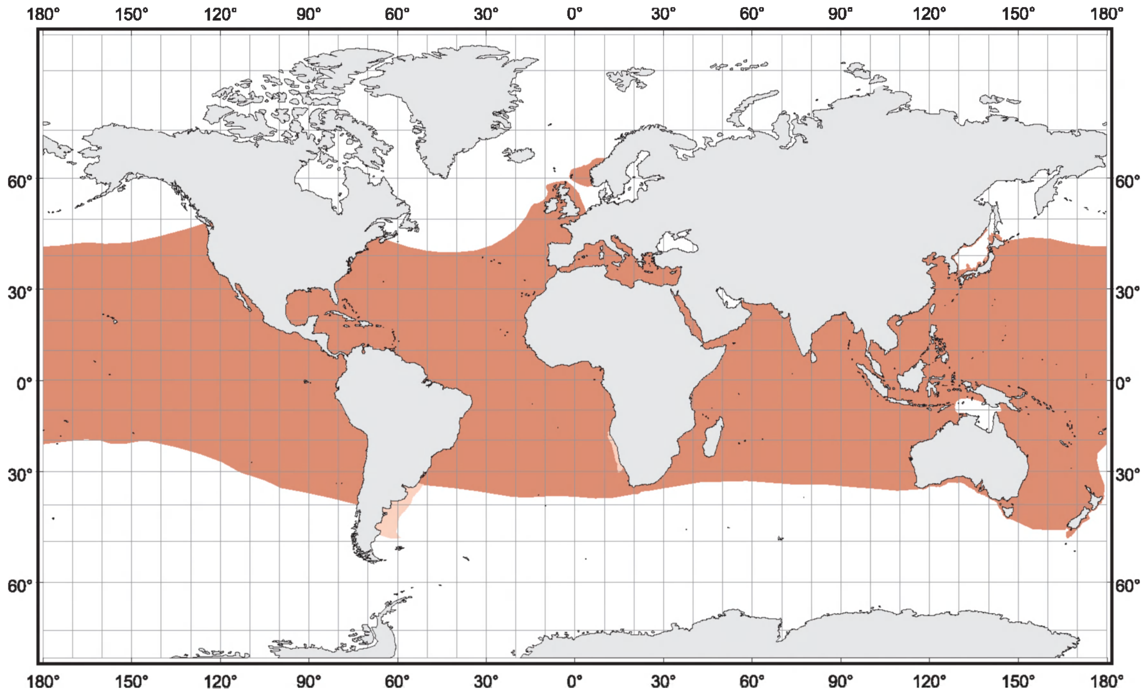
UNDERSIDE OF HEAD

Fig. 74 *Isurus oxyrinchus*

Field Marks: Spindle-shaped body, long, acutely conical snout, large blade-like teeth without cusplets or serrations, pectoral fins rather narrow-tipped and with anterior margins less than head length, large first dorsal fin and minute, pivoting second dorsal and anal fins, strong keels on caudal peduncle, no secondary keels on caudal base, crescentic caudal fin, ventral surface of body usually white.

Diagnostic Features: Snout acutely pointed. Eyes relatively small. Mouth U-shaped. Lower anterior teeth strongly protruding and horizontal on jaws even when mouth is closed; anterior teeth with narrow, more oblique cusps with flexed tips; cusps of first upper anterior teeth with incomplete cutting edges; intermediate teeth with curved oblique distally hooked cusps. Body moderately slender but more fusiform than in ***Isurus paucus***. Pectoral fins semifalcate and with tips relatively narrow, anterior margins about 16 to 22% of total length and shorter than head length. Origin of first dorsal fin over or just behind the pectoral free rear tip; first dorsal-fin apex broadly rounded in young but more angular and narrowly rounded in large juveniles and adults; first dorsal-fin height greater than base length in large individuals but equal or smaller in young below 185 cm. Total vertebral count 182 to 195, mostly below 190. **Colour** (except Azores 'marrajo criollo'): dorsolateral coloration brilliant blue or purplish in life, white below underside of snout in young and adults; dark colour of head partially covering gill septa, lower part of second and third gill septa white; dark colour of flanks not extending ventrally onto abdomen; pelvic fins dark on anterior halves, white on posterior halves, undersides white and sometimes with thin dark margin; first dorsal fin with pale centre (more obvious in young than adults); anal fin dark only on anterior half and white on posterior half.

Distribution: Coastal and oceanic, circumglobal in all temperate and tropical seas. Western Atlantic: Gulf of Maine to southern Brazil and possibly northern Argentina, including Bermuda, Gulf of Mexico and Caribbean. Eastern Atlantic: Norway, British Isles and Mediterranean to Morocco, Azores, Western Sahara, Mauritania, Senegal, Côte d'Ivoire, Ghana, southern Angola, probably Namibia, and South Africa (west coast). Indo-West Pacific: South Africa (east coast), Mozambique, Madagascar, Mauritius and Kenya north to Red Sea and east to Maldives, Iran, Oman, Pakistan, India, Indonesia, Viet Nam, China, Taiwan (Province of China), North Korea, South Korea, Japan, Russia (Primorskiyi Kray), Australia (all states and entire coast except for Arafura Sea, Gulf of Carpentaria and Torres Strait), New Zealand (including Norfolk Island), New Caledonia, Fiji. Central Pacific: From south of Aleutian Islands to Society Islands, including Hawaiian Islands. Eastern Pacific: USA (Washington and California) south to Mexico, Costa Rica, Ecuador, Peru and central Chile.



Habitat: The shortfin mako is a common, extremely active, offshore littoral and epipelagic species found in tropical and warm-temperate seas but seldom occurring in waters below 16°C. This shark occurs from the surface down to at least 500 m. It occurs well offshore but penetrates the inshore littoral just off the surf zone in places such as parts of KwaZulu-Natal, South Africa, where the continental shelves are very narrow. Shark meshing data off South Africa suggests that this species prefers clear water to turbid water and is caught at a range of water temperatures from 17 to 22°C. In the western North Atlantic it prefers a similar range of temperatures, and only moves onto the continental shelf when surface temperatures exceed 17°C. In the eastern North Pacific juveniles range into southern California waters and tend to stay near the surface, with little tendency to descend into cold subsurface waters, and use these offshore continental waters as nursery areas. Telemetered small sharks in this area tended to stay near the surface above 20 m depth and in waters 20 to 21°C, and mostly avoided the thermocline and cold deeper waters (Holts and Bedford, 1992).

Biology: The peregrine falcon of the shark world, the shortfin mako may be the fastest shark and one of the swiftest and most active fishes. It is famed as a jumper, leaping several times its length from the water, and is capable of extreme bursts of speed when hooked and in pursuit of prey. Sonic telemetry of small (1.7 to 1.8 m and 32 to 36 kg) makos off southern California showed a relatively slow cruise speed (Holts and Bedford, 1992) between 1.3 and 2.6 km/h, with short increases up to 4.5 and 5.6 km/h and slowing to less than 1 km/h at night. No fast dashes were recorded during the periods monitored. Similar speeds were recorded over a track of 280 km off Florida by a larger (about 180 kg) shortfin mako (Casey and Kohler, 1992).

Shortfin makos are endothermic and maintain higher temperatures than surrounding water temperatures in their body musculature, brains, eyes and viscera with countercurrent vascular heat exchangers (Carey and Teal, 1969; Carey et al., 1972; Carey, 1982, 1992; Block and Carey, 1985). Body muscle may run 1 to 10°C higher than ambient temperature. Central temperatures in the body musculature of the shortfin mako are highest relative to water temperature in cooler water (between 19 and 25° in water 15°C), but approach ambient in warm water (27 to 29° in water 27°C). Endothermy is particularly advantageous in maintaining elevated swimming, visual, central nervous system and digestive functions when the makos are in cooler waters in higher latitudes or when diving below the thermocline in warm waters.

The shortfin mako is highly migratory and in the extreme northern and southern parts of its range, has a tendency to follow movements of warm water masses polewards in the summer. Off South Africa catches in the KwaZulu-Natal shark nets indicate inshore movements from deeper water over the continental slopes, which in the area is relatively close to shore because of the narrow shelves.

Long-range movements of this shark are not well known and are being slowly elucidated by conventional tagging in the North Atlantic. Casey and Kohler (1992) reported on 2 459 shortfin makos tagged off the western North Atlantic coast of the USA between 1962 and 1989, with a recapture rate of 9.4% to date. About 64% were recaptured within 500 km of where they were tagged, but 13% travelled over 1 600 km with several recaptures in the Azores and one even travelling about 4 000 km to Spain. Casey and Kohler suggested that makos may travel up the Gulf Stream and around the Sargasso Sea to return to the East Coast of North America, with few crossing the Mid-Atlantic Ridge and reaching European waters. The authors hypothesized that the western North Atlantic makos form a separate population or stock to those in the eastern Atlantic although intermixing is possible as shown by crossings to the Azores and Europe. There are problems in understanding the population structure of western North Atlantic makos because large adults, particularly females, are little-known in the area although juveniles are abundant.

This species is ovoviviparous and a uterine cannibal (oophagous), with 4 to 25 and possibly 30 young (mostly 10 to 18) in a litter, with larger females having larger litters. Sex ratios from beach-meshed sharks off KwaZulu-Natal, South Africa, varied monthly, with male-female ratios ranging from 0.6:1 to 2.5:1 and with males more abundant than females for most of the year except January and August; with a sample of 171 sharks, males were significantly more abundant than females with an overall ratio of 1.4:1. Birth occurs mostly in late winter to midsummer in both hemispheres. Off KwaZulu-Natal birth occurred offshore in late spring (November), and mating occurs in autumn (March to June). Estimates of gestation period vary, but recent estimates suggest it may be 15 to 18 months within a reproductive cycle of three years (including a year break between pregnancies; Mollet et al., 2000). Adult males show seasonal changes in gonadosomatic index (gonad weight as % of body weight), with males having the heaviest gonads in the summer and the lightest in winter. Gonadosomatic index is positively correlated with hepatosomatic index (liver weight as % of body weight) in adult females, with females with large ovaries having larger livers than those with small ovaries.

Makos may mature at a minimum age of 7 to 8 years old, based on yearly addition of growth rings on vertebral centra, with the oldest known with 18 rings corresponding to at least 18 years at 321 cm, and an estimated maximum age of 45 years (Cailliet et al., 1983). Pratt and Casey (1983) assumed that two growth rings were formed each year on the vertebral central of shortfin makos, though Cailliet et al. (1983) suggested that one ring per year was formed. Stillwell (1990) suggested that makos were faster-growing, and achieved adult size in 4.5 years for males and 7 years for females.

The shortfin mako primarily feeds on other fishes, with a wide variety of prey recorded. Prey items are typically much smaller than the mako, and off South Africa range between 10 and 35% of the length of the predator. However, Stillwell (1990) suggested that large makos shifted to large prey near their own size, with swordfish (***Xiphias***) weighing 180 kg or more being commonly taken by large and presumably adult makos (males about 136 kg and females 337 kg) in the western North Atlantic.

The mako eats both pelagic and demersal bony fishes, including freshwater eels (Anguillidae), eel-pouts (Zoarcidae), anchovies (Engraulidae), menhaden, sardines and other herring (Clupeidae), grunts (Haemulidae), lancetfish (Alepisauridae), needlefish (Belonidae), sauries (Scomberesocidae), cod, ling, whiting and other cod-like fishes (Gadidae), hake (Merlucciidae), alfonsinos (Berycidae), croakers (Sciaenidae), mullet (Mugilidae), Australian salmon (***Arripis***), butterfishes (Stromateidae), bluefish (***Pomatomus saltatrix***, Pomatomidae), yellowtails, jack mackerel and other jacks (Carangidae), sea bass (Serranidae), porgies or sea breams (Sparidae), scabbardfish (Trichiuridae), snake mackerel (Gempylidae), swordfish (***Xiphias gladius***, Xiphiidae), sailfish (***Istiophorus platypterus***, Istiophoridae), mackerel, tuna, bonito, skipjack, and other scombrids (Scombridae), medusafishes (Centrolophidae), rockfish (***Sebastes***, Scorpaenidae), sea robins (Triglidae), and even seahorses (Syngnathidae), puffers (Tetraodontidae), porcupine fish (Diodontidae), and boxfish (Ostraciidae). In the western North Atlantic, bluefish are the most important food and comprise about 78% of the shortfin mako's diet (Stillwell and Kohler, 1982), but the same species (called taylor in Australia) was not recorded from makos off New South Wales (Stevens, 1984).

Elasmobranchs taken by the shortfin mako include blue sharks (***Prionace glauca***), grey sharks (***Carcharhinus obscurus***, ***C. brevipinna***, ***C. sealei*** and ***C. limbatus***), milk sharks (***Rhizoprionodon acutus***), hammerheads (***Sphyrna lewini*** and ***S. zygaena***, skates (Rajidae), spotted eagle rays (***Aetobatus narinari***, Myliobatidae), and cownose rays (Rhinopteridae). Off KwaZulu-Natal, South Africa, small sharks less than 1.3 m long including the young of large species such as ***Carcharhinus obscurus*** are more important food items for the mako than large sharks and rays, which is a function possibly of high availability as well as preference for smaller prey items. Off South Africa elasmobranchs were the most important prey, followed by teleosts and cephalopods (squid), but in the western North Atlantic and New South Wales teleosts were the most important prey while elasmobranchs were virtually unrepresented.

Cephalopods are important prey and include a variety of inshore and oceanic and deep-benthic squids including ***Loligo*** (Loliginidae), ***Ancistrocheirus*** (Ancistrocheiridae), ***Lycoteuthis*** (Lycoteuthidae), ***Octopoteuthis*** (Octopoteuthidae), ***Histioteuthis*** (Histioteuthidae), Gonatidae, and ***Illex*** and other ommastrephids (Ommastrephidae), as well as cuttlefish (***Sepia***, Sepiidae). Other food includes sea turtle heads (uncertain if these were scavenged or if the turtles were decapitated by the makos), unidentified small cetacean material (including a pelagic dolphin), salps, isopods, penaeid shrimp, sponges, sargassum weed, and occasional stones and other detritus. Marine mammals are rarely reported in the diet of the shortfin mako and may be scavenged, but very large individuals occasionally catch small pelagic cetaceans (dolphins). Very large shortfin makos over 3 m long have somewhat broader, more flattened and triangular upper teeth, perhaps more suitable for handling small cetaceans than the awl-shaped teeth of smaller makos. Pinnipeds have not been recorded as mako food so far (although they could be eaten in places where their distribution overlaps that of large makos), and makos have not been seen scavenging on dead whales as with white sharks or tiger sharks.

From prey types and other information, makos apparently feed at or near the surface and well below it, and may feed on bottom prey when close inshore. Stillwell and Kohler (1982) estimated that a 68 kg mako might consume about 2 kg of prey per day, and could eat about 8 to 11 times its body weight per year. Stillwell (1990) suggested that makos might consume up to 15 times their weight per year.

This is a bold and responsive shark when a feeding stimulus (such as speared fish or a bait station) is present, and individuals have *charged* divers repeatedly at high speed (usually veering off at the last moment) as well as *chasing* off less dominant (possibly smaller?) conspecifics from baits. About a fourth of some 156 makos examined from the shark nets off KwaZulu-Natal, South Africa, had injuries, including missing fin tips, clasper tips, and mako bite patterns on the belly, flanks, pectoral fins, and gill regions. Some injuries were due to scavenging by other sharks, but mako-induced tooth cuts are likely to be both from combat and mating, as with similar cuts on white and sand tiger sharks, including pectoral fin injuries that may be due to a male holding onto a female with its mouth during courtship. Open-mouth *gaping* at divers by these sharks may be a threat display as in the white shark. Another possible threat display under non-baited conditions may be *porpoising* or low short leaps at the surface, followed by *figure 8 looping* at speed. Behaviour is otherwise sketchily known, but it is suspected that a variety of behavioural elements, including varied social interactions, may be present in this species as in the white shark. Shark netting data off South Africa suggests that makos were generally caught singly off beaches, though two occurred in the same net on the same day and a small group of five was caught in adjacent nets over nine days.

The shortfin mako apparently has relatively few natural predators, perhaps because of its high activity level, speed and large size. Their chief predators are humans, in the form of commercial fisheries. It is not immune from predation by its larger cousin the white shark, which is very fast when chasing prey or conspecifics. Off California and in the Mediterranean Sea small (less than 2 m long) makos have been found in white shark stomachs. In South Africa the fresh head of a mako (cut off at the pectoral fins) was found on a beach with unmistakable white shark wounds indicating a predation bout and no evidence of scavenging from fishing gear such as hook or net injuries. A live South African mako was caught with injuries suggesting that a white shark grabbed it by the caudal fin and either lost it or let it go. Sailfish and swordfish may stab makos with their beaks, presumably in self-defence; one adult female South African mako was found with a beak of a small sailfish sticking out of one eye. Makos caught in the KwaZulu-Natal shark nets were mostly dead (only 6% still alive when examined), vs. 16% alive for white sharks and 33% for spotted ragged-tooth sharks (***Carcharias taurus***). This probably reflects different activity levels and oxygen requirements, with the mako (presumably with obligate ram-ventilation of its gills) having the highest levels and the more sluggish ragged-tooth (which can hover motionless) the least.

Size: Maximum about 396 cm, estimated maximum total length about 408 cm. Size at birth between 60 and 70 cm, with free-living individuals as small as 71 cm. Males adolescent at about 140 to 199 cm and maturing between 203 and 215 cm and reaching about 296 cm; females adolescent at about 233 to 286 cm, maturing at about 275 to 293 cm and reaching at least 394 cm. Females apparently mature at smaller sizes in the Southern Hemisphere than in the western North Atlantic (Mollet et al., 2000). Several length-weight equations exist for this species and include:

Stevens (1983): $W(kg) = 4.832 \times 10^{-6} \times TL(cm)^{3.10}$ (n = 80, TL = 58 to 343 cm, Australia)

Guitart (1975): $W(kg) = 1.193 \times 10^{-6} \times TL(cm)^{3.46}$ (n = 23, TL = 160 to 260 cm, Cuba)

Strasburg (1958): $\log W(lb) = -4.608 + 2.925 \times \log TL(cm)$ (Central Pacific)

Cliff, Dudley and Davis (1990): $W(kg) = 1.47 \times 10^{-5} \times PCL(cm)^{2.98}$ (n = 143, PCL = 84 to 260 cm, South Africa)

Kohler, Casey and Turner (1995): $W(kg) = 5.2432 \times 10^{-6} \times FL(cm)^{3.1407}$ (n = 2081, western North Atlantic)
where $FL(cm) = 0.9286 \times TL(cm) - 1.7101$ (n = 199)

Mollet et al. (2000): $W(kg) = 7.2999 \times TL\ (m)^{3.224}$ (n = 63, for females TL = 2.0 to 3.7 m, western North Atlantic)

and $W(kg) = 6.824 \times TL(m)^{3.137}$ (n = 64, for females TL = 2.0 to 3.4 m, Southern Hemisphere).

Interest to Fisheries and Human Impact: The shortfin mako is an important species for pelagic longline fisheries wherever it occurs, because of its relative abundance and high quality meat, but is also caught in fisheries using drifting and set gill nets, and is taken by hook-and-line. It is taken as a utilized bycatch of tuna and swordfish longline fisheries worldwide, with carcasses as well as fins being retained for market. The meat is utilized fresh, frozen, smoked and dried-salted for human consumption; the oil is extracted for vitamins; the fins used for shark-fin soup; the hides are processed into leather and the jaws and teeth are used for ornaments.

Considerable fisheries for shortfin mako exist or existed in the Mediterranean Sea, off Cuba, in the Gulf of Mexico and Caribbean, off southern California, and in the western and central Pacific. It has been estimated that the Spanish longline fleet caught about 750 t/y of shortfin makos in the Atlantic Ocean and Mediterranean Sea in the early 1990s (Bonfil, 1994). Off California, early juvenile shortfin makos were targeted by a short-lived experimental drift longline fishery and are a very welcomed bycatch in the driftnet fishery for swordfish (Cailliet et al., 1993). Up to 475 t of shortfin makos were taken jointly by these fisheries in 1987, and although CPUE did not show a declining trend concerns over the heavy exploitation of immature fish prompted the closure of the experimental longline fishery in 1992 (O'Brien and Sunada, 1994). The total bycatch of shortfin makos in the former high-seas driftnet fisheries in the North Pacific in the early 1990s was estimated at about 360 t/y (Bonfil, 1994). This species is apparently very common in the tuna fisheries of Indonesia: unconfirmed reports indicate that landings of shortfin makos from Indonesian waters attained 5 200 t in 1995 and that the estimated potential is about 16 000 t/y (Priyono, 1998). The Brazilian longlining fleet based in Santos landed between 13.3 and 138.3 t of shortfin makos annually between 1971 and 1990 (Costa et al., 1996). Despite increasing fishing effort during this period, the CPUE of shortfin makos has remained relatively stable with an initial slight decreasing trend followed by a slight increasing trend.

Despite the role of shortfin makos in worldwide pelagic fisheries, catches are currently poorly reported to FAO at least. Brazil, New Zealand and the United States reported very small catches (2 to 76 t) to FAO from 1987 to 1997 (FAO FishStat Plus database, 2000).

Big-game sports angling for mako sharks is widespread, with New Zealand and South Africa being traditional places for offshore sports fishing for makos with heavy gear. The International Game Fish Association lists the shortfin mako as a record game fish. In the 1980s mako angling became popular in the USA off southern California, with numerous anglers involved and mako tournaments rivalling competitive angling for marlin.

Makos rarely bite divers and swimmers and few biting incidents are reliably reported. This suggests that the mako is not normally inclined to bite people without an exciting stimulus or provocation and does not normally eat marine mammalian prey (except perhaps large females preying on small pelagic dolphins), however it should be treated with respect. The mostly offshore habitat of this species probably prevents it from coming in contact with recreational swimmers except under exceptional circumstances such as places where makos visit the vicinity of beaches with a narrow continental shelf. Its speed, power, large teeth, and boldness when a feeding stimulus is present should be cause for divers, especially spearfishers, to treat the mako with caution and observe what it is doing if it approaches. Divers should not dispute it for possession of a shot fish and should back off if it is directing *gapes* their way, swimming in *figure-8s*, or giving bluff-*charges*. The shortfin mako tends to respond vigorously when hooked or harassed, and it should not be speared or otherwise provoked underwater. A defensive response by this animate torpedo when provoked may be far too quick for directed anti-shark weapons such as powerheads or repellent squirters to be effective. Steel-mesh armour suits were penetrated by the powerful jaws and teeth of these sharks in tests. Electronic shark repellent devices worn by divers may be effective in thwarting oral contact by these sharks but may not be needed if the shark's activities are correctly gauged.

Makos occasionally bite boats, and mako boat incidents are second in number only to those involving the white shark. Most of these incidents have occurred while makos were being played by anglers and should be regarded as human-provoked and abnormal. The angling and popular literature is rife with 'mako stories', in which these sharks bite, jump into, or even smash right through the boats of their assailants. Anglers who suddenly find themselves sharing a boat with an aroused and vigorous mako have been known to leap into the water!

Makos have become the subject of ecotouristic diving in recent years, with most of the mako dive sites being off southern California from the Los Angeles Basin to San Diego, but with sites also in South Africa and the Maldives. The sight of this sleek, beautiful, graceful shark underwater may be one of the high points for the shark-watching diver. The writer does not know offhand of any attempts to display shortfin makos in public oceanaria, but small makos have been kept for physiological research in hydrodynamic tunnels at Scripps Institution of Oceanography in southern California (United States).

The conservation status of the shortfin mako is of moderate concern despite its relative abundance and vast distribution. It has been preliminarily assessed as a *Lower Risk/Near Threatened* species by the IUCN Shark Specialist Group. The shortfin mako was found to have a midrange intrinsic rebound potential (a measure of its ability to recover from exploitation) among 26 shark species analysed (Smith, Au and Show, 1998). Fisheries are regulated and limited in the United States and New Zealand, but not elsewhere where intensive epipelagic longline fisheries can have a major impact on it. Obviously international and regional management is needed to maintain sustainable catches. It is not known what the effects of the former pelagic gill net fishery for scombroids was on makos and other oceanic sharks. Declines in landings have been recorded off the United States (east and west coasts) and in the eastern Atlantic by the Azorean 'marrajo' fleet, but trends are little known elsewhere. Castro, Woodley and Brudek (1999) suggest that although it is very difficult to assess the conservation status of this shark because it is caught in numerous fisheries worldwide, it is reasonable to assume that decreases are occurring in those areas for which there is limited data or none whatsoever.

Local Names: Mako (original Maori name for this species, New Zealand); Shortfinned mako shark, Mako shark, Mako, Atlantic mako shark, Pacific mako shark, Pacific bonito shark, Pacific mako, Mackerel shark, Blue shark, Sharp nosed, Sharpnosed or Sharp-nosed mackerel shark, Mackerel porbeagle, Mediterranean mackerel shark (English); Ossirina dello spallanzani, Meanto, Pisci tunnu, Piscicani, Cani di mari, Cane di mare di Messina, Cagnia (Italy); Psina cavlozuba, Psina dugonoska (Adriatic); Anequin (Portugal); Marracho, Rinquim, Mako, Shortfin mako, Marrajo criollo (Azores); Sobraig, Sobratg, Ludia marraco, Marraquet, Marrajo, Tiburón (Spain); Alecrín (Mexico); Dentudo, Dientuso azul (Cuba); Ganumu sorrah (India, Tamil); Blue pointer, Mako shark, Snapper shark (Australia); Porpoise shark, Blue porpoise shark, Sharpnose mako, Mambone, Moro (South Africa); Aozame, Morozame, Awozame (Japan); Bonito shark (California); Anequin barbatana curta (Mozambique).

Remarks: Moreno and Morón (1992b) give detailed descriptions of the coloration of typical ***I. oxyrinchus*** and the Azores 'marrajo criollo' mako, which was long recognized by Azores fishermen as a separate form as distinguished from typical ***I. oxyrinchus*** or marrajo, and marrajo negro or ***I. paucus***. Apparently Cuban and Japanese fishermen recognized the longfin and shortfin makos as being distinct long before scientists were aware of their existence.

Literature: Garman (1913); Barnard (1925); Fowler (1936, 1941); Whitley (1940); Bigelow and Schroeder (1948); Smith (1949, 1957d); Strasburg (1958); Farquhar (1963); Stead (1963); Garrick and Schultz (1963); Randall (1963); Applegate (1966, 1977); Guitart (1966, 1975); Garrick (1967); Carey and Teal (1969); Lineaweaver and Backus (1970); Mundus and Wisner (1971); Carey et al. (1972); Gubanov (1974, 1978); Bass, D'Aubrey and Kistnasamy (1975a); Ellis (1976); Penrith (1978); Glikman and Dolganov (1980); Cadenat and Blache (1981); Stillwell and Kohler (1982); Cadenat and Blache (1981); Carey (1982, 1990); Pratt and Casey (1983); Gilmore (1983); Stevens (1983, 1984, 1990, 1992); Cailliet and Bedford (1983); Compagno (1984, 1990a, b); Nakaya (1984); Block and Carey (1985); Compagno, Ebert and Smale (1989); Quero (1984); Paulin et al. (1989); Springer (1990); Fischer et al. (1990); Cliff, Dudley and Davis (1990); Stillwell (1990); Compagno, Ebert and Cowley (1991); Casey and Kohler (1992); Moreno and Morón (1992b); Holts and Bedford (1992); Anderson and Ahmed (1993); Cailliet, Holts and Bedford (1993); Francis and Randall (1993); Michael (1993); Bonfil (1994);

Last and Stevens (1994); Seret (1994); Costa et al. (1996); Priyono (1998); Smith, Au and Show (1998); Castro, Woodley and Brudek (1999); Mollet et al. (2000); H. Mollet (pers. comm.).

Isurus paucus Guitart, 1966

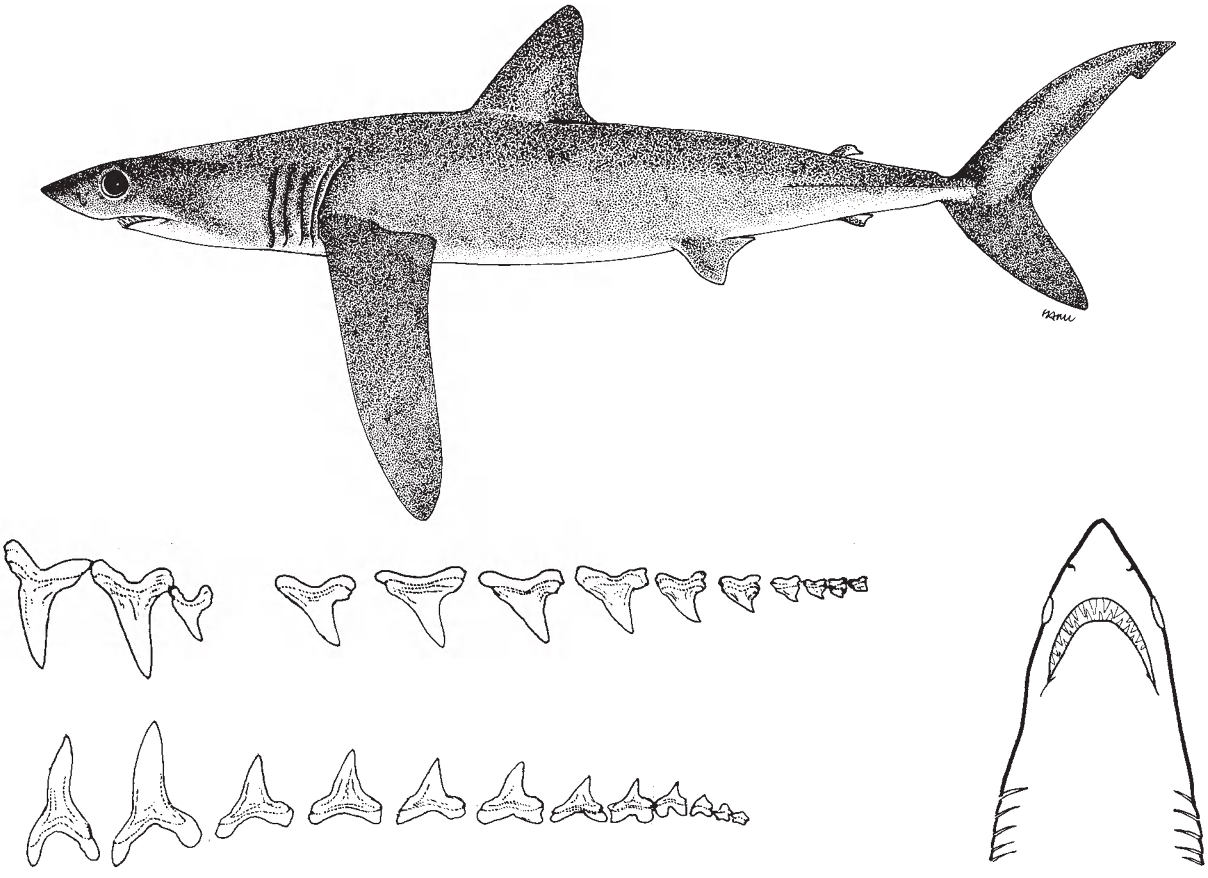
Fig. 75

Isurus paucus Guitart, 1966, *Poeyana*, Ser. A, (15): 3, figs. 1, 2A, 3A, 3C. Syntypes: 2 260 mm PCL adult female, 2 030 mm PCL adult male, and 1 955 mm PCL adult female, possibly in the Instituto de Biología or Instituto de Oceanología, Cuba, collected in the Caribbean near Cuba. No types known according to Eschmeyer (1998: CD-ROM).

Synonyms: ?***Lamiostoma belyaevi*** Glikman, 1964: 105. Syntypes: a set of fossil tooth crowns from the bottom of the West-Central Pacific at 5 120 m depth, 13°00′ N, 176°04′ E. Syntypes doubtfully referred to the living species (see remarks below). ***Isurus alatus*** Garrick, 1967: 677. Holotype: US National Museum of Natural History, USNM-197427, 1 233 mm TL immature male, Indo-Pacific, no precise locality. Status confirmed by Howe and Springer (1993: 3).

Other Combinations: None.

FAO Names: En - Longfin mako; **Fr** - Petit taupe; **Sp** - Marrajo carite.



UPPER AND LOWER TEETH ON LEFT SIDE

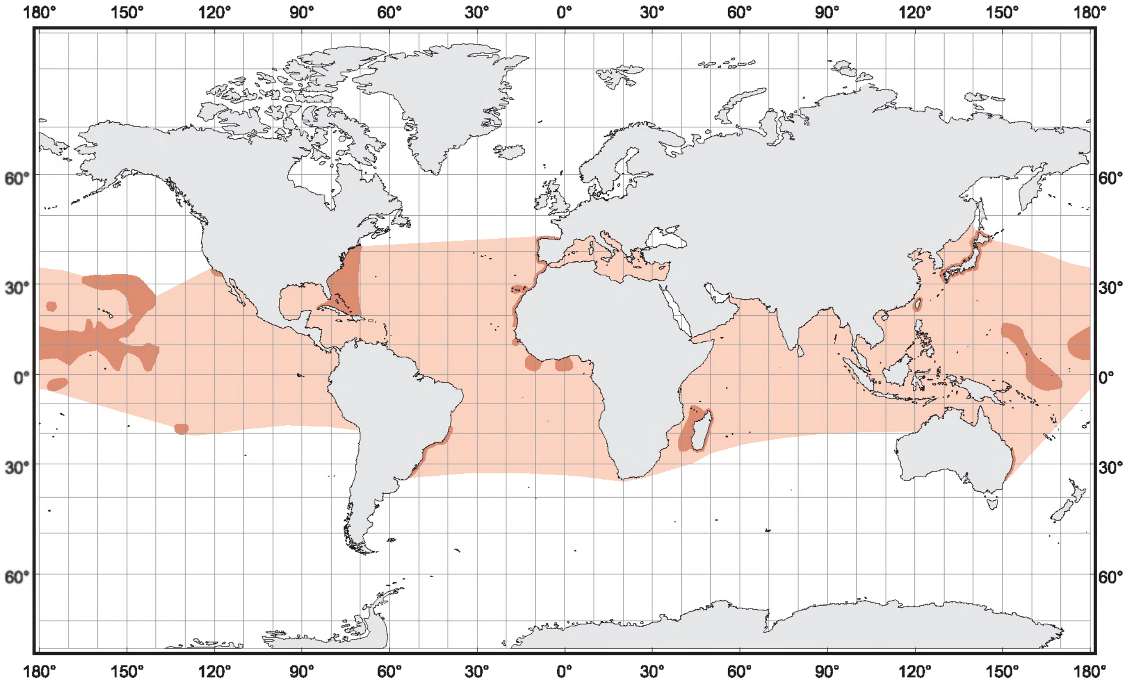
UNDERSIDE OF HEAD

Fig. 75 *Isurus paucus*

Field Marks: Slender, spindle-shaped body, moderately long conical snout, large blade-like teeth without lateral cusplets or serrations, long gill slits, pectoral fins broad-tipped and as long or longer than head, large first dorsal fin with light free rear tip, minute, pivoting second dorsal and anal fins, strong keels on caudal peduncle, short secondary keels on caudal base, crescentic caudal fin, ventral surface of body dusky on underside of head.

Diagnostic Features: Snout broadly pointed. Eyes relatively large. Mouth parabolic in shape. Lower anterior teeth slightly protruding from jaws and in line with the laterals; anterior teeth with relatively broad, nearly straight cusps with unflexed tips; cusps of first upper anterior teeth with complete cutting edges; intermediate teeth with nearly straight or slightly hooked cusps. Body slender and elongated. Pectoral fins nearly straight and very broad-tipped, anterior margins about 23 to 31% of total length and equal to or greater than head length. Origin of first dorsal fin well behind the pectoral free rear tip; first dorsal-fin apex broadly rounded and hardly angular at all stages; first dorsal-fin height greater than base length at all stages (smaller in term foetuses). Vertebral total count 195 to 197. **Colour:** dorsolateral coloration dark slaty blue or grey-black in life, underside white but with underside of snout and jaws dark in adults and large juveniles though not in young; dark colour of head entirely covering gill septa; dark colour of flanks extending ventrally onto abdomen in adults; pelvic fin completely dark, underside white with prominent dark margin; first dorsal fin as dark as back; anal fin dark except for white free rear tip and posterior margin.

Distribution: Oceanic and tropical, probably circumtropical but records sporadic and distribution sketchily known, probably often mistaken for the apparently far more common ***Isurus oxyrinchus*** or included with records for it. Western Atlantic: Florida, Gulf Stream off eastern USA, Cuba, southern Brazil. Eastern Atlantic: Spain, Portugal, probably Mediterranean, Morocco, Western Sahara, Canary Islands, Mauritania, Guinea-Bissau, Liberia, Ghana, ?Cape Verde Islands. Western Indian Ocean: ? South Africa, Madagascar. Western Pacific: Japan, Taiwan (Province of China), Australia (Queensland and northern New South Wales, also possibly off northern Australia). Central Pacific: Northeast of Micronesia, between Solomon and Nauru Islands, area south of Johnston and Hawaiian Islands, near Phoenix Island, and north of Hawaiian Islands. Eastern Pacific: United States (southern California).



Habitat: A little-known epipelagic, tropical and warm-temperate shark, apparently common in the western Atlantic and possibly in the Central Pacific, but rare elsewhere. Said to be deep-dwelling but bathymetric data was not available.

Biology: The biology of the longfin mako is poorly known. In the eastern Atlantic this species is possibly rare compared to ***I. oxyrinchus***, and landings of longfin mako in Spanish fishing ports sampled by Moreno and Morón (1992) included only 51 specimens compared with 45 679 shortfin mako (0.1%). The often slimmer build and broad, long pectoral fins of this shark suggest that it is slower and less active than its better-known relative, the shortfin mako (J. Casey, pers. comm.). Its macroceanic morphology suggests similar slow cruising in the epipelagic zone as in the oceanic whitetip (***Carcharhinus longimanus***) and the blue shark (***Prionace glauca***) rather than the more active, scombroid-like swimming of ***Isurus oxyrinchus***. The longfin mako is apparently endothermic, with countercurrent vascular heat exchangers for its body musculature, eyes, brain and viscera as in other lamnids (Carey, 1982), but the levels of temperature elevation it can achieve above ambient conditions have apparently not been measured.

The longfin mako is ovoviviparous, with uterine cannibalism; foetuses are larger than those of ***I. oxyrinchus***, are full-term at 92 to 120 cm, and occur as a litter of 2 to 8 young. It may approach land to give birth.

Food of this shark is presumably schooling fish and pelagic cephalopods. Michael (1993) noted that one was found with a swordfish sword stuck in its abdomen, though it is not known if swordfish are an important item of this mako's diet as with the shortfin mako.

Size: Maximum reported 417 cm; size at birth between 97 and 120 cm; a male (Central Pacific) was adult at 245 cm; adult females (western North Atlantic) were 245 to 417 cm long.

Interest to Fisheries and Human Impact: Probably taken regularly in tropical pelagic longline fisheries for tuna and swordfish as bycatch (with some marketed in Tokyo). Historically it was often taken in the Cuban longline fishery for sharks off the north coast of Cuba and averaged about a sixth of the total weight of sharks caught there in 1971-1972. Whether it is still as common there at present is unknown. It is utilized fresh, frozen and dried-salted for human consumption but the meat is of lower quality than the shortfin mako and it is often finned and discarded at sea. In addition to longlines, the species is taken with hook-and-line and with anchored gill nets.

This species has not bitten people or boats and has not, to the writer's knowledge, been observed underwater or kept in captivity.

The conservation status of this species is uncertain but needs urgent investigation. It has probably been captured as bycatch in oceanic fisheries wherever it occurs and is a minor bycatch of fisheries targeting shortfin makos in the eastern Atlantic. No trends are obvious for the species as there are no catch statistics for it except off Cuba and the United States and these are not long-term. The United States reported small catches (2 to 12 t in 1987 to 1997) to FAO (FAO FishStat Plus database, 2000). Problems for the longfin mako include the rarity or uncommonness of this shark in most places (except perhaps the western Atlantic in the 1970s at least); limited knowledge of its biology; large maximum size; apparently lower fecundity than the shortfin mako; and occurrence as a limited but complementary bycatch of high-intensity oceanic fisheries targeting shortfin makos, other sharks, and pelagic scombroid fishes. These problems should arouse the concern of conservation and fisheries organizations, because of increased mortality of an uncommon or rare species due to finning and possibly capture trauma.

Local Names: Longfinned mako shark, Taupe longue aile (France); Dientuso prieto (Cuba); Marrajo negro (Azores); Bake-aozame (Japan).

Remarks: Garrick (1967), Compagno and Vergara (1978), and Compagno (1981a) thought that the species ***Lamiostoma belyaevi*** Glikman, 1964 might prove to be an earlier name for ***I. paucus***, particularly because a stuffed ***Isurus*** illustrated in a photograph in Glikman (1964, figs 31-32) and labelled ***L. belyaevi*** appeared to be a longfin mako. This may be irrelevant even if correct. A translation of Glikman's description of ***L. belyaevi*** (pp. 105, 132-133) by Mrs L.J. Dempster with the aid of Dr V.V. Barsukov (noted in Compagno, 1984) revealed that Glikman deliberately refrained from naming the stuffed ***Isurus*** as holotype of ***L. belyaevi*** but instead picked one lot of teeth crowns dredged from the ocean bottom 5 120 m deep at *RV VITYAZ* station 5128, 13°00′ N, 176°04′E in the Central Pacific southwest of the Hawaiian Islands (Glikman, 1964, pl. 31, figs 13, 14, 18, 19) for this role. Examination of Glikman's photos did not convince Compagno (1984) that the shark or sharks represented by these teeth were necessarily conspecific with ***I. paucus*** and were not conspecific with ***I. oxyrinchus*** or even some extinct ***Isurus*** species. Hence the substitution of the species name ***belyaevi*** for ***paucus*** was rejected, especially because the former is based on such poor material. It is uncertain if the stuffed specimen illustrated by Glikman is ***I. paucus*** also, because some of the characters ascribed to it (snout very long and acute, pectoral fins falcate, and pectoral fin length slightly less than the distance from snout tip to upper margin of first gill opening, vs. snout short and bluntly conical, pectoral fins not strongly falcate, and pectoral-fin length much longer than the distance from snout tip to upper margin of first gill opening in ***I. paucus***) indicate that it might be a specimen of ***I. oxyrinchus*** instead.

Literature: Glikman (1964); Guitart (1966, 1968, 1975); Garrick (1967); Bass, D'Aubrey and Kistnasamy (1975a); Fourmanoir and Laboute (1978); Dodrill and Gilmore (1979); Gilmore (1983, 1993); Pinchuk (1983); Compagno (1984); Nakaya (1984); Quero (1984); Sadowsky, Amorim and Arfelli (1986); Killam and Parsons (1986); Joung, Wu and Chen (1989); Springer (1990); Moreno and Morón (1992); Michael (1993); Seret (1994); Stevens and Scott (1995); Stevens and Wayte (1998); Castro, Woodley and Brudek. (1999); Mollet et al. (2000); R. Bonfil (pers. comm.); H. Mollet (pers. comm.); D. Ebert (pers. comm. on California record).

Lamna Cuvier, 1816

Genus: Subgenus ***Lamna*** Cuvier, 1816 (Genus ***Squalus*** Linnaeus, 1758), *Reg. Anim.*, ed. 1, 2: 126.

Type Species: ***Squalus cornubicus*** Bloch and Schneider, 1801 by monotypy, equals ***S. cornubicus*** Gmelin, 1788: 1497, and a junior synonym of ***S. nasus*** Bonnaterre, 1788.

Number of Recognized Species: 2.

Synonyms: Genus ***Lamia*** Risso, 1827: 123. Type species, "***L. cornubicus*** L" = ***Squalus cornubicus*** Gmelin, 1788 by monotypy. A junior homonym of ***Lamia*** Fabricius, 1775 in Coeloptera (Insecta). Genus ***Selanonius*** Fleming, 1828: 169. Type species, ***Selanonius walkeri*** Fleming, 1828 by monotypy (Eschmeyer, 1998: CD-ROM), junior synonym of ***Squalus nasus*** Bonnaterre, 1788. Genus ***Exoles*** Gistel, 1848: ix. Replacement name for ***Lamia*** Risso, 1827, and hence taking the same type species, ***Squalus cornubicus*** Gmelin, 1788.

Diagnostic Features: Snout very bluntly conical to acutely conical. Eyes large, 1.6 to 2.8% of total length. Nostrils situated medial to horizontal head rim in ventral view. Mouth width 1.4 to 2.3 times its length. Anterior teeth not enlarged; anterior and intermediate teeth not compressed but upper lateral teeth somewhat compressed, teeth not forming a continuous cutting edge; intermediate teeth small and about half height of adjacent anteriors, intermediate teeth with normal cusps directed posterodistally or vertically; second lower anterior teeth moderately enlarged and taller than second upper anterior tooth. Total tooth count 49 to 60; roots of anterior teeth deeply arched, with narrow short lobes; lateral cusplets present on teeth at all stages except newborn sharks; teeth smooth-edged; cusps of anterior teeth not strongly flexed. Body very stout. First dorsal-fin origin over or just behind the pectoral-fin insertions. Anal-fin origin about under second dorsal-fin origin.

Secondary caudal keels present and strong. Total vertebral count 150 to 173. Cranium with rostral cartilages more or less expanded and hypercalcified. Intestinal valve of ring type with count 38 to 41. Length of adults 1.5 to at least 3.1 m. No black axillary spot at pectoral-fin insertions; pectoral-fin tips not abruptly black on their ventral surfaces but sometimes with dark margins.

Local Names: Porbeagles, Mackerel sharks, Salmon sharks.

Remarks: As with the makos (***Isurus***) there has been confusion in the past as to the number of valid species of mackerel sharks (***Lamna***). Material examined by the writer and the accounts of Bigelow and Schroeder (1948), Nakaya (1971), Stevens, Dunning and Machira (1983), and Compagno (1984, 1990b, c), suggest that there are only two species, ***L. ditropis*** and ***L. nasus***, with ***L. philippi*** from Chile and ***L. whitleyi*** from New Zealand and Australia most probably being synonyms of ***L. nasus***. ***Lamna ditropis*** was compared in detail to ***L. nasus*** by Nakaya (1971) and the two are readily separable in external morphology and coloration. Nakaya (1971) also noted differences between the dentitions of the two species, with ***L. ditropis*** having more oblique-cusped upper first lateral teeth. This needs to be confirmed by a comprehensive study of the dentition of ***Lamna*** from different areas, as some Southern Hemisphere ***L. nasus*** have upper first lateral teeth about as oblique-cusped as ***L. ditropis.*** Compagno (1984 and this volume) noted differences in the colour of the first dorsal rear tip and the flanks between the two species (see below), while Compagno (1990b) described and illustrated striking differences in their cranial morphology.

Pillai and Honma (1978) reported ***L. ditropis*** from the southern Indian Ocean without data confirming their identification. Compagno (1984) suggested that the species in question was ***L. nasus***, and had examined a specimen from the southern Indian Ocean (open sea between Kerguelen and St. Paul Islands, *ANTON BRUUN* Cruise 5, Sta. 309, 960 mm immature female, 42°23'S, 74°56'E, in collections of the California Academy of Sciences). There are also records from near Kerguelen Island (Duhamel and Ozouf-Costaz, 1982). Records of ***L. nasus*** from sub-Antarctic seas were summarized by Duhamel and Compagno (1985) and Compagno (1990c).

A few specimens of large ***L. nasus*** (1.6 to 2.1 m long) have subsequently been examined by the writer from the Southern Hemisphere, off the Western Cape, South Africa, off Marion Island, and between the Prince Edward and Crozet Islands. These specimens agreed with ***L. nasus*** from the North Atlantic in having more elongated snouts, moderately hypercalcified rostra, no light flank markings, and a light first dorsal rear tip, but agree with ***L. ditropis*** in having dusky or blackish faces with dark coloration on the underside of the head and a spotted, dusky abdomen. Stevens, Dunning and Machira (1983) illustrated a similar colour pattern in a porbeagle from the Tasman Sea. These 'black-faced' porbeagles resemble the 'marrajo criollo' makos from the Azores (***Isurus oxyrinchus***), which have a colour pattern similar to ***I. paucus*** (see above). It may be that black-faced ***Lamna nasus*** have been misidentified as ***L. ditropis*** in the Southern Hemisphere, but it is not known if large southern ***L. nasus*** are exclusively dark-faced, or if this dark form is geographically restricted within the vast southern range of the porbeagle. Apparently it is necessary to conduct comparative studies of porbeagles from different areas, including molecular research, to sort out these problems. One aspect of this is to determine if separate populations or subpopulations exist for ***L. nasus***, within contiguous ranges and north or south of the Equator.

It is an interesting irony of nomenclature that the names ***Lamna*** Cuvier, 1816 and its synonym ***Lamia*** Risso, 1827, based on the classical ***Lamia*** (***Carcharodon carcharias***) and connoting a frightful anthropophagous monster, should be used for the rather less assertive porbeagles and salmon sharks.

Key to Species:

1a. Snout relatively long, distance from snout tip to eye 50% or more of the distance from eye to first gill opening (Fig. 76); free rear tip of first dorsal fin abruptly white; sides above pectoral-fin bases dark, without an extension of the white abdominal area . . . . ***Lamna nasus***

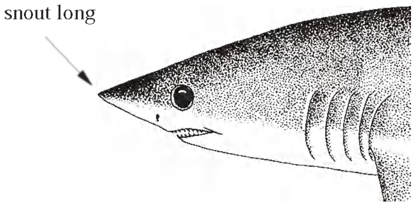


Fig. 76 *Lamna nasus*

1b. Snout shorter, distance from snout tip to eye 40% or less of the distance from eye to first gill opening (Fig. 77); free rear tip of first dorsal fin dark; sides above pectoral-fin bases marked with a white patch extending forward from the abdominal area . . . . ***Lamna ditropis***

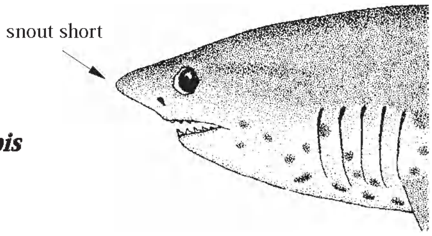


Fig. 77 *Lamna ditropis*

Lamna ditropis Hubbs and Follett, 1947

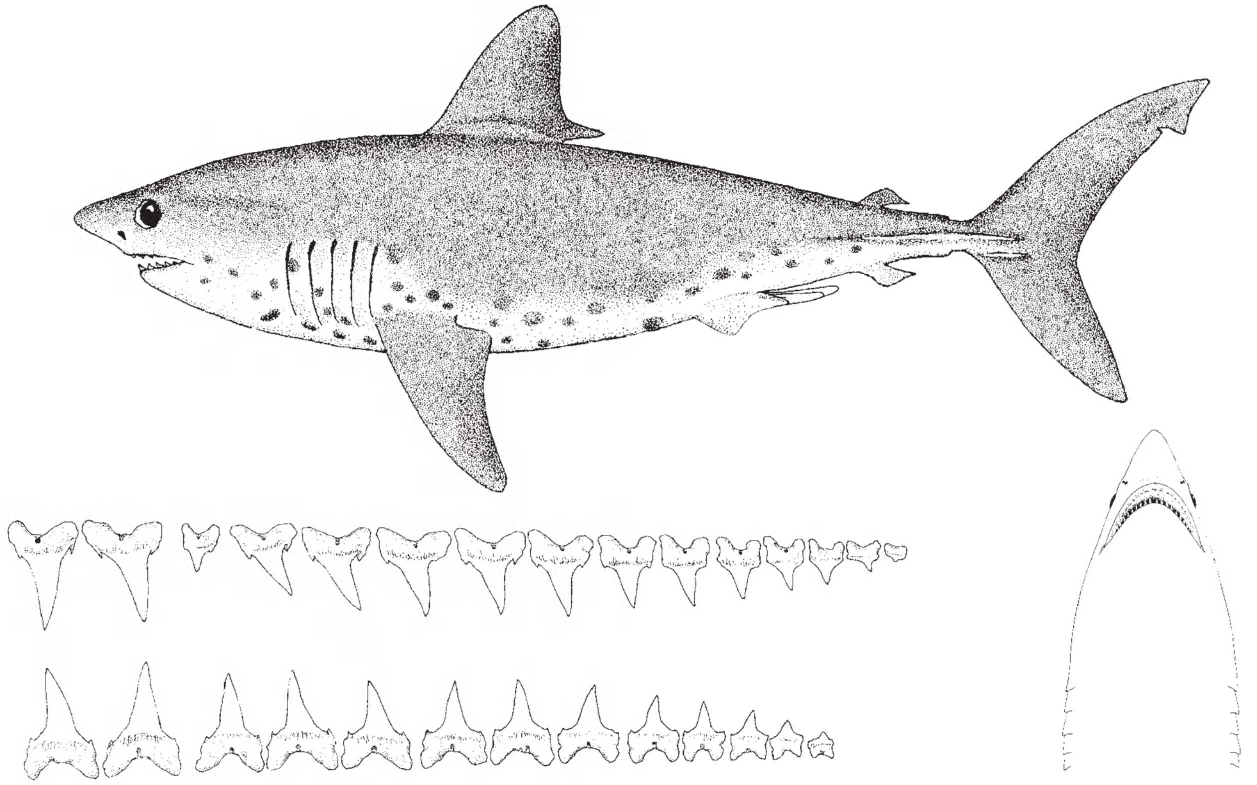
Fig. 78

Lamna ditropis Hubbs and Follett, 1947, *Copeia*, 1947(3): 194. Holotype, Museum of Comparative Zoology, Harvard University, MCZ-36471, adult male (partial specimen, size uncertain); type locality, La Jolla, California, 92 to 107 m off the La Jolla Beach Club in shallow water.

Synonyms: None.

Other Combinations: None.

FAO Names: En - Salmon shark; **Fr** - Requin-taupe saumon; **Sp** - Marrajo salmón.



UPPER AND LOWER TEETH ON RIGHT SIDE, LINGUAL VIEW

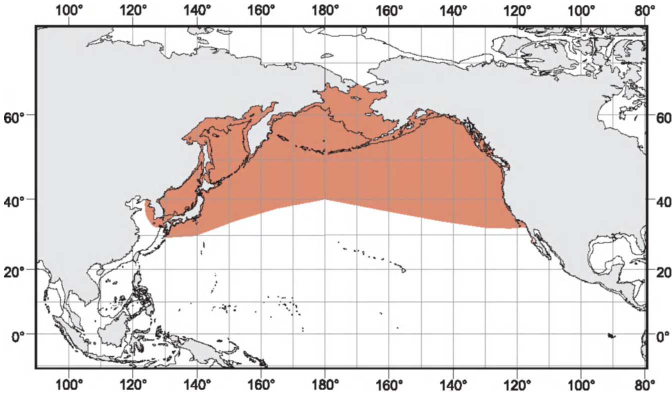
UNDERSIDE OF HEAD

Fig. 78 *Lamna ditropis*

Field Marks: Heavy spindle-shaped body, short conical snout, moderately large blade-like teeth with lateral cusplets, long gill slits, large first dorsal fin with dark free rear tip, minute, pivoting second dorsal and anal fins, strong keels on caudal peduncle, short secondary keels on caudal base, crescentic caudal fin, underside of preoral snout dark, often dusky blotches on ventral surface of body and white patches over pectoral bases.

Diagnostic Features: Snout short and bluntly pointed, with preoral length 4.5 to 7.6% of total length (adults 4.5 to 5.0%), space from eye to first gill slit 1.3 to 1.9 times preorbital length. First upper lateral teeth with oblique cusps. Total vertebral count 170, precaudal vertebral count 103. Cranial rostrum expanded as a huge hypercalcified knob which engulfs most of the rostral cartilages except bases in adults. **Colour**: dark grey or blackish on dorsolateral surface of body, white below, with white abdominal colour extending anteriorly over pectoral bases as a broad wedge-shaped band; first dorsal fin without a white free rear tip; ventral surface of head dusky and abdomen with dusky blotches in adults but not in young.

Distribution: Coastal and oceanic. North Pacific: Japan (including Sea of Japan), North Korea, South Korea, and the Pacific coast of Russia (including Sea of Okhotsk) to Bering Sea and the eastern Pacific coast of the USA and Canada (Alaska south to British Columbia, Washington, Oregon, and southern California) and probably Mexico (northern Baja California).



Habitat: A common coastal-littoral, offshore and epipelagic shark with a preference for boreal to cool temperate waters, found at depths from the surface to below 152 m. One was photographed at 255 m near the bottom in Monterey Canyon using an underwater camera, while a diver in a submersible saw one at 224 m off Alaska. Salmon sharks are common in continental offshore waters but range inshore to just off beaches; they also are abundant far from land in the North Pacific Ocean basin, along with their pelagic fish prey.

Biology: Salmon sharks are common and are often encountered by oceanic and coastal fisheries but are sketchily known biologically. Behaviour and sociobiology are little-known. They occur singly and in schools or feeding aggregations of several individuals and in some areas are seen at or near the surface. Water temperatures where salmon sharks were caught ranged from 2.5° to 24°C. They are swift-swimming sharks, maintaining a body temperature well above ambient water temperature. Recent studies suggest that salmon sharks may have the highest body temperature of any shark. Body temperature elevations of 8° to 11°C above that of the surrounding water have been reported for smaller specimens, while elevations up to 13.6°C have been recorded in larger ones (Smith and Rhodes 1983; Goldman and Human, *in press*). Salmon sharks are migratory, with segregation by size and sex, and with larger sharks ranging more northerly than young. In the western North Pacific large sharks migrate from Japanese waters (where they breed) in the wintertime, move north to the Sea of Okhotsk and the western Bering Sea when the water warms, and return to Japan in the autumn or early winter (for a one-way distance of 3 220 km). In the eastern Pacific females apparently migrate south to pup in the spring off Oregon and California, USA, as suggested by commercial fish catch records, washed up (beached) young of the year and anecdotal information. A strong sexual segregation appears to exist across the Pacific Ocean basin, with males dominating the western North Pacific and females dominating the eastern North Pacific (K.J. Goldman and J. A. Musick, pers. comm.).

This shark reproduces by aplacental viviparity, with uterine cannibalism (oophagy); litter size is 2 to 5 young. Length of gestation period might be nine months; length of entire reproductive cycle unknown. Breeding occurs in late summer and into autumn, and females bear young in spring. Breeding and nursery areas may be localized in the offshore western North Pacific between about 156° and 180°E in the open ocean, off the southern Kuril region, and in the Sea of Okhotsk, where young below 60 cm (possibly newborn) occur and juveniles up to 110 to 120 cm long also are found. Age 0 and 1 salmon sharks occur off California, USA, suggesting that a breeding and nursery ground might exist in the eastern North Pacific (K.J. Goldman and J.A. Musick, pers. comm.). Males may mature at 5 years and about 182 cm TL, and females at 8 to 10 years and about 221 cm TL (Tanaka, 1980). Females in the eastern North Pacific live to at least 20 years of age, males to at least 27 years; preliminary indications are that female salmon sharks mature at an earlier age and are heavier in the eastern North Pacific relative to those living in the western North Pacific (K.J. Goldman and J.A. Musick, pers. comm.).

Salmon sharks are opportunistic feeders and eat a variety of pelagic and demersal bony fishes including Pacific salmon and steelhead trout (Salmonidae), herring and sardines (Clupeidae), pollock, Alaska cod and tomcod (Gadidae), lancetfishes (Alepisauridae), daggerteeth (Anotopteridae), sauries (Scombresocidae), lanternfishes (Myctophidae), pomfrets (Stromateidae), mackerel (***Scomber***; Scombridae), lumpfishes (Cyclopteridae), sculpins (Cottidae), possibly rockfish (***Sebastes***, Scorpaenidae), possibly sablefish (Anoplopomatidae), and Atka mackerel (***Pleurogrammus***, Hexagrammidae). Salmon sharks also feed on spiny dogfish (***Squalus acanthias***, Squalidae) and several species of pelagic squid, and have been attracted to bycatch offal dumped by shrimp trawlers.

The salmon shark is generally considered to be one of the principal predators of Pacific salmon (***Oncorhynchus***) apart from humans and is depicted as voraciously feeding on salmon. This is apparently the case around the Aleutians and the Gulf of Alaska, where peaks in abundance in salmon sharks follow maximum catches of salmon and the distribution and migrations of the two appear to be strongly correlated as predator and prey. Salmon sharks caught by Japanese pelagic salmon gill netters in this area have had salmon in their stomachs and little else. However Blagoderov (1994) suggested that this relationship is highly unlikely, and cited major differences in areal distribution between salmon and salmon sharks in the western North Pacific, with most salmon sharks concentrated south of the main migration path of salmon and very few within it. In the western North Pacific these sharks congregate in areas with breeding aggregations of herring and sardines and may be selecting these fishes rather than salmon.

Size: Maximum total length about 305 cm; anecdotal accounts mention sizes of 3.7 to 4.3 m TL but cannot be confirmed, and confusion with the larger white shark is possible and has happened. Size at birth between 40 and 50 cm and 85 cm TL, with the largest foetuses at least 70 cm long and the smallest free-ranging young between 40 and 50 cm. Males maturing at about 182 cm TL (5 years) and females at about 221 cm TL (8 to 10 years); both sexes adult over about 210 to 220 cm TL.

Interest to Fisheries and Human Impact: This species has been fished in the North Pacific in the past by Japanese coastal and oceanic longliners. Salmon sharks are commonly caught by Japanese, United States and Canadian offshore salmon gill netters as bycatch but are generally discarded (except for fins). They are also caught in salmon seines, by salmon trollers towing hooks, and possibly by bottom trawlers off Alaska; Russian research vessels have regularly caught them in pelagic trawls in the western North Pacific. They are occasionally trammel-netted by halibut fishermen off California and have showed up in numbers as bycatch in gill nets set for swordfish and threshers off California but have usually not been marketed there. Sports anglers in Alaska and Canada catch salmon sharks using rod and reel much like porbeagle anglers in the North Atlantic.

Salmon sharks are generally considered a nuisance for the damage they do to salmon nets and other fishing gear. A commercial fishery was initiated off Alaska but this did not succeed. FAO catch statistics for recent salmon shark landings were not available (FAO FishStat Plus database, 2000) but available data (Makihara, 1980) indicates that Japanese fishers landed 100 to 41 000 t during 1952-1978 (with one very high catch year, 41 000 t in 1954, but mostly below 10 000 t and averaging about 6 900 t). Bycatch of salmon sharks in the flying squid and large-mesh driftnet fisheries of the North Pacific in 1990, just before high-seas driftnets were internationally banned was estimated to be about 5 400 t and 71 t respectively.

The flesh of the salmon shark is used fresh for human consumption in Japan, where it is processed into various fish products, and to a lesser extent in Alaska and California, United States, where it is seldom marketed and has in the past (California) been occasionally sold as swordfish. Presumably its flesh is less desirable than that of the shortfin mako. Its oil, skin (for leather), and fins (for shark fin soup) are utilized also. The heart of the salmon shark is highly appreciated in a local sashimi dish in the northern fishing port of Kesennuma, where most of the landings of salmon sharks occur in Japan (R. Bonfil, pers. comm.).

The salmon shark has been regarded as potentially injurious to people because of its large size and relationship to other species that occasionally bite people, but has never been positively identified in shark-bite incidents. There are a few unsubstantiated incidents reported for the species, but possibly by confusion with the white shark. Salmon sharks are reported as occasionally circling, approaching and bumping fishing vessels and sports boats off southeastern Alaska (Paust and Smith, 1985), but their identity needs to be confirmed to eliminate white sharks as being involved in such activities. Divers have seen and photographed schools of adult salmon sharks underwater, with no agonistic overtures on the part of the sharks (R. Lea, pers. comm.). An ecotouristic dive site at Roca Partida, Socorro Islands, Mexico has reported "***Lamna nasus***", but it is not known if salmon sharks or other lamnids are being viewed there. The salmon shark is not currently held in captivity in large oceanaria, nor does the writer know of any attempts to keep salmon sharks in the past.

Recently (1997) there has been numerous strandings of small salmon sharks, ca. 1 m long, off north-central and southern California (R. Lea, pers. comm.), which was of rare occurrence in the 1970s and 1980s. Whether this has to do with human-induced environmental problems such as pollution or unusual water conditions is not known.

The conservation status of this species is of concern because it is heavily fished as largely discarded but complementary bycatch (with finning) in major pelagic fisheries in the North Pacific. Unlike ***Lamna nasus***, this species has limited fisheries statistics (with no country reporting catch statistics to FAO in 1997) and no regulation of the largely pelagic fishery in international waters, so that trends in abundance are unknown. It also has a negative image as an abundant and low-value pest that avidly eats or damages valuable salmon and wrecks gear, which encourages fishers to kill it and add to mortality from finning and capture trauma. Knowledge of its biology is limited despite its abundance, which invites neglect, but its fecundity is very low and probably cannot sustain current fishing pressure for extended periods.

The Alaska Board of Fisheries has closed all commercial shark fishing and has heavily regulated the sport fishery in Alaska state waters since 1997 in view of the lack of biological information at a time when there was a small amount of commercial fishing and a large increased interest in sport fishing for salmon sharks (Goldman and Human, *in press*). The North Pacific Fishery Management Council is currently considering closure of commercial fishing for sharks in Federal waters as no Federal Management plan exists specifically for sharks in the Gulf of Alaska and the Aleutian Islands. Currently, salmon sharks are allowed as bycatch, and are included in the commercial bycatch TAC (Total Allowable Catch) for Alaska Federal waters. Sport fishing regulations in Alaska include EEZ waters and are two sharks per person per year, one in possession at any time (one per day).

Local Names: Nezumizame, Mokazame, Radukazame, Sakezame, Japanese mackerel shark (Japan); Salmon shark, Porbeagle, Mackerel shark (English).

Literature: Hubbs and Follett (1947); Bigelow and Schroeder (1948); Roedel and Ripley (1950); Strasburg (1958); Lindberg and Legeza (1959); Sano (1962); Farquhar (1963); Larkins (1964); Kato, Springer and Wagner (1967); Nakaya (1971, 1984); Miller and Lea (1972); Hart (1973); Makihara (1980); Tanaka (1980); Urquhart (1981); Smith and Rhodes (1983); Compagno (1984); Paust and Smith (1986); Paust (1987); Brodeur (1988); Applegate et al. (1989); Hanan, Holts and Coan (1993); Blagoderov (1994); Bonfil (1994); Nagasawa (1998); Castro, Woodley and Brudek (1999); Goldman and Human, (in press); K.G. Goldman and J. A. Musick (pers. comm.); S. Kato (pers. comm.); R. Lea (pers. comm.); T. Neal (pers. comm.); H. Mollet, (pers. comm.).

Lamna nasus **(Bonnaterre, 1788)**

Fig. 79

Squalus nasus Bonnaterre, 1788, *Tabl. Encyclop. Method. Trois Reg. Nat., Ichthyol., Paris*: 10, pl. 85, fig. 350. Holotype unknown, type locality probably Cornwall, England (Eschmeyer, 1998: *Cat. Fish.*: CD-ROM).

Synonyms: ***Squalus glaucus*** Gunnerus, 1768: 1, pl. 1. Type locality, Norway. A junior homonym of ***S. glaucus*** Linnaeus, 1758 (= ***Prionace glauca***). ***Squalus cornubicus*** Gmelin, 1788: 1497. No types known according to Eschmeyer (1998: CD-ROM). Type locality: Cornwall, England. ***Squalus pennanti*** Walbaum, 1792: 517. Type locality: Atlantic. No types according to Eschmeyer (1998: CD-ROM). ***Squalus monensis*** Shaw, 1804: 350. Based on the 'Beaumaris Shark' of

Pennant, a 2.33 m (7 ft) shark observed and reported by the Rev. Hugh Davies, of Beaumaris, Isle of Anglesey, Wales. No types known according to Eschmeyer (1998: CD-ROM). Shaw thought that his ***S. monensis*** might be the same as ***Squalus cornubicus*** Gmelin, 1788 (= ***Lamna nasus***), and that differences between them might be attributable to sexual dimorphism. ***Squalus cornubiensis*** Pennant, 1812: 152. Type locality: Cornwall. Variant spelling of ***S. cornubicus*** Gmelin, 1788 according to Eschmeyer (1998: CD-ROM). ***Squalus selanonus*** Leach, 1818: 64, pl. 2, fig. 2. Holotype: University of Edinburgh, ca. 2.6 m TL adult male, Lochfyne, Scotland (also, Eschmeyer, 1998: CD-ROM). ***Selanonius walkeri*** Fleming, 1828: 169. Argyll, Scotland. Based on ***Squalus selanonus*** of Walker, 1769 (manuscript name) according to Eschmeyer (1998: CD-ROM). ***Lamna punctata*** Storer, 1839: 185, pl. 3, fig. 2. Also Storer, 1839: 534, pl. 8. New combination for and misinterpretation of ***Squalus punctatus*** Mitchill, 1815 (= ***Carcharhinus isodon***), itself a junior homonym of ***S. punctatus*** Bloch and Schneider, 1801(= ***Ginglymostoma cirratum***). Type locality: Massachusetts Bay; cf. Eschmeyer (1998: CD-ROM). ***Lamna pennanti*** Desvaux, 1851: 23. Possibly new combination based on ***Squalus pennanti*** Walbaum, 1792. ***Oxyrhina daekayi*** Gill, 1862a: 60. New name for ***Lamna punctata*** Storer, 1839 according to Eschmeyer (1998: CD-ROM). ***Isuropsis dekayi*** Gill, 1873: 813 (emended spelling of specific name). ***Lamna philippi*** Perez Canto, 1886: 1. Type locality, Chile. Types? ***Lamna whitleyi*** Phillipps, 1935: 239, fig. 3. Syntypes: Whereabouts unknown according to Eschmeyer (1998: CD-ROM). Type Locality, Island Bay, Wellington, New Zealand.

Other Combinations: ***Lamna cornubica*** (Gmelin, 1788).

FAO Names: En - Porbeagle; **Fr** - Requin-taupe commun; **Sp** - Marrajo sardinero.

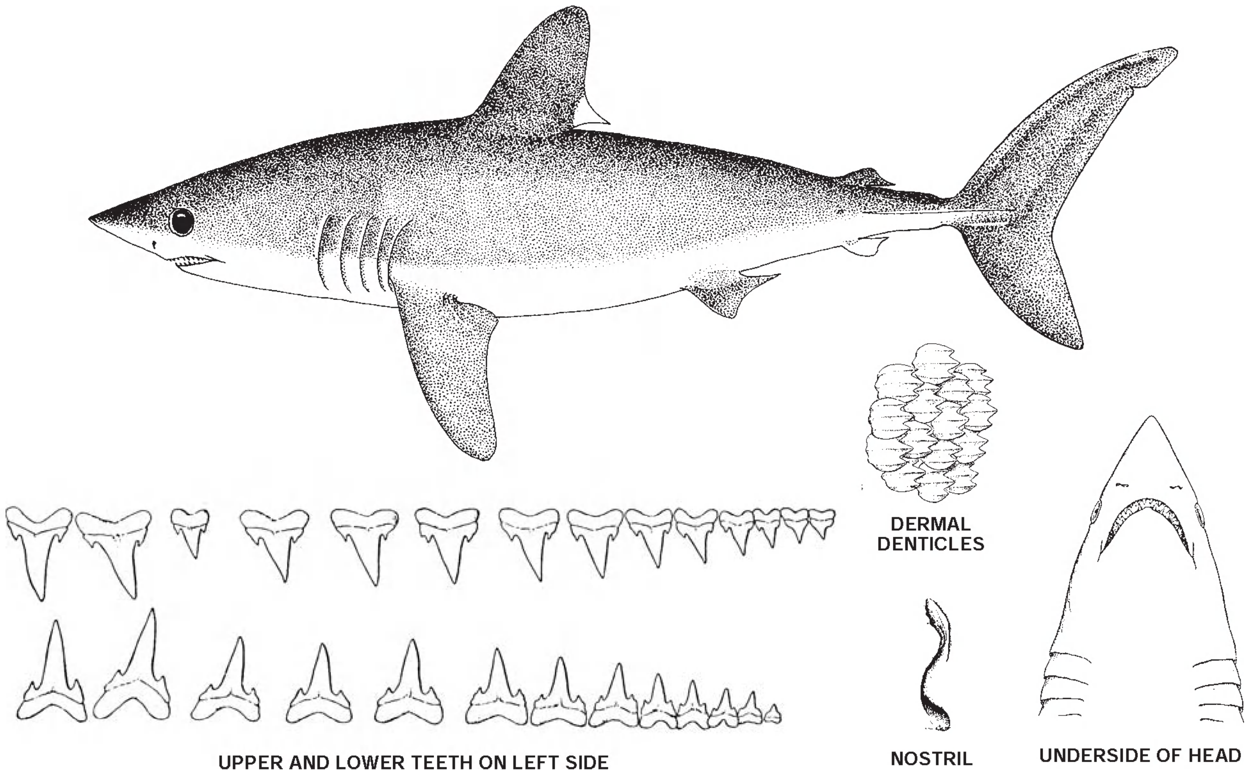
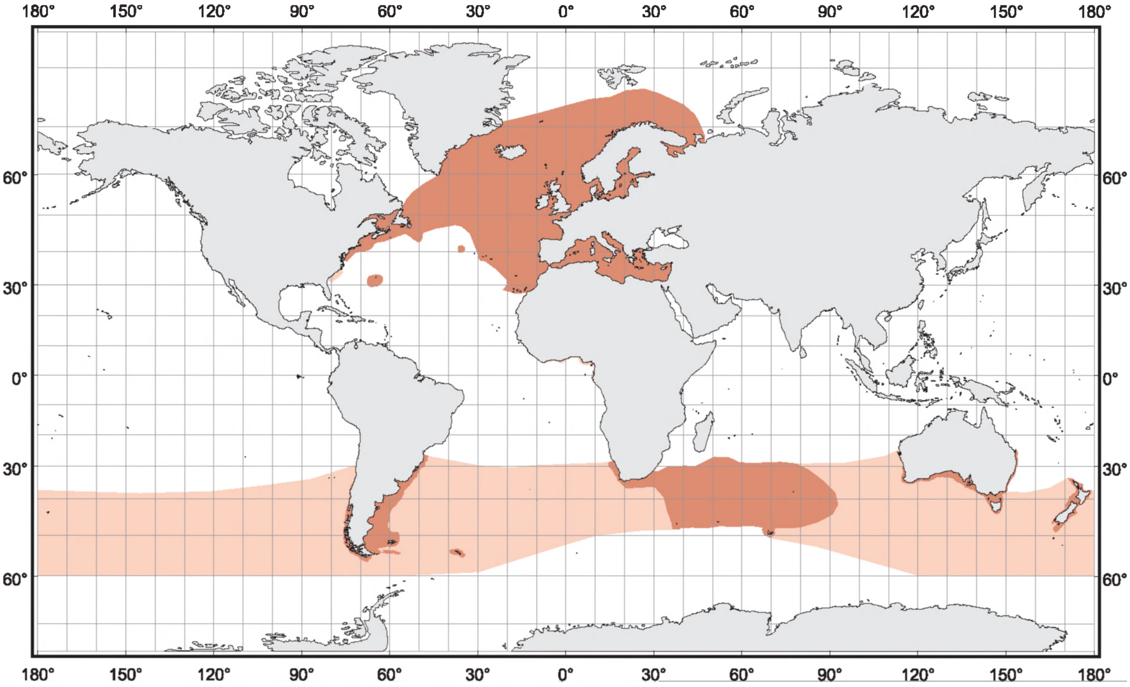


Fig. 79 ***Lamna nasus***

Field Marks: Heavy spindle-shaped body, moderately long conical snout, moderately large blade-like teeth with lateral cusplets, long gill slits, large first dorsal fin with abruptly white free rear tip, minute, pivoting second dorsal and anal fins, strong keels on caudal peduncle, short secondary keels on caudal base, crescentic caudal fin, ventral surface of body white and not extending over pectoral bases as white patches.

Diagnostic Features: Snout long and sharply pointed, with preoral length 5.9 to 9.0% of total length (adults 5.9 to 7.3%) and space from eye to first gill slit 1.7 to 2.5 times preorbital length. First upper lateral teeth with nearly straight cusps. Total vertebral count 150 to 162, precaudal vertebral count 85 to 91. Cranial rostrum with enlarged but discrete hypercalcified rostral cartilages, not forming a massive knob. **Colour:** grey or bluish grey to blackish above, white below, with white abdominal colour terminating at rear end of pectoral bases; first dorsal fin with an abruptly white or greyish white free rear tip; ventral surface of head white and abdomen without dusky blotches in adults of typical Northern Hemisphere porbeagles, but underside of head dark and abdomen blotched in some Southern Hemisphere adults.

Distribution: Coastal and oceanic, amphitemperate, with centres of distribution in the North Atlantic and in a circumglobal band of temperate water of the southern Atlantic, southern Indian Ocean, southern Pacific and Antarctic Ocean. Western Atlantic: Greenland, Canada (Newfoundland Banks, Gulf of St. Lawrence and Nova Scotia), United States (Maine, Massachusetts, Rhode Island, rarely New York, New Jersey and possibly South Carolina), and Bermuda; southern Brazil and Uruguay to southern Argentina. Eastern Atlantic: Iceland and western Barents Sea to Baltic and North Seas, English Channel, Straits of Gibraltar, and Mediterranean Sea, including Russia, Norway, Sweden, Denmark, Germany, Holland, Scotland, England, Wales, Ireland, the Orkney Islands, France, Portugal, Spain, and Gibraltar; entire coast of Mediterranean Sea but not in Black Sea; Morocco, Madeira, Azores, possibly the Gulf of Guinea, and off South Africa (Western Cape). Indo-West Pacific: South-central Indian Ocean from South Africa (Eastern Cape and possibly KwaZulu-Natal) eastward to between Prince Edward and Crozet Islands, between Kerguelen and St. Paul Islands, and the southern coast of Australia (southern Western Australia and South Australia, Victoria, Tasmania, New South Wales and southern Queensland), New Zealand (including Stewart Island). Subantarctic waters off South Georgia, Marion, Prince and Kerguelen Islands. Eastern South Pacific: southern Chile south to Cape Horn.



Habitat: A common littoral and epipelagic shark, most abundant on the continental offshore fishing banks but also found far from land in ocean basins and occasionally close inshore. It was recently caught at the mouth of a brackish estuary in Argentina but does not penetrate fresh water. This shark usually occurs in cold water, less than 18° and down to 1°C, but was once recorded in water 23°C. It does not occur in equatorial seas as far as is known. The porbeagle ranges in depth from the surface and inshore waters less than 1 m deep down to at least 700 m.

Biology: The porbeagle is described as very active and strong-swimming in pursuit of prey or when viewed by divers underwater but does not engage in spectacular leaps like the shortfin mako (***Isurus oxyrinchus***) when hooked. Behaviour and sociobiology are poorly known, and most data available has a fisheries context.

The porbeagle is found at the surface down to the bottom, singly and in schools and feeding aggregations. Porbeagles may come inshore and to the surface in summer, but will winter offshore and beneath the surface. Fisheries catches in Europe indicate that the porbeagle has populational segregation by size (age) and sex.

Porbeagles of the western North Atlantic seem to constitute a single stock that undertakes extensive migrations between southern Newfoundland (Canada) in summer to at least Massachusetts (USA) in the winter. Longterm tagging data suggest there is no mixing between this population and that of the eastern North Atlantic.

Porbeagles breed on both sides of the North Atlantic, off the Atlantic coast of Europe and the British Isles, where females have embryos during most of the year except July through September, and off North America from Massachusetts to Maine, where females can be found with young at all times of year. Young are apparently born in the spring off Europe, in either winter-spring or late summer off North America, and probably from April to September (peak June-July [winter]) in the Southern Hemisphere. Mating in European waters occurs in late summer, and breeding there probably occurs every year. An extended mating period seems to exist for Southern Hemisphere populations around Australia and New Zealand.

The porbeagle is ovoviviparous and a uterine cannibal (oophagous), with litters of 1 to 5 young but the majority of litters are of four young. The foetuses grow enormously by feeding on fertilized eggs, and develop grotesquely expanded abdomens and branchial regions. Small porbeagle embryos posses fang-like functional teeth to tear open egg capsules and release the contained ova; the fangs are shed at 34 to 38 cm FL (Francis and Stevens, 2000). The gestation period has been estimated at about 8 or 9 months for North Atlantic and South Pacific populations. The length of the entire reproductive cycle is not known. Pupping and nursery areas may be in continental waters, but are little-documented. In the western North Atlantic, mating is believed to take place off southern Newfoundland.

Tag-recapture data and tetracycline injected sharks at liberty have been used to validate age determinations for porbeagles in the western North Atlantic up to age 10, but longevity could be as much as 30 to 45 years (Natanson, Mello and Campana, in press). Preliminary studies in this region suggest that males mature at about 175 cm FL (~ Age 7) and females at around 212 cm FL (~ Age 14) (Campana et al. 1999). Newborn porbeagles grow an estimated 15 to 20 cm per year (FL) during the first three years of life in the South Pacific. Prior to the intensive fishery that greatly reduced the numbers of this shark in European waters, the annual mortality for the species was an estimated 18% under low human exploitation and probably minimal predation pressure from other species. Recent research in Atlantic Canada indicates that the instantaneous natural mortality rate of porbeagles is about 0.1.

This shark is a proverbially voracious feeder on small to moderate-sized pelagic schooling fishes, including mackerel (***Scomber***, Scombridae) and pilchards and herring (Clupeidae), but also feeds on demersal fishes including various gadoids such as cod, haddock, cusk, whiting (Gadidae) and hake (Merlucciidae), icefishes (Channichthyidae), and John dories (Zeidae). Chondrichthyan prey include dogfish (***Squalus acanthias***, Squalidae) and tope sharks (***Galeorhinus galeus***, Triakidae). Cephalopod prey includes squid and cuttlefish. It will scavenge hooked fishes including cod from longlines.

Predators of the porbeagle are little known (apart from humans). A small specimen from Argentina had tooth marks suggestive of a carcharhinid, perhaps ***Carcharhinus brachyurus***, but it is uncertain if these were from a predation bout or agonistic encounter. The white shark and orca are obvious candidates for porbeagle predators, but records of predation by either on porbeagles are not known to the author.

Size: Maximum total length 300+ cm, possibly to 370 cm but most smaller; size at birth between 60 and 75 cm TL (69 to 80 cm TL in South Pacific); males maturing at about 150 to 200 cm TL (196 cm TL in the western North Atlantic) and reaching at least 262 cm; females maturing at about 200 to 250 cm TL (with one reported at only 152 cm), to possibly 370 cm (with most less than 300 cm). Females mature at about 237 cm TL in the western North Atlantic and at about 185 to 202 cm TL in the South Pacific. There are several morphometric and L-W equations for porbeagles:

Kohler, Casey and Turner (1995): $W(kg) = 1.4823 \times 10^{-5} \times FL(cm)^{2.9641}$ (n = 15, western North Atlantic)
where: $FL(cm) = 1.7939 + 0.8971 \times TL(cm)$ (n = 13)

Campana et al. (1999): $W(kg) = 0.5 \times 10^{-4} \times FL(cm)^{2.713}$ (n = 286, western North Atlantic)
where: $FL(cm) = 0.99 + 0.885 \times TL(cm)$ (n = 361)

Campana et al. (1999): $FL(cm) = 4.96 \times IDL(cm)^{0.901}$ (n = 358)

Campana et al. (1999): $FL(cm) = 1.7 + 1.12\ PCL(cm)$ (n = 360)

Francis and Stevens (2000): $PCL(cm) = -1.366 + 0.907\ FL(cm)$ (n = 866, FL = 61 to 223 cm, New Zealand)

Francis and Stevens (2000): $TL(cm) = 4.165 + 1.098\ FL(cm)$ (n = 173, FL = 63 to 180 cm, Australia)

Interest to Fisheries and Human Impact: This species has been heavily fished commercially and utilized for human consumption in the temperate North Atlantic and the Mediterranean, but is also caught as bycatch in the Southern Hemisphere where it is the second most common shark as bycatch of the New Zealand longline fishery. World catches of porbeagles have been reported to FAO by a number of countries, including Canada, Denmark, the Channel and Faeroe Islands, France, Germany, Iceland, Malta, New Zealand, Norway, Portugal, Spain, Saint Pierre and Miquelon Islands, Sweden, the United Kingdom, and the United States. World catches per annum ranged from 346 to 9 674 t from 1951 through 1997 (mean 2 102 t) with 1 736 t reported in 1997 (FAO FishStat Plus database, 2000). The major peak was in the middle 1960s and was followed by a declining trend with peaks and declines in the 1970s and 1980s to a level between 1 000 and 2 500 t in the 1990s.

Stocks in the North Atlantic have shown signs of serious overfishing in the form of greatly declining catches. Scandinavian fishers have caught porbeagles since the early nineteenth century, but only intensively during the twentieth century. Norway and to a lesser extent Denmark have been the principle fishers of porbeagles in the North Atlantic. Norwegian catches have varied wildly during the twentieth century, increasing from 279 t in 1926 to 3 884 t in 1933, then declining steadily to low levels during the second world war. Intensive fishing resumed in 1945 and peaked at 2 824 t in 1947, but then steadily declined to 207 t in 1970 and only 25 t in 1994. Porbeagles became scarce off Europe and the Norwegian fishery spread to the western North Atlantic, but eventually the fishery shifted to other species such as shortfin mako and swordfish. Small regulated catches exist at present for Norway (200 t allocated in European Community waters per year) and New Zealand, with the species protected in United States waters and regulated in the European Community. Canadian catches of porbeagles were less than 100 t/y until 1990 but landings increased in 1992 and catches have oscillated around 1 300 t/y since 1994. The western Atlantic stock is currently considered overexploited, with declining catch rates, and a fishing mortality beyond the replacement level. A Canadian management plan that limits the number of licenses, types of gear, fishing areas and seasons, prohibits finning, and restricts recreational fishing to catch-and-release only, has been in force since 1995. A TAC of 1 000 t/y was introduced in the commercial fishery for the period 1997-1999 pending better scientific information about resource status. In the past porbeagles were considered a nuisance to commercial fishermen because they wrecked light gear set for bony fishes (such as cod nets) and bit fish off hooks, but probably not so much at present with greatly depleted porbeagle stocks and decimated stocks of some of its prey species (including cod).

A considerable bycatch fishery for porbeagle by Japanese longliners and probably the pelagic fishing fleets of other countries has existed in the southern Indian Ocean and probably elsewhere in the Southern Hemisphere. The catch is poorly known and may be little-utilized except for fins. It has figured as complementary bycatch (fins utilized) of the Japanese longline fishery for southern bluefin tuna off Tasmania. It is used fresh and dried-salted for human consumption; for oil and fishmeal for fertilizer; and for fins for shark-fin soup. The species is primarily caught with pelagic longlines; also pelagic and bottom trawls, handlines and gill nets. It has recently showed up as bycatch of demersal longlines for Patagonian toothfish (***Dissostichus eleginoides***, Nototheniidae) in the southern Indian Ocean. Statistics for the Southern Hemisphere porbeagle fishery are only reported to FAO by New Zealand (21 t in 1997), which suggests that the southern catch is largely unreported.

This species has been described as a relatively less active game fish compared to the shortfin mako and white shark. However, the porbeagle has been regularly sought by sportsfishing anglers in the United Kingdom, Ireland and the United States and is a strong fighter (especially on light tackle from a small boat). It is listed as a record game fish by the International Game Fish Association.

The porbeagle seldom if ever bites people in the water or boats (unlike its close relatives the shortfin mako and white sharks). An older anecdotal account mentions a provoked encounter by a porbeagle that leapt at and bit a piece of clothing from a fisherman who was attempting to capture it. A swimmer was reported as being bitten by a 'mackerel shark', but this was not confirmed and could have resulted from mistaking a white shark or shortfin mako for a porbeagle or mackerel shark. Recently adult porbeagles have been filmed underwater making fast rushes at divers servicing oil platforms in the North Sea, with the sharks sometimes brushing the divers and making light contact without hurting them (I. Fergusson, pers. comm.). The motivation of this activity is uncertain but is apparently nonpredatory and possibly agonistic or exploratory. To the writer's knowledge porbeagles have not figured in ecotouristic diving, nor have they been kept in captivity.

The conservation status of the porbeagle is of major concern because of the drastic decline in catches from targeted fisheries in the North Atlantic and continuing exposure of the species to intensive high-seas pelagic longline fisheries (with finning and capture trauma contributing to mortality) wherever it occurs. North Atlantic fisheries are relatively well-documented and under regulation, but not those of the Southern Hemisphere with the exception of New Zealand.

Local Names: Mackerel shark, Common porbeagle, Porbeagle shark, Atlantic mackerel shark, Common Atlantic mackerel shark, Salmon shark, Atlantic porbeagle, Swordfin, Blue dog, American porbeagle, Beaumaris shark, Blue shark, Bottle-nosed shark (England and USA); Le squale nez, Le lamie long nez, Lamie, Nez, Touille, Touilele boeuf taupe, Requin long nez, Loutre de mer, Nas llarg, Melantoun (France); Neushaai (Holland); Sillhaj or Herring shark, Sildehaaen (Denmark); Morgi mawr (Wales); Haabranden, Haamar (Sweden); Smeriglio, Lamna smeriglio, Isuro muso acuto, Cagnia, Smeriglio, Sorglio pisci tunnu, Pisci cani, Cani di mer (Italy); Psina atlantska (Adriatic); Calderon, El marrago, Ludia, Marraco, Marraquet, Marrraix, Marrajo, Taulo (Spain); Anequim, Arrequim, Marracho, Sardo (Portugal); Marracho, Porbeagle (Azores); Requim, Nequim (Madeira); Akula sel devaia (Russia); Haringhaai (South Africa).

Literature: Shann (1911, 1923); Garman (1913); Lahille (1928); Fowler (1936, 1941); Whitley (1939, 1940); Bigelow and Schroeder (1948); Smith (1949); Aasen (1961, 1963); Farquhar (1963); Garrick and Schultz (1963); Templeman (1963); Kato, Springer and Wagner (1967); Nakaya (1971); Stevens (1973); Baldridge (1974); Schwartz and Burgess (1975); Sadowsky and Amorim (1977); Svetlov (1978); Duhamel and Ozouf-Costaz (1982); Stevens, Dunning and Machida (1983); Compagno (1984, 1990b, c); Quero (1984); Duhamel and Compagno (1985); Sadowsky, Arfelli and Amorim (1985); Paust and Smith (1986); Stevens (1990); Last and Stevens (1994); Santos, Porteiro and Barreiros (1997); Lucifora and Menni (1997); O'Boyle et al. (1998); Castro, Woodley and Brudek (1999); Campana et al. (1999); Francis and Stevens (2000); Natanson, Mello and Campana, (in press); I. Fergusson, (pers. comm.).

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2.3 Order ORECTOLOBIFORMES - Carpet sharks

Order: Orectolobiformes: Compagno, 1973, *J. Linn. Soc. (Zool.)*, 53, suppl. 1: 28; also Applegate, 1974, *J. Mar. Biol. Ass. India*, 14(2): 743.

Number of Recognized Families: 7.

Synonyms: [Part] 1 Squali, Abtheilung [Division] 1: Müller and Henle, 1838d: 3. [Part] 1 Squali, Abtheilung [Division] 2, Unterabtheilung [Subdivision] 3: Müller and Henle, 1839: 66. Ordo Plagiostomi, Subordo Squalini, Sectio Proktopterides, Tribus Dinotopterini: Bleeker, 1859: xi. Order Squali, Suborder Squali: Gill, 1862b: 394, 396. Order Squali, Suborder Galei: Gill, 1872: 22, 23. Order Plagiostomi diplospondyli, Suborder Plagiostomi asterospondyli, Group 1 Scyllia: Hasse, 1879: 52. Order Plagiostomi diplospondyli, Suborder Plagiostomi asterospondyli, Group 2 Scylliolamnidae: Hasse, 1879: 51. Order Selachii, Suborder Asterospondyli: Woodward, 1889: 157. Order Asterospondyli, suborder unnamed: Gill, 1893: 130; Fowler, 1941: 4, 13; Smith, 1949: 37, 39. Order Asterospondyli, Suborder Galei: Jordan and Evermann, 1896: 19, 21. Order Euselachii, Suborder Pleurotremata, Division Galeoidei: Regan, 1906a: 723. Order Selachii, Group 2, Division B, Subdivision 1, Suborder Scylliodei: Goodrich, 1909: 148. Order Pleurotremata, Suborder Galeoidei: Engelhardt, 1913: 97. Order Plagiostoma, Suborder Antacea, "Group" Catuloidei: Garman, 1913: 11, 12. Order Plagiostoma, Suborder Antacea, "Group" Isuroidei: Garman, 1913: 10, 12. Order Euselachii, Suborder Galei, [Series] Scyllioidei: Jordan, 1923: 97. Order Plagiostomi, Suborder Galeiformes: Lozano y Rey, 1928: 280. Order Galea, Suborder Isurida, Superfamily Orectoloboidea: White, 1936: 4; White, 1937: 36, tab. 1. Order Euselachii, Suborder Scylliformes: Bertin, 1939a: 9. Order Lamniformes, Suborder Lamnoidei: Berg, 1940: 137; Berg and Svetovidov, 1955: 65; Patterson, 1967: 670; Lindberg, 1971: 8, 257; Nelson, 1976: 33; Nelson, 1984: 51. Order Euselachii, Suborder Galeoidei, Superfamily Orectoloboidea: Whitley, 1940: 68-69. Order Selachii, Suborder Galeoidea: Romer, 1945: 576; Bigelow and Schroeder, 1948: 77, 95; Romer, 1966: 350. Order Lamnoidea, Suborder Galeoidea: Schultz and Stern, 1948: 224. Order Lamnida, Suborder Lamnina: Matsubara, 1955: 1-789. Order Galeiformes, Suborder Isuroidei: Arambourg and Bertin, 1958: 2030. Order Pleurotrema, Suborder Galeoidea: Norman, 1966: 7. Order Carchariida, Suborder Carchariina, Superfamily Orectolobicae: Fowler, 1967a: 89. Order Carchariida, Suborder Carchariina, Superfamily Lamnicae: Fowler, 1967a: 104. Order Squatinida, Suborder Ginglymostomatoidei: Glikman, 1967: 216. Order Euselachii, Suborder Galeoidei: Blot, 1969: 702-776. Order Pleurotremata, Suborder Galeiformes: Budker and Whitehead, 1971: 5, tab. 2. Order Carcharhiniformes: Rass and Lindberg, 1971: 304; Gubanov, Kondyurin and Myagkov, 1986: 3, 61. Order Orectolobiformes: Chu and Meng, 1979: 114, tab. 2; Compagno, 1984: 165; Cappetta, 1987: 26, 71; Compagno, 1988: 382; Eschmeyer, 1990: 435; Nelson, 1994: 45; de Carvalho, 1996: 55; Shirai, 1996: 32; Eschmeyer, 1998: CD-ROM. Order Orectolobiformes, Suborder Orectoloboidei: Applegate, 1974: 74. Order Orectolobiformes, Suborder Parascylloidei: Applegate, 1974: 749. Order Orectolobiformes, Suborder Rhincodontoidei: Applegate, 1974: 744. Order Orectolobiformes, Suborder Rhincodontoidea: Chu and Meng, 1979: 114, tab. 2. Order Orectolobiformes, Suborder Orectoloboidea: Chu and Meng, 1979: 114, tab. 2. Order Galeomorpha, Suborder Heterodontoidea: Carroll, 1988: 598.

FAO Names: En - Carpet sharks; **Fr** - Requins-tapis; **Sp** - Tiburones tapiceros and Gatas nodrizas.

Field Marks: Moderate-sized to gigantic, sluggish, demersal to active sharks without nictitating eyelids, with barbels and nasoral grooves, nostrils connected with mouth, short mouths that end in front of eyes, usually without enlarged anterior teeth and without a gap or small intermediate teeth between anteriors and lateral teeth on each side of the upper jaw, five narrow to broad gill openings, two spineless dorsal fins and an anal fin.

Diagnostic Features: Head conical to greatly depressed, expanded laterally or not. Snout short to very short, truncated to flattened-conical, not greatly elongated nor blade-like and without lateral teeth or rostral barbels. Eyes usually dorsolateral on head but lateral in a few derived taxa (***Stegostoma***, ***Nebrius*** and ***Rhincodon***), without nictitating lower eyelids or secondary lower eyelids, but with shallow subocular pouches in some taxa; upper eyelids not fused to eyeball. Spiracles small to large, close behind and about opposite level of eyes. Five pairs of gill openings present on sides of head, with the posteriormost two to four above pectoral-fin origins. Nostrils longitudinal on snout, usually with barbels (rudimentary in ***Rhincodon***), circumnarial grooves primitively present around incurrent aperture but absent in some derived taxa; nasoral grooves present and connecting excurrent apertures of nostrils with mouth; anterior nasal flaps short to elongate and reaching mouth. Mouth small to large, usually subterminal (terminal in ***Rhincodon***), arched to nearly transverse and short, ending in front of eyes. Labial furrows well-developed on both jaws. Teeth weakly to strongly differentiated along the jaws, with (Orectolobidae) or usually without enlarged anterior teeth and without enlarged molariform posterior teeth; without a gap or small intermediate teeth between anterior and lateral teeth in the upper jaw; teeth primitively with orthodont histological structure but osteodont in ***Ginglymostoma*** and ***Nebrius***. Trunk cylindrical to depressed and somewhat ray-like (Orectolobidae). Caudal peduncle with or without lateral dermal ridges or lateral keels on caudal peduncle. Dermal denticles covering entire body, not enlarged as thorns or spines. Pectoral fins small to large, somewhat expanded and ray-like in some Orectolobidae, without triangular anterior lobes that cover the gill slits. Pectoral girdle (scapulocoracoid) fairly high, U-shaped, without a medial joint, and with superscapulae directed posterodorsally and not contacting vertebral column. Pectoral-fin skeleton primitively tribasal (dibasal in some taxa), with propterygium in contact with radials and metapterygium without a proximal segment; pectoral fins primitively aplesodic, with radials confined to the fin bases, but plesodic in derived taxa and supporting the fin webs; radial count 14 to 28, with 2 to 10 segments. Pelvic fins small to large, with vent usually continuous with their inner margins (may be separate in Orectolobidae). Claspers generally with siphons in the abdomen but without clasper sacs; clasper glans with a pseudosiphon (sometimes absent), cover rhipidion (sometimes reduced), rhipidion (sometimes absent), exorhipidion, and often lateral clasper spurs or spines; dorsal and ventral marginals of clasper skeleton rolled into a tube for the clasper canal. Two spineless dorsal fins present, with origin of first dorsal fin varying from anterior to pelvic-fin origins to behind pelvic-fin insertions; dorsal-fin skeleton with segmented radials but without segmented basal plates. Anal fin present. Caudal fin with a long dorsal lobe and the ventral lobe strong to absent; vertebral axis weakly to strongly elevated into the dorsal caudal-fin lobe (heterocercal caudal fin). Vertebral calcification strong, secondary calcification usually in form of strong branched radii in intermedial spaces although sometimes wedge-shaped and solid (Parascylliidae), intermedialia sometimes with annular rings (Rhincodontidae), usually without diagonal lamellae in the basal spaces (present in ***Rhincodon*** and ***Parascyllium***). Total vertebral count 117 to 243, precaudal vertebrae 69 to 138. Neurocranium with a short to rudimentary monopodal rostrum consisting of a ventral rostral cartilage without ventral keel, rostral space open dorsally; nasal capsules trumpet-shaped and more or less flattened, without subnasal fenestrae (basal communicating canals) or antorbital cartilages; orbits with incomplete preorbital walls, usually strong supraorbital crests (greatly reduced in Parascylliidae), usually strong suborbital shelves (greatly reduced in Parascylliidae), separate foramina for superficial ophthalmic nerves but not for hyomandibular nerves, and incomplete postorbital walls without lateral commissures for lateral head vein; occipital condyles low, occipital hemicentrum present between them. Jaws short to moderately elongated, upper jaws (palatoquadrates) with low, ridge-like orbital processes that articulate with nasal capsules and orbits in horizontal grooves contacting ethmoid region, basal plate and suborbital shelves; orbital processes not penetrating supraorbital crests. Hyobranchial skeleton with moderately broad, short to elongated basihyoid; posterior two pharyngobranchials and last epibranchial fused into a yoke-shaped element. Head muscles include vertical broad preorbitalis; short levator palatoquadrati and separate first dorsal constrictors that do not extend behind the postorbital processes, adductor mandibulae muscles segmented into two or three groups of divergently biased fibres, not notched anteriorly for mouth gape; no craniomandibular muscle between the lower jaw and orbital walls; no mandibulocutaneous muscle between upper jaw and skin; and no postocular eyelid muscles (an anterior palpebral depressor muscle present in Parascylliidae). Intestinal valve of conicospiral or (usually) ring type, with 6 to 74 turns. Reproduction oviparous in some species, which lay eggs in oval cases; other species are ovoviviparous (aplacental viviparous), with foetal nutriment from the yolk sack or from uterine cannibalism (oophagy or egg-eating in ***Nebrius***), but without placental vivipary or nutritive trophonemata.

Distribution: Circumglobal in warm-temperate and tropical seas, absent or marginal in cold-temperate areas and not reaching cold boreal and subantarctic waters. Most species occur in tropical seas and are most diverse in the western Pacific. The whale shark is circumglobal, and some large carpet sharks have wide ranges in the Atlantic and eastern Pacific (***Ginglymostoma***), or the Indo-West Pacific (***Nebrius*** and ***Stegostoma***). Most carpet sharks have more limited ranges in the Indo-West Pacific, with several species confined to Australia and New Guinea and a few occurring only off Taiwan (Province of China) or Japan.

Habitat: Carpet sharks or orectoloboids occur in a variety of marine habitats from shallow open and enclosed bays, rocky and coral reefs, estuaries, and sandy beaches on the continental shelves to the outer shelves, uppermost slopes, and the epipelagic zone (Rhincodontidae). They range in depth from the intertidal to the outer shelves and exceptionally between 200 and 435 m on the upper slopes (Parascylliidae) and in the epipelagic zone at the surface (whale shark, ***Rhincodon***). Although many species are found in shallow inshore waters only a few species of Hemiscylliidae may penetrate the lower brackish reaches of rivers but are not definitely recorded from freshwater rivers and lakes. No carpet sharks are specialized deep-slope or oceanic species.

Biology: Carpet sharks are small to gigantic, rather varied sharks that are mostly small, benthic, and sluggish, while larger species are generally more active swimmers. Morphotypes (Compagno, 1990a) include generalized benthic and littoral species (Ginglymostomatidae and Brachaeluridae), elongated leptobenthic bottom-dwelling species (Parascylliidae and Hemiscylliidae), squatinobenthic depressed specialists (Orectolobidae), and a macroceanic, filter-feeder (Rhincodontidae). The squatinobenthic wobbegongs are ambush-hunters that take relatively large prey, swallowed whole, and parallel the mostly allopatric angel sharks (Squatinidae). The prey of orectoloboids includes microscopic zooplankton, small to moderate-sized bony fishes, smaller chondrichthyans, crabs, lobsters, shrimp, octopuses, cuttlefish, squid, gastropods, bivalves, sea urchins, sea anemones, and corals. Information on movements is limited or absent for most species; the whale shark is highly migratory, and seasonally visits favoured areas including concentrations of food (reefs with plankton blooms.) The whale shark is apparently social and forms aggregations, but the sociobiology of most species is poorly known. Modes of reproduction include oviparity (egg-laying, in Parascylliidae, Hemiscylliidae, and Stegostomatidae), ovoviviparity or aplacental vivipary (Brachaeluridae, Orectolobidae, Rhincodontidae, ***Ginglymostoma***), and uterine cannibalism or cannibal vivipary in the form of egg-eating or oophagy (***Nebrius***).

Interest to Fisheries and Human Impact: Several families of orectoloboids are minor to important fisheries sharks in coastal and oceanic waters, particularly members of the Orectolobidae, Hemiscylliidae, Stegostomatidae and Ginglymostomatidae. These are regular components of targeted shark fisheries and as bycatch of other fisheries targeting teleost fishes or marine invertebrates. Some species are discarded bycatch of demersal fisheries (Parascylliidae), while the whale shark is targeted by specialized fisheries. Orectoloboids are caught in bottom trawls, in fixed and possibly pelagic gill nets, in fish traps, on bottom longlines, with harpoons, and with hook-and-line and rod-and-reel. Several species are used for human consumption; the flesh of some species is excellent, and large fins are of high value in the oriental soup-fin trade. Whale sharks were formerly caught by very small artisanal fisheries for local use, but values of whale shark fins, flesh and other products for the international market have soared during the last decade and have encouraged intensive targeted fisheries in certain countries (India, Philippines, and Taiwan (Province of China)). Several inshore and offshore species are caught by sportsfishing anglers.

Wobbegongs and larger nurse sharks (Ginglymostomatidae) rarely bite people. Whale sharks occasionally butt fishing boats, but are more often run down and injured or killed by ships.

Whale sharks, nurse sharks, wobbegongs, and zebra sharks are currently sought by ecotouristic divers and film-makers in the tropics, with whale sharks the subject of dedicated dive tours in the Indo-Pacific from South Africa to Costa Rica. Orectoloboids as a group are very hardy in captivity and are among the most important aquarium sharks, both for public viewing and for home aquaria. Most species have been kept in captivity, with the wobbegongs (Orectolobidae), bamboo sharks (Hemiscylliidae), nurse sharks (Ginglymostomatidae), and zebra sharks (Stegostomatidae) being the most popular orectoloboids for public aquaria and oceanaria. Whale sharks are kept in a few Japanese oceanaria with sufficiently huge tanks to accommodate them.

The diversity of orectoloboid sharks is greatest in inshore and offshore continental waters of the tropical Indo-West Pacific, where intensive fisheries occur. The conservation problems facing the whale shark are the most urgent and widely publicized, but most species of orectoloboids are taken in targeted and bycatch demersal fisheries and several species are coral-reef dwellers that are adversely affected by reef destruction. Some species have limited geographic and bathymetric distributions in continental inshore and offshore tropical waters (some Parascylliidae, Orectolobidae, Brachaeluridae and Hemiscylliidae) and are at potential risk from habitat degradation and fisheries. Fisheries statistics are unavailable for almost all species, including catches of carpet sharks for the aquarium trade. The whale shark is included on the IUCN Red List and protected off Belize, Honduras, the Philippines, and the USA (east coast) while nurse sharks (***Ginglymostoma***) are protected off the east coast of the United States.

Remarks: The concept of the orectoloboids as a discrete, monophyletic group is relatively recent and stems from the work of Regan (1906a), White (1936, 1937), Compagno (1973) and Applegate (1974). Most researchers in the nineteenth and twentieth centuries followed Müller and Henle (1839) in placing the highly distinctive whale shark (***Rhincodon***) in a separate, monotypic family (Rhincodontidae or its synonyms). Müller and Henle (1838d) included orectoloboids other than the whale shark in the carcharhinoid catshark family (Scyliorhinidae or its synonyms), and this was followed by several earlier authors (Müller, 1845; Gray, 1851; Bleeker, 1859; Dumeril, 1865; Günther, 1870; Jordan and Gilbert, 1883; Woodward, 1889; Goodrich, 1909; Bertin, 1939a).

Gill (1862b, 1872) divided the orectoloboids into the families Rhinodontoidae (Rhinodontidae) for the whale shark, Ginglymostomatidae for the nurse sharks (***Ginglymostoma***, ***Nebrius***), Crossorhinoidae for the wobbegongs (***Orectolobus***), and Scylliorhinoidae for other orectoloboids and the scyliorhinid catsharks. Gill (1862b) subdivided the Scylliorhinoidae into the subfamilies Scylliorhininae for the catsharks and Parascylliinae, Hemiscylliinae, Chiloscylliinae, and Stegostomatinae for other orectoloboids, and later (Gill, 1893) transferred the Stegostomatinae to the Ginglymostomatidae. Hasse (1879) named a "Group 2 Scylliolamnidae" as a family for ***Stegostoma***, ***Ginglymostoma***, and ***Orectolobus*** and a "Family Chiloscyllium" for the hemiscylliid orectoloboid ***Chiloscyllium***.

Regan (1906a; followed by Engelhardt, 1913 and Berg, 1940) was the first author to associate the whale shark with other orectoloboids in a common family Orectolobidae. White (1936, 1937) expanded Regan's arrangement by placing the whale shark (Rhincodontidae) and the carpet sharks (Orectolobidae) in a common superfamily Orectoloboidea. White was followed by Whitley (1940), who further subdivided the Orectoloboidea into the families Hemiscylliidae, Orectolobidae, Ginglymostomatidae and Rhincodontidae in the superfamily Orectoloboidea. This arrangement and the orectoloboid families and subfamilies of Gill (1862b, 1872, 1893) were revived and expanded by Compagno (1973) and Applegate (1974), who proposed a common order Orectolobiformes for all orectoloboids, and recognized the separate families Parascylliidae, Brachaeluridae, Orectolobidae, Hemiscylliidae, Stegostomatidae, Ginglymostomatidae and Rhiniodontidae, while Applegate (1974) proposed an additional family Cirrhoscylliidae (here ranked as a synonym of Parascylliidae). This was followed by several authors (Compagno, 1981b, 1982, 1984, 1988, 1999; Cappetta, 1987; Nelson, 1994; Eschmeyer, 1990, 1998; de Carvalho, 1996; Helfman, Collette and Facey, 1997). Dingerkus (1986) and Shirai (1996) modified this classification by synonymizing the Ginglymostomatidae and Stegostomatidae with the family Rhincodontidae. Chu and Meng (1979) recognized the order Orectolobiformes with three families, Orectolobidae, Cirrhoscylliidae and Rhincodontidae. Carroll (1988) recognized a suborder Orectoloboidea for the families Orectolobidae, Rhinocodontidae [sic], Hemiscylliidae and Parascylliidae.

There are several alternative arrangements for the classification of orectoloboids. Orectoloboids were often included in a common and undifferentiated 'galeoid' group along with the lamnoids and carcharhinoids (and occasionally the heterodontoids) as the families Orectolobidae and Rhincodontidae (Fowler, 1941; Romer, 1945, 1966; Bigelow and Schroeder, 1948; Schultz and Stern, 1948; Smith, 1949; Matsubara, 1955; Garrick and Schultz, 1963; Norman, 1966; Blot, 1969; Pinchuk, 1972). Some authors associated the Rhincodontidae or equivalents with more derived lamnoids or all of the lamnoids in a common group (Bonaparte, 1838; Goodrich, 1909; Garman, 1913; Fowler, 1947, 1967a; Berg and Svetovidov, 1955; Nelson, 1976, 1984). Arambourg and Bertin (1958) included all orectoloboids with the lamnoids in a common higher group. Glikman (1964, 1967) included the orectoloboids with most of the squalomorph sharks (squatinoids, squaloids, and pristiophoroids). Jordan (1923) named a Series Scyllioidei for the orectoloboid families Hemiscylliidae, Orectolobidae, Ginglystomidae (sic.), and Rhincodontidae, which also included the carcharhinoid catsharks. Rass and Lindberg (1971) and Gubanov, Kondyurin and Myagkov (1986) grouped the orectoloboids in a common, undifferentiated order Carcharhiniformes with certain lamnoids (***Cetorhinus***, ***Megachasma***), and the carcharhinoids.

Continuing work on the morphology of orectoloboid sharks by the writer as an extension of previous research (Compagno, 1979, 1984, 1988) supports the recognition of the Orectolobiformes as a monophyletic if morphologically varied group. The arrangement of orectoloboid families recognized in Compagno (1973, 1984) are retained here, but one notes that Dingerkus' (1986) cladistic classification united the more derived orectoloboids in a single family Rhincodontidae. Compagno's (1988) cladistic analysis of orectoloboids was at variance with Dingerkus (1986) but supported the monophyly of the group of 'higher' orectoloboids placed in his Rhincodontidae (***Stegostoma***, ***Pseudoginglymostoma***, ***Nebrius***, ***Ginglymostoma*** and ***Rhincodon***). A problem remains on the familial position of the genus ***Pseudoginglymostoma***, which is retained provisionally in Ginglymostomatidae here. Alternative cladograms (Dingerkus, 1986, Compagno, 1988) suggested that this genus may be either the plesiomorphic sister group of all other 'higher' orectoloboids (which seems more likely), or alternatively is the plesiomorphic sister group of ***Stegostoma***. Alternatives include placing ***Pseudoginglymostoma*** in its own family, in the Stegostomatidae, or accepting Dingerkus' arrangement of an expanded and morphologically diverse Rhincodontidae. The writer favours the former arrangement, but reserves action for the completion of a detailed study of the anatomy of ***Pseudoginglymostoma*** and comparison with other higher orectoloboids.

Key to Families:

1a. Mouth huge and nearly terminal; external gill slits very large, internal gill slits inside mouth cavity with filter screens; caudal peduncle with strong lateral keels; caudal fin with a strong ventral lobe, but without a strong terminal lobe and subterminal notch (Fig. 80) . . . . ***family Rhincodontidae***

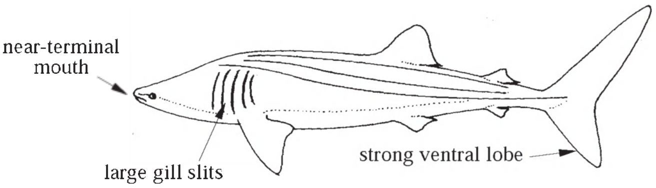


Fig. 80 Rhincodontidae

1b. Mouth smaller and subterminal; external gill slits small, internal gill slits without filter screens; caudal peduncle without strong lateral keels; caudal fin with a weak ventral lobe or none, but with a strong terminal lobe and subterminal notch (Fig. 81) . . . .→ ***2***

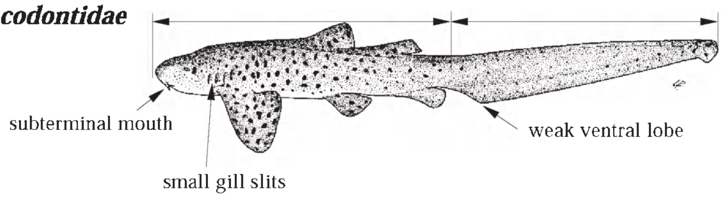


Fig. 81 Stegostomatidae

2a. Caudal fin about as long as rest of shark (Fig. 81) . . . . ***family Stegostomatidae***

2b. Caudal fin much shorter than rest of shark . . . .→ ***3***

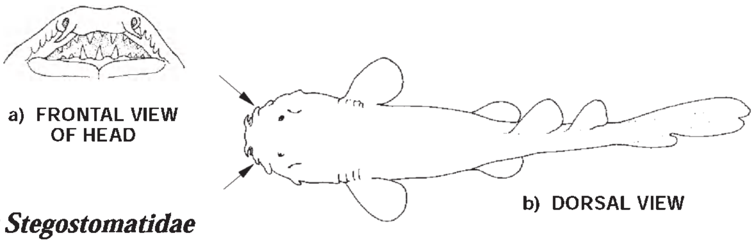
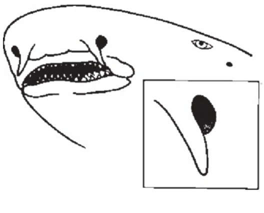


Fig. 82 Orectolobidae

3a. Head and body greatly flattened, head with skin flaps on sides; two rows of large, fang-like teeth at symphysis of upper jaw and three in lower jaw (Fig. 82) . . . . ***family Orectolobidae***

3b. Head and body cylindrical or moderately flattened, head without skin flaps; teeth small, not enlarged and fang-like at symphysis . . . .→ ***4***

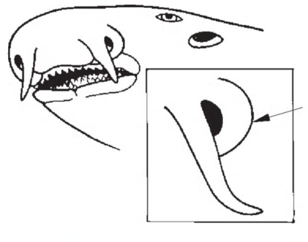


HEAD AND DETAIL OF NOSTRIL

Fig. 83 Ginglymostomatidae

4a. No circumnarial lobe and groove around outer edges of nostrils (Fig. 83). ***family Ginglymostomatidae***

4b. A circumnarial lobe and groove around outer edges of nostrils (Fig. 84) . . . .→ ***5***



HEAD AND DETAIL OF NOSTRIL

Fig. 84

5a. Spiracles minute; origin of anal fin well in front of second dorsal-fin origin, separated from lower caudal-fin origin by space equal or greater than its base length (Fig. 85) . . . . ***family Parascylliidae***

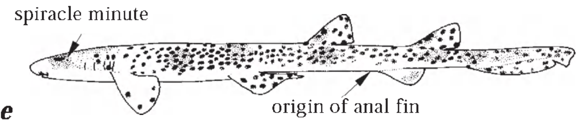


Fig. 85 Parascylliidae

5b. Spiracles large; origin of anal fin well behind second dorsal-fin origin, separated from lower caudal-fin origin by space less than its base length (Fig. 86) . . . . → ***6***

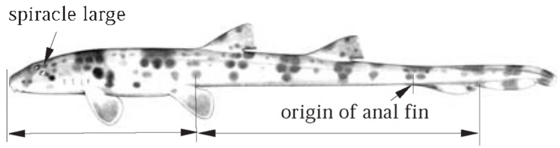
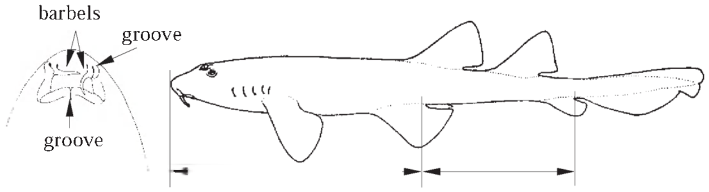


Fig. 86 Hemiscylliidae

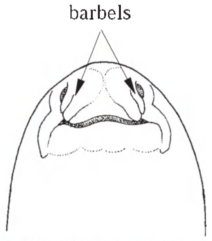


a) UNDERSIDE OF HEAD **b) LATERAL VIEW**

Fig. 87 Brachaeluridae

6a. Nasal barbels very long; longitudinal groove on middle of chin; anal fin high and angular; distance from vent to lower caudal-fin origin shorter than distance from snout to vent (Fig. 87). . . . . ***family Brachaeluridae***

6b. Nasal barbels short; no groove on chin; anal fin low, rounded and keel-like; distance from vent to lower caudal-fin origin longer than distance from snout to vent (Figs 86 and 88) . . . . ***family Hemiscylliidae***



UNDERSIDE OF HEAD

Fig. 88 Hemiscylliidae

2.3.1 Family PARASCYLLIIDAE

Family: Subfamily Parascylliinae Gill, 1862b, *Ann. Lyceum Nat. Hist. New York*, 7(32): 407, 408, 412 (Family Scylliorhinoidae Gill, 1862). Also as Subfamily Parascylliinae Fowler, 1934, *Proc. Acad. Nat. Sci. Philadelphia*, 85: 238 (Family Orectolobidae).

Type Genus: ***Parascyllium*** Gill, 1862.

Number of Recognized Genera: 2.

Synonyms: Family Parascylliidae Applegate, 1974: 749. Type genus: ***Parascyllium*** Gill, 1862. Independently proposed as a family. Family Cirrhoscylliidae Applegate, 1974: 749; Chu and Meng, 1979: 37, 114, tab. 2 (independently proposed from Applegate, 1974). Type genus: ***Cirrhoscyllium*** Smith and Radcliffe, 1913.

FAO Names: En - Collared carpet sharks; **Fr** - Requins-carpettes; **Sp** - Alfombreras.

Field Marks: Small sharks, superficially similar to members of the family Scyliorhinidae in their slender form, cat-like eyes with subocular pockets, first dorsal-fin origin behind pelvic-fin bases, and fin proportions, but differing in having their mouths entirely in front of eyes and in having narrow nasoral grooves, circumnarial grooves and folds around the nostrils, and medial barbels not derived from the anterior nasal flaps. Their mouth and nostril structures, two spineless dorsal fins and an anal fin, anal-fin origin well ahead of second dorsal-fin origin, and minute spiracles distinguish them from other sharks.

Diagnostic Features: Head narrow and somewhat flattened, without lateral flaps of skin. Snout broadly rounded to slightly pointed. Eyes dorsolaterally situated on head and with strong subocular ridges below them. Eyes with movable upper eyelids and shallow subocular pockets and ridges. Spiracles minute and much smaller than eyes, without raised external rims; spiracles somewhat behind but not below eyes. Gill slits small, fifth gill slit overlapping fourth; internal gill slits without filter screens. Nostrils with short, pointed barbels, circumnarial folds and circumnarial grooves around outer edges of incurrent apertures. Nasoral grooves long and strongly developed. Mouth small, moderately arched, and subterminal on head. Lower lip not trilobate and without lateral orolabial grooves connecting edge of lip with medial ends of lower labial furrows; no symphysial groove on chin. Lower labial furrows ending well lateral to symphysis, not connected medially by a mental groove nor mental groove and flap. Teeth not strongly differentiated in upper and lower jaws, with symphysial teeth not enlarged and fang-like. Tooth row count 23 to 54/22 to 49. Teeth with a strong medial cusp, a pair of short lateral cusplets, and strong labial root lobes. Teeth orthodont with a central pulp cavity and no plug of osteodentine. Body cylindrical or slightly depressed, without ridges on sides. Precaudal tail about as long as body or slightly longer. Caudal peduncle without lateral keels or precaudal pits. Pectoral fins small, broad and rounded. Pectoral fins aplesodic and with fin radials not expanded into fin web. Pectoral propterygium small and fused with mesopterygium; pectoral-fin radial segments mostly 3 or (rarely) 2 or 4, and with longest distal segments less than 0.3 of length of longest proximal segments. Pelvic fins about as large as dorsal fins and slightly larger than anal fin, noticeably smaller than pectorals and with anterior margins 0.6 to 0.8 of pectoral-fin anterior margins. Claspers with unique mesospurs, claws and dactyls (Compagno, 1988). Dorsal fins equal-sized. First dorsal-fin origin and insertion well behind the pelvic-fin bases. Anal fin somewhat smaller than second dorsal fin, with broad base, angular apex, origin well ahead of second dorsal-fin origin, and insertion separated by a space much greater than its base length from lower caudal origin. Caudal fin horizontally elongated and not crescentic, weakly heterocercal and with its upper lobe hardly elevated above the body axis; dorsal caudal-fin margin less than one-fourth as long as the entire shark. Caudal fin with a strong terminal lobe and subterminal notch but without a ventral lobe, preventral and postventral margins not differentiated but forming a continuous curve. Vertebral centra without radii, with solid or hollow intermedialia and diagonal calcified knobs present or absent. Total vertebral count 159 to 199, monospondylous precaudal count 35 to 48, diplospondylous precaudal count 72 to 95, diplospondylous caudal count 51 to 65, and precaudal count 111 to 138. Cranium narrow and not greatly expanded laterally. Medial rostral cartilage moderately long and not reduced to a low nubbin. Nasal capsules elevated and not greatly depressed but strongly fenestrated, internarial septum high and compressed. Orbits with enlarged fenestrae for preorbital canals, medial walls greatly fenestrated around the optic nerve foramina. Supraorbital crests absent from cranium. Suborbital shelves strongly reduced. Cranial roof with a continuous fenestra from the anterior fontanelle to the parietal fossa. Basal plate of cranium with a pair of internal carotid foramina but no stapedial foramina. Adductor mandibulae muscle of jaws with two divisions. Preorbitalis muscles not extending onto posterodorsal surface of cranium. Anterodorsal palpebral depressor, rostromandibular, rostronuchal and ethmonuchal muscles present (Compagno, 1988) and unique to the family. Valvular intestine of conicospiral type with 6 to 9 turns. Development oviparous. Size small with adults 34 to 91 cm. Colour pattern of obscure or prominent dark saddles, with or without numerous small to large black or white spots, blotches and collar markings around branchial region.

Distribution: These are little-known sharks of inshore to deepish temperate and tropical, continental waters of the western Pacific. One genus (***Parascyllium***) is confined to Australian waters while the second (***Cirrhoscyllium***) occurs in the South China sea from Viet Nam north to Taiwan (Province of China) and Japan.

Habitat: These sharks occur on the bottom from close inshore to at least 435 m deep offshore. They are found on muddy, sandy or rocky bottom.

Biology: These small, harmless bottom sharks are rare to common in some areas but are poorly known biologically. They apparently can change colour somewhat to match the bottom type. All species are small, less than a metre long when mature. At least some and possibly all of the species are oviparous, depositing eggs in elongated, flattened egg cases on the bottom. Food habits are little known, but probably these sharks include small fishes, crustaceans, and other bottom invertebrates in their diet.

Interest to Fisheries and Human Impact: Several species are taken in bottom trawls as incidental and minimal bycatch, but utilization is probably minimal. They are harmless to people. Conservation status is uncertain, but should be monitored as they have restricted and localized distributions and some of them occur in areas of heavy inshore and offshore fishing activity, including demersal trawling. Some members of the family have been kept in captivity in public aquaria and make attractive displays, particularly the spectacularly marked ***Parascyllium variolatum***. Michael (1993) suggested that these sharks are suitable for captive breeding programmes, being small and hardy in captivity.

Local Names: Collared carpet sharks, Australian cat sharks.

Remarks: Applegate (1974) proposed a separate family for the genus ***Cirrhoscyllium***, but external and anatomical studies (Compagno, 1984, 1988) suggested that this genus is closely related to ***Parascyllium*** although readily distinguishable from it, and that both genera are referable to a single family Parascylliidae. These sharks are remote from other orectoloboids and are distinguishable from them by their unique, carcharhinoid-like teeth with strong labial root lobes and low basal ledges, arched mouths, position of the anal-fin origin well anterior to the second dorsal-fin origin, cranial morphology, extraordinarily derived cranial muscles, and spiral intestinal valves with few turns. The clasper morphology of parascylliids is unique and highly derived, with a unique, medial, finger-like, spur-bearing lobe (dactyl) supported by the dorsal terminal cartilage as well as a row of unique clasper hooks on the ventral terminal cartilage.

Applegate (1974) placed the two parascylliid genera in a separate suborder of the Orectolobiformes, emphasizing their distinctiveness. Compagno (1988) suggested that the Parascylliidae is the plesiomorphic sister group of all other orectoloboids. Dingerkus (1986), in contrast made Parascylliidae the sister group of Orectolobidae and Brachaeluridae only.

Literature: Regan (1908a); Smith (1913); Garman (1913); Whitley (1940); Fowler (1941, 1967a); Stead (1963); Compagno (1973, 1984, 1988); Applegate (1974); Dingerkus (1986); Last and Stevens (1994); Goto and Nakaya (1996).

Key to Genera:

1a. A pair of barbels on throat (Fig. 89); colour pattern of dark saddles, no light or dark spots . . . . ***Cirrhoscyllium***

1b. No barbels on throat (Fig. 90); colour pattern of saddles, dark spots, or dark and light spots . . . . ***Parascyllium***

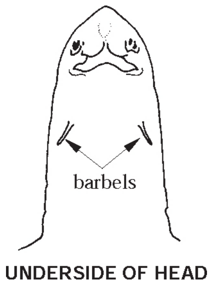


Fig. 89 ***Cirrhoscyllium***

Fig. 90 ***Parascyllium***

Cirrhoscyllium Smith and Radcliffe, 1913

Genus: ***Cirrhoscyllium*** Smith and Radcliffe *in* Smith, 1913, *Proc. U.S. Natl. Mus.*, 45(1997): 568.

Type Species: ***Cirrhoscyllium expolitum*** Smith and Radcliffe, 1913, by original designation.

Number of Recognized Species: 3.

Synonyms: Genus ***Zev*** Whitley, 1927: 289. Unjustified replacement name for ***Cirrhoscyllium*** Smith and Radcliffe, 1913, thought by Whitley to be a junior synonym of ***Cirriscyllium*** Ogilby, 1908 = ***Brachaelurus*** Ogilby, 1907. Type species: ***Cirrhoscyllium expolitum*** Smith and Radcliffe, 1913, by replacement and by original designation.

Diagnostic Features: Snout relatively long, narrow and pointed, head broad and flattened. A pair of cartilage-cored barbels present on ventrolateral surface of throat below rear corners of eyes, unique to this genus and found in no other sharks. Eyes horizontally oval. Tooth count 23 to 32/22 to 27 in adults and subadult juveniles. Pectoral fins relatively thin and rather large, their anterior margins nearly equal to head length and to distance between bases of pectoral and pelvic fins. Vertebrae few, total count 159 to 175. Size small, adults 34 to 49 cm long. Colour pattern of dark saddles present, but no spots on body or collar markings around gills.

Remarks: Data for the three species of ***Cirrhoscyllium*** are from Smith and Radcliffe *in* Smith (1913), Kamohara (1943), Teng (1959b), Shiino (1972), Compagno (1984), Nakaya and Shirai (1984), Goto, Nakaya and Amaoka (1994), and Goto and Nakaya (1996), who reviewed the genus. Compagno (1984) based keys and diagnoses for the three species of ***Cirrhoscyllium*** on Smith and Radcliffe (1913), Kamohara (1943), and Teng (1959b) as well as on examination of the holotype of ***C. expolitum***, but noted: "It is not certain at present whether the characters used to distinguish the three species are valid, and if so, if the three species are synonyms. Pending further studies on the genus these species are provisionally recognized."

Goto and Nakaya (1996) examined a sample of 22 ***C. japonicum*** as well as the 11 paratypes of ***C. formosanum*** and the holotype of ***C. expolitum***. They indicated that the characters used by Compagno (1984) were variable and not entirely diagnostic. These characters include position of first dorsal-fin origin relative to the pelvic fins, position of first dorsal-fin origin relative to the snout tip and subterminal notch, position of anal-fin insertion relative to second dorsal fin, size of anal-fin base relative to the dorso-caudal space, and number of dark saddle markings on sides. They provided additional morphometric and colour characters (adopted here) to separate the three species. Their account suggests that ***C. japonicum*** is readily separable from the two other species, but that additional comparative material of ***C. expolitum*** and ***C. formosanum*** is desirable to determine if the morphometric and vertebral count characters of these species are valid. The humped back suggested by Compagno (1984) as a characteristic of ***Cirrhoscyllium*** was thought by Goto and Nakaya (1996) to be an artefact of preservation.

Key to Species (modified from Goto and Nakaya, 1996):

1a. Saddle-markings bold, saddles on back over abdomen discrete C-shaped; second dorsal-fin base usually shorter and rarely equal to anal-caudal space; precaudal vertebral count 117 to 123 (Fig. 91). . . . . . ***Cirrhoscyllium japonicum***

1b. Saddle-markings diffuse, saddles on back over abdomen rounded and confluent with saddles over pelvic fins; second dorsal-fin base equal to or longer than anal-caudal space (Fig. 92); precaudal vertebral count 108 to 117 . . . . → ***2***

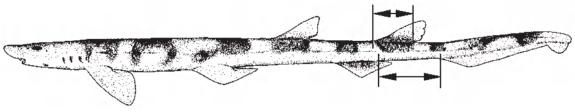


Fig. 91 *Cirrhoscyllium japonicum*

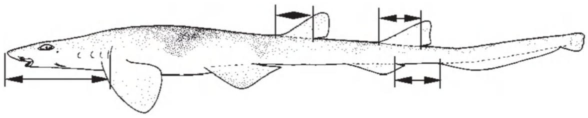


Fig. 92 *Cirrhoscyllium expolitum*

2a. Head length 3.0 times first dorsal-fin base (Fig. 92); total vertebral count 154, precaudal vertebral count 108 . . . . . . ***Cirrhoscyllium expolitum***

2b. Head length 2.3 to 2.6 times first dorsal-fin base (Fig. 93); total vertebral count 159 to 167, precaudal vertebral count 112 to 117 . . . . ***Cirrhoscyllium formosanum***

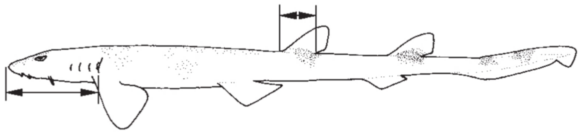


Fig. 93 *Cirrhoscyllium formosanum*

Cirrhoscyllium expolitum Smith and Radcliffe, 1913

Fig. 94

Cirrhoscyllium expolitum Smith and Radcliffe *in* Smith, 1913, *Proc. U.S. Natl. Mus.*, 45(1997): 568, figs 1-2, pl. 45. Holotype: US National Museum of Natural History, USNM-74603, 335 mm adult female, 21° 33′ N, 116° 13′ E, South China Sea between northern Luzon, Philippines, and China, 183 m. Status and correction in longitude from Howe and Springer (1993, *Smiths. Contr. Zool.*, [540]: 7); also by author's examination of the holotype.

Synonyms: None.

Other Combinations: None.

FAO Names: En - Barbelthroat carpet shark; **Fr** - Requin-carpette á moustache; **Sp** - Alfombrera barbuda.

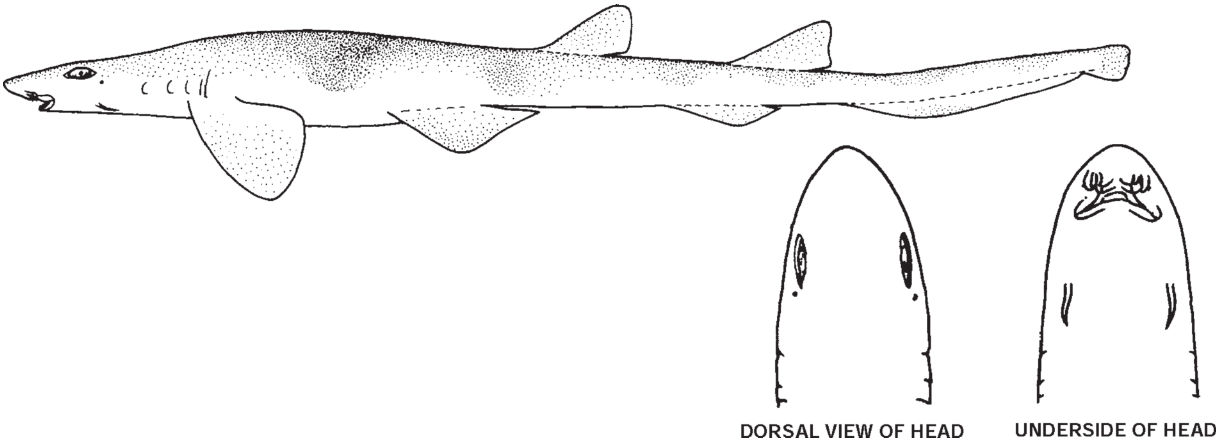
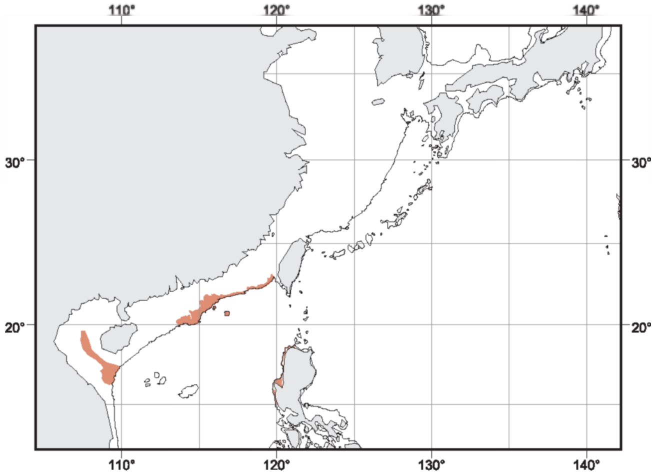


Fig. 94 *Cirrhoscyllium expolitum*

Field Marks: Barbels on throat, nasoral grooves, mouth in front of eyes, six or possibly ten diffuse saddle marks on dorsal surface, saddles above abdomen rounded and continuing above pelvic-fin bases, not C-shaped, head length three times first dorsal-fin base.

Diagnostic Features: Head length 3.0 times first dorsal-fin base. Anal-caudal space 7.7% of total length, 43% of head length. Second dorsal-fin base equal to or longer than anal-caudal space. Precaudal vertebral count 108, total count 154. **Colour:** six to possibly ten indistinct pairs of saddle markings on sides of back and tail; an elongated rounded saddle on each side of back between bases of pectoral and pelvic fins and extending over pelvic-fin bases.

Distribution: Western North Pacific: South China Sea off the coast of China between China and Luzon, Philippines, and in the Gulf of Tonkin off Viet Nam. Nominal from Okinawa (Uchida, 1982) but record uncertain, possibly *C. japonicum*?



Habitat: Outer continental shelf, South China Sea on bottom at 183 to 190 m depth.

Biology: A little-known and presumably rare or uncommon tropical bottom shark. Probably oviparous, judging from large nidamental glands. Food habits unknown.

Size: The adult female holotype is 335 mm long while a Vietnamese female (maturity stage unknown) is 306 cm long (Kharin, 1987).

Interest to Fisheries and Human Impact: Interest to fisheries unknown, probably taken as discarded bycatch of offshore trawl fisheries in the area, conservation status unknown.

Local Names: Higezame (Japan).

Literature: Smith (1913); Fowler (1941); Teng (1959b); Compagno (1984); Kharin (1987); Goto and Nakaya (1996).

Cirrhoscyllium formosanum Teng, 1959

Fig. 95

Cirrhoscyllium formosanum Teng, 1959b, *Taiwan Fish. Res. Inst., Keelung, Lab. Fish. Biol. Rep.*, (7): 1, pl. 1. Holotype: Taiwan Fisheries Research Institute, TFRI 3574, 367 mm female, off Kao-hsiung, Taiwan (Province of China), 110 m.

Synonyms: None.

Other Combinations: None.

FAO Names: En - Taiwan saddled carpet shark; **Fr** - Requin-carpette chin; **Sp** - Alfombrera de Taiwan.

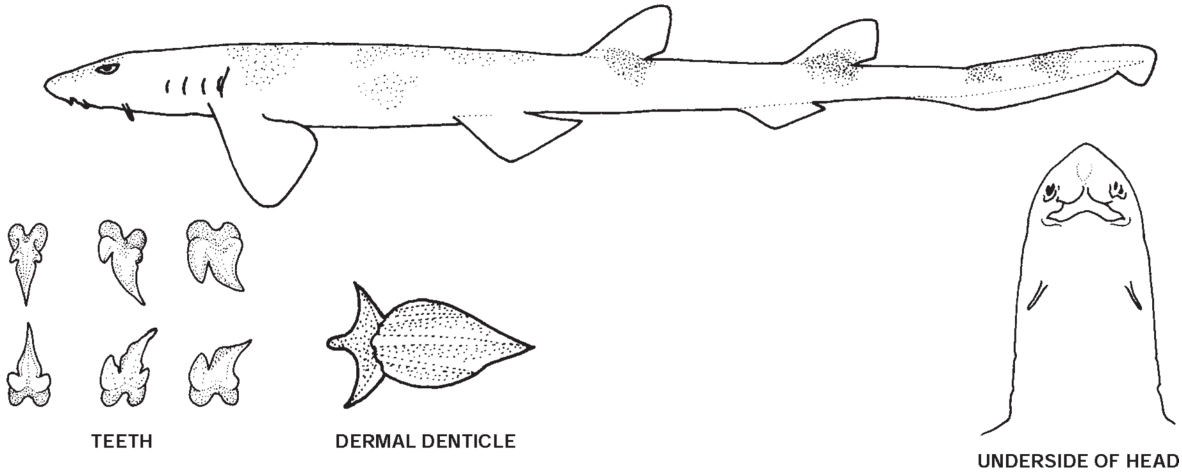
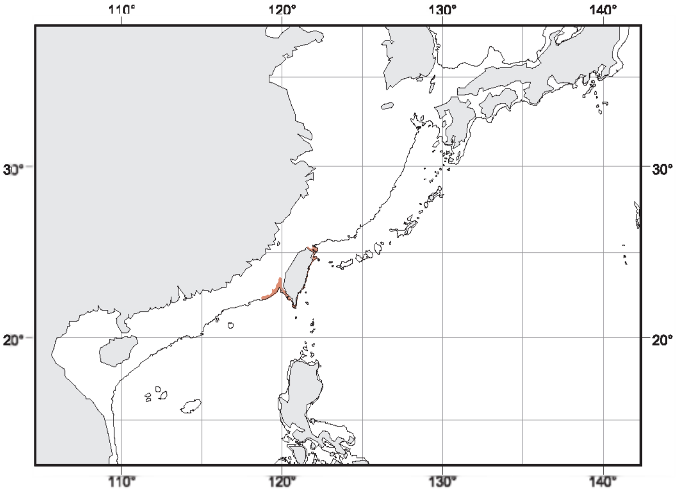


Fig. 95 ***Cirrhoscyllium formosanum***

Field Marks: Barbels on throat, nasoral grooves, mouth in front of eyes, six diffuse saddle marks on dorsal surface, saddles above abdomen rounded and continuing above pelvic-fin bases, not C-shaped, head length 2.3 to 2.6 times first dorsal-fin base.

Diagnostic Features: Head length 2.3 to 2.6 times first dorsal-fin base. Anal-caudal space 6.8 to 7.7% of total length, 38 to 45% of head length. Second dorsal-fin base equal to or longer than anal-caudal space. Precaudal vertebral count 112 to 117, total count 159 to 167. **Colour:** six pairs of indistinct saddle markings on sides of back and tail; an elongated rounded saddle on each side of back between bases of pectoral and pelvic fins and extending over pelvic-fin bases.

Distribution: Western North Pacific: Taiwan Island (Province of China).



Habitat: Outer shelf of Taiwan (Province of China) at depth of about 110 m.

Biology: A little-known small, tropical or subtropical shark, biology essentially unknown. Twelve specimens (11 paratypes and the holotype) are in the Taiwan Fisheries Research Institute, all collected off Kao-hsiung, Taiwan (Province of China). That all the paratypes were collected in one day on longlines suggests that the species may be or was common although possibly localized.

Size: Maximum 39 cm; eight males 35.2 to 37.7 cm; one paratype male 35.9 cm TL from this series was adult according to Goto and Nakaya (1996), and presumably the larger males were also mature. Females 35.2 to 38.5 cm possibly adult if adult females attain a size similar to ***C. expolitum***.

Interest to Fisheries and Human Impact: Interest to fisheries unknown, taken on bottom longlines off Taiwan (Province of China), presumably also as discarded trawl bycatch. Conservation status unknown.

Literature: Teng (1959b); Compagno (1984); Goto and Nakaya (1996).

Cirrhoscyllium japonicum Kamohara, 1943

Fig. 96

Cirrhoscyllium japonicum Kamohara, 1943, *Bull. Biogeogr. Soc. Japan*, 13(17): 126, fig. 1. Holotype: 485 mm female from Mimase, Shikoku, Japan, possibly at Kochi University, Kochi City, Japan (Dr T. Abe, pers. comm.). According to Goto and Nakaya (1996: 205), Kamohara (1961, *Rep. Usa Mar. Biol. St.* 8: 1-9, not seen) designated a neotype (Kochi University, Department of Biology, Faculty of Science, BSKU-3656, 291 mm immature female, from Mimase Fish Market) to replace the holotype, which was destroyed during the second world war. Goto and Nakaya suggested that Kamohara's designation was invalid according to the International Code of Zoological Nomenclature (1985, Art. 75b[i] and 75d[1,2]), but redesignated the same specimen as neotype.

Synonyms: None.

Other Combinations: None.

FAO Names: **En** - Saddled carpet shark; **Fr** - Requin-carpette chat; **Sp** - Alfombrera japonesa.

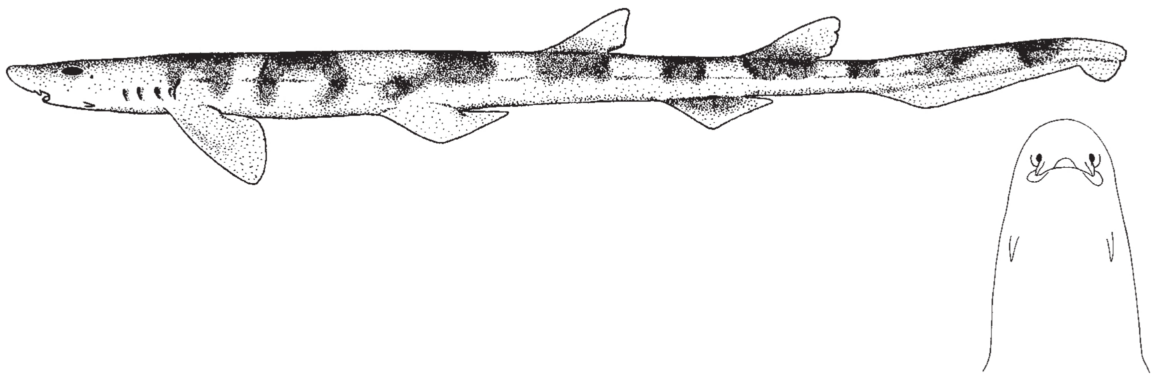
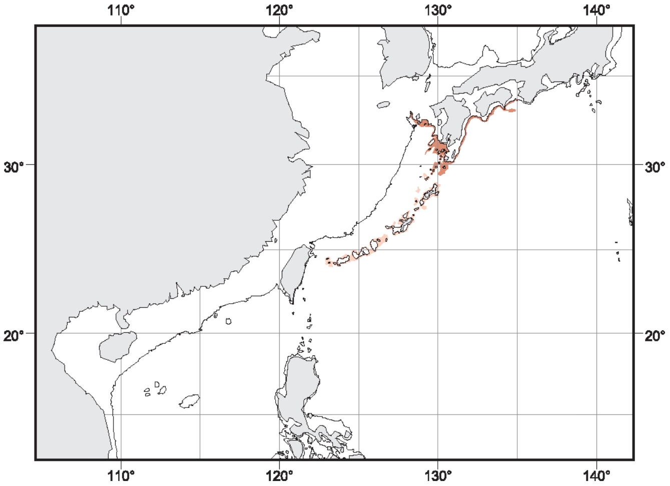


Fig. 96 ***Cirrhoscyllium japonicum***

Field Marks: Barbels on throat, nasoral grooves, mouth in front of eyes, nine well-defined saddle marks on sides of body, with C-shaped saddles on abdomen.

Diagnostic Features: Head length 2.2 to 2.6 times first dorsal-fin base. Anal-caudal space 7.5 to 9.7% of total length. Anal-caudal space 45 to 62% of head length. Second dorsal-fin base usually shorter and rarely equal to anal-caudal space. Precaudal vertebral count 117 to 123. Total vertebral count 165 to 175. **Colour:** nine well-defined pairs of saddle-markings on sides of back and tail; a strongly marked C-shaped saddle on each side of back between pectoral and pelvic-fin bases and discrete from saddles over pelvic-fin bases.



Distribution: Western North Pacific: Japan, off southwest coast from Shikoku and Kyushu southwest to Yakushima Island and possibly the Riu-Kyu Islands.

Habitat: Uppermost slope of southwestern Japan at depths of 250 to 290 m.

Biology: Biology poorly known. Apparently oviparous, as cased eggs were discovered in a 445 mm female. A morphological study of the throat barbels of this shark (Goto, Nakaya and Amaoka, 1994) suggested that they were mechanical sensors, without obvious chemical or other sense organs, and that they were unique to the genus ***Cirrhoscyllium***.

Size: Maximum 48.5 cm; females immature at 25.7 to 42.4 cm, adolescent at 43.1 cm, and adult at 44.5 cm, maximum 48.5 cm; males immature at 22.8 cm, adolescent at 36.6 cm, and adult at 36.7 to 40.7 cm.

Interest to Fisheries and Human Impact: Interest to fisheries unknown. Possibly taken as a bycatch of trawl fisheries. Conservation status unknown.

Local Names: Kurakake-zame, or Kurakakezame, Higezame, Saddled catshark (Japan).

Remarks: A female specimen nominally referred to ***C. expolitum*** (Uchida, 1982) was collected off the Riu-Kyu Islands and kept in an aquarium in Okinawa where it laid eggs; it may refer to this species.

Literature: Kamohara (1943); Teng (1959b); Uchida (1982); Compagno (1984); Goto, Nakaya and Amaoka (1994); Goto and Nakaya (1996).

Parascyllium **Gill, 1862**

Genus: ***Parascyllium*** Gill, 1862b, *Ann. Lyceum Nat. Hist. New York*, 7(32): 408, 412.

Type Species: ***Hemiscyllium variolatum*** Dumeril, 1853, by original designation.

Number of Recognized Species: 4.

Synonyms: Subgenus ***Neoparascyllium*** Whitley, 1939: 227 (Genus ***Parascyllium*** Gill, 1862). Type species: ***Parascyllium multimaculatum*** Scott, 1935, by original designation.

Diagnostic Features: Snout relatively short, thick, and broadly rounded, head narrow and cylindrical. No barbels on throat. Eyes more elongated and slit-like. Tooth count 37 to 54/33 to 49 in adults. Pectoral fins thick, muscular, and rather small, their anterior margins much less than head length and than distance between pectoral and pelvic-fin bases. Vertebrae numerous, total count 188 to 199. Size of adults 60 to 91 cm long. Colour pattern of light or dark spots present, sometimes with dark saddles, black blotches, and collar markings around gills.

Remarks: The present arrangement of the species of ***Parascyllium*** follows Whitley (1940), Compagno (1984), and Last and Stevens (1994) in most details.

Key to Species (after Compagno, 1984, and Last and Stevens, 1994):

1a. Gill region with a prominent dark collar marking dotted with dense white spots; body with brown blotches and small white spots; fins with very prominent large black blotches (Fig. 97) . . . . . . ***Parascyllium variolatum***

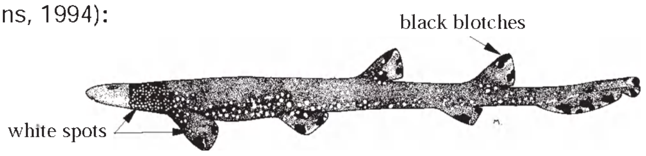


Fig. 97 ***Parascyllium variolatum***

1b. Gill region with or without an indistinct to prominent dusky collar marking, with or without a few brown spots but lacking white spots; body with small to moderately large brown spots but no blotches; fins without black blotches (Fig. 98) . . . . → ***2***

Fig. 98 ***Parascyllium collare***

2a. Gill region with a prominent dusky collar, sharply delimited from front of head; dark spots absent from pectoral fins (Fig. 98) . . . . ***Parascyllium collare***

2b. Gill region with collar marking absent, pale or obscure, not sharply delimited from front of head; dark spots usually present on pectoral fins . . . . → ***3***

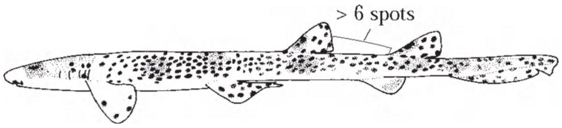


Fig. 99 ***Parascyllium ferrugineum***

3a. More than six spots on flanks between dorsal fins (Fig. 99); a littoral species on the continental shelves . . . . . ***Parascyllium ferrugineum***

3b. Less than six dark spots on flanks between dorsal fins (Fig. 100); a deepwater species on the continental slopes . . . . ***Parascyllium sp. A***

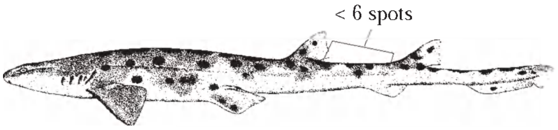


Fig. 100 ***Parascyllium*** **sp. A**

Parascyllium collare Ramsay and Ogilby, 1888 Fig. 101

Parascyllium collare Ramsay and Ogilby, 1888, *Proc. Linn. Soc. New South Wales*, ser. 2, 3: 1310. Holotype: Australian Museum, Sydney, AMS-I.1874, > 76 cm (30 in) TL adult male, in deep water off Port Jackson, New South Wales, Australia.

Synonyms: None.

Other Combinations: None.

FAO Names: En - Collared carpet shark; **Fr** - Requin-carpette à collarette; **Sp** - Alfombrera collareja.

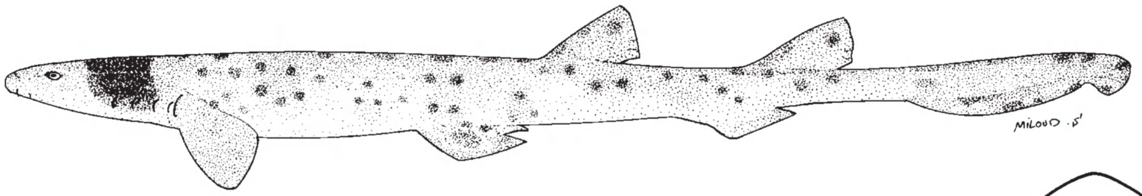


Fig. 101 ***Parascyllium collare***

UNDERSIDE OF HEAD

Field Marks: Prominent dark, unspotted, sharp-edged collar mark around the gills, dusky saddles on back and tail, and sparse, large dark spots on body, tail and fins; nasal barbels, nasoral and circumnarial grooves present; mouth in front of eyes, two equal-sized, spineless dorsal fins and an anal fin, the first dorsal-fin origin behind the pelvic-fin bases, the anal-fin origin well in front of the second dorsal-fin origin.

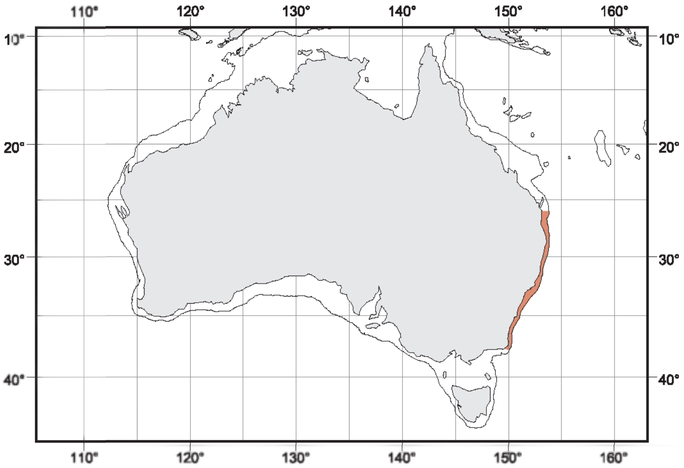
Diagnostic Features: Colour: light yellowish to reddish brown with five dusky saddles on trunk and tail; a prominent dark, unspotted collar marking around gill region; no white spots on body; no bold black blotches and spots on fins; sparse, scattered, large dark brown spots on sides and fins, except for pectoral fins, no more than two or three irregular longitudinal rows of spots on sides and less than six spots on sides of tail between the dorsal fins.

Distribution: Western South Pacific: confined to the east coast of Australia (Victoria, New South Wales, and southern Queensland from Gabo Island to Mooloolaba).

Habitat: A little-known temperate bottom shark of the eastern Australian continental shelf, found at depths of 20 to 160 m on hard bottom including inshore rocky reefs and hard-bottomed trawling grounds.

Biology: Development oviparous, but details little-known. Eggcase described as flattened and elongate, but details not given. Apparently common or formerly common on hard bottom at depths of 55 to 128 m on trawling grounds off New South Wales.

Size: Maximum about 87 cm; adult males 80 to 85 cm long; adult females 85 to 87 cm.



Interest to Fisheries and Human Impact: Interest to fisheries essentially none, not utilized but taken as bycatch by commercial vessels, including trawlers and possibly line boats. Conservation status unknown.

Local Names: Collared catshark or Cat shark, Collared carpet shark.

Remarks: According to Last and Stevens (1994) this species was confused with other species of ***Parascyllium*** and is somewhat less wide-ranging than previously thought. It was recorded from Tasmania but these records are apparently based on ***P. ferrugineum.***

Literature: McCulloch (1911); Whitley (1940); Fowler (1941); Stead (1963); Compagno (1984); Last and Stevens (1994).

Parascyllium ferrugineum McCulloch, 1911

Fig. 102

Parascyllium ferrugineum McCulloch, 1911, *Zool. Resul. Fish. Exper. F.I.S. "ENDEAVOUR"*, 1: 7, pl. 2, fig. 2, text fig. 2. Holotype: Australian Museum, Sydney, possibly AMS E.4604 (Eschmeyer, 1998, *Cat. Fish.*: CD-ROM), 730 mm female, outside Port Phillip Heads, Victoria.

Synonyms: ***Parascyllium multimaculatum*** Scott, 1935: 63, fig. 1. Holotype: Queen Victoria Museum and Art Gallery, Launceston, Tasmania, QVM old no. H.T.983 (mounted, missing in 1974 according to Eschmeyer, 1998: CD-ROM), 710 mm adult male, Tamar Heads, Devon Dorset, Tasmania, Australia. Synonymy after Last and Stevens (1994: 120).

Other Combinations: None.

FAO Names: En - Rusty carpet shark; **Fr** - Requin-carpette roux; **Sp** - Alfombrera mohosa.

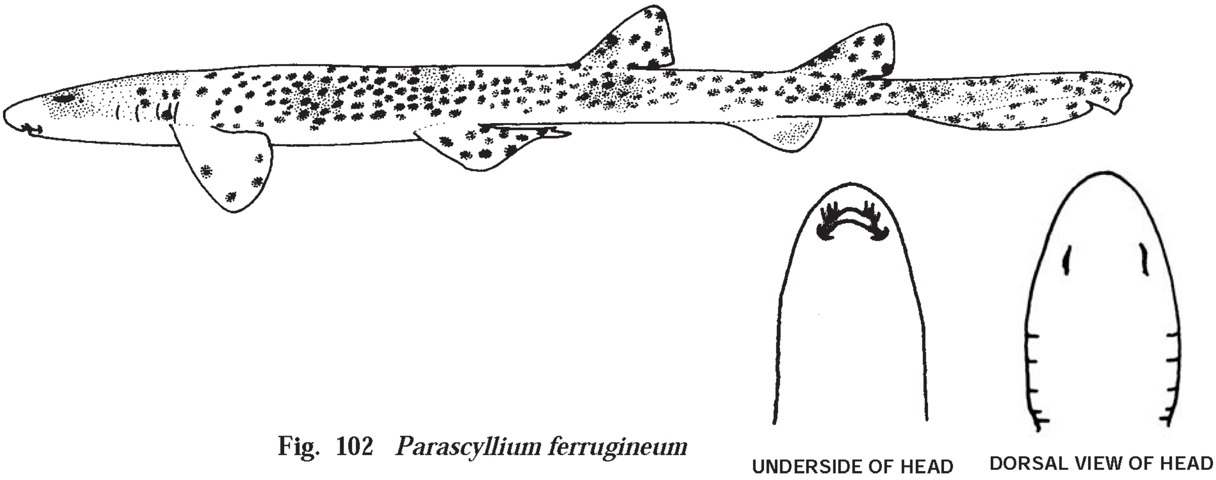
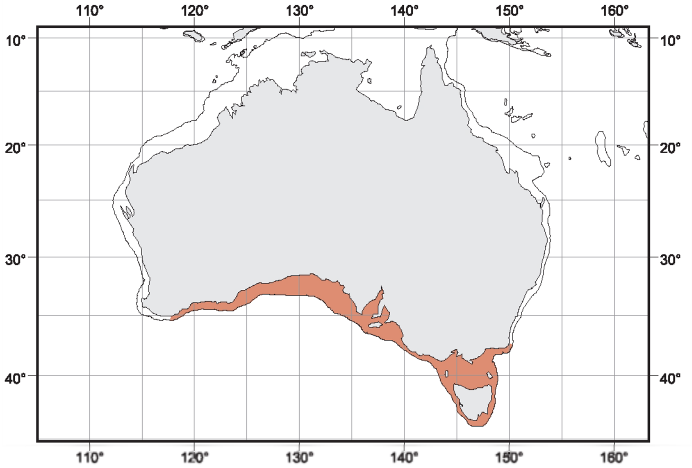


Fig. 102 *Parascyllium ferrugineum*

Field Marks: Inconspicuous dusky collar around the gills, with or without three or four dark spots; six or seven dusky saddles on back and tail; moderately sparse to dense, large to small dark brown or blackish spots on body, tail and fins, more than six dark spots on the sides of the tail between the dorsal fins; nasal barbels, nasoral and circumnarial grooves present, mouth in front of eyes; two equal-sized, spineless dorsal fins and an anal fin, the first dorsal-fin origin behind the pelvic-fin bases, the anal-fin origin well in front of the second dorsal-fin origin.

Diagnostic Features: Colour: grey-brown with six dusky saddles on trunk, tail and caudal fin; an indistinct dark, collar marking around gill region, unspotted or with up to three or four dark spots; no white spots on body; no bold large black blotches on fins though unpaired fins usually have small to large rounded black spots on them; moderately sparse to dense, scattered, large dark brown spots on body and fins, three or four (mainland) to five or six (Tasmania) irregular longitudinal rows of dark spots on sides, and more than six spots on the sides of the tail between the dorsal fins.

Distribution: Western South Pacific: Confined to the south and east coasts of Australia (Western Australia, South Australia, Victoria, from Albany to Gabo Island, and Tasmania).



Habitat: A little-known temperate-water shark of the Australian continental shelf, on or near the bottom at depths of 5 to 150 m. Off Tasmania close inshore near rocks and river mouths. Occurs in beds of algae on reefs or in seagrass. Hides in rocky caves and ledges during the day.

Biology: A poorly known nocturnal shark. Oviparous, lays eggs in yellow cases with long tendrils during the summer. Feeds on bottom-dwelling crustaceans and molluscs.

Size: Maximum about 80 cm; possible hatchling about 17 cm; males mature by 60 cm, adult males recorded at 71 to 75 cm; adolescent female 74 cm.

Interest to Fisheries and Human Impact: Interest to fisheries essentially none, not utilized but taken as bycatch by commercial vessels, captured in bottom trawls and possibly by line gear. Conservation status unknown.

Local Names: Rusty carpet shark, Rusty catshark or Cat shark, Tasmanian spotted catshark or Cat shark, Tasmanian carpet shark, Requin-carpette tacheté, Alfombrera tasmánica.

Remarks: Scott (1935) named ***Parascyllium multimaculatum*** as a distinct species for an adult female specimen of ***Parascyllium*** from Tasmania with densely scattered small dark spots. Whitley (1939, 1940) recognized this species and proposed a new subgenus, ***Neoparascyllium*** Whitley, 1939, for it because it differed from other species in having the first dorsal "insertion" (= origin) behind the middle of the total length and by its markings (more numerous small dark brown spots). Compagno (1984) examined specimens of ***Parascyllium multimaculatum*** from Tasmania and recognized the species, but noted that the species differed little from ***P. ferrugineum*** and ***P. collare*** except in colour pattern and did not warrant a separate subgenus. The morphometric character was thought to be invalid by Compagno (1984), as two Tasmanian specimens from Green's Beach near the Tamar River mouth with numerous spots (one of these was illustrated in Compagno, 1984) varied in this character (PD1 60% TL in an adult female vs. 48% TL in the illustrated adult male). This suggests that the position of the dorsal fin relative to the middle of the total length may be individually variable and may also vary according to size and even sex in this shark and in other species of ***Parascyllium***. Compagno (1984) distinguished ***P. ferrugineum*** and ***P. multimaculatum*** by colour pattern only as follows:

> ***P. ferrugineum:*** Sparse, scattered, large dark brown spots on sides and fins, no more than three or four irregular rows of spots on sides.
>
> ***P. multimaculatum:*** Numerous small to large dark brown spots on sides and fins, five or six irregular rows of spots on sides.

Last and Stevens (1994) synonymized ***P. multimaculatum*** with ***P. ferrugineum***, and noted that "Tasmanian specimens [of ***P. ferrugineum***] have a variable but greater average density of spots which has led to their recognition as a separate species." The present account follows Last and Stevens' synonymy while noting that it is desirable to learn more about the nature of variation (including ontogenetic changes) in the colour pattern of these poorly-known sharks. Genetic comparisons between Tasmanian and mainland animals are also desirable.

Literature: McCulloch (1911); Whitley (1939, 1940); Fowler (1941); Scott (1961); Stead (1963); Compagno (1984); Michael (1993); Last and Stevens (1994).

Parascyllium variolatum (Dumeril, 1853) Fig. 103

Hemiscyllium variolatum Dumeril, 1853, *Rev. Mag. Zool.* (2) 5: 121, fig. 1. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN-1004, 36 cm TL female, from "côtes de l'Australie" (= Tasmania).

Synonyms: ***Parascyllium nuchalis*** McCoy, 1874: 15, pl. 2. Holotype: National Museum of Victoria, Melbourne, Australia, NMV no number (apparently lost according to Eschmeyer, 1998: CD-ROM), 84 cm adult female, Hobson's Bay, Victoria, Australia.

Other Combinations: None.

FAO Names: En - Necklace carpet shark; **Fr** - Requin-carpette à collier; **Sp** - Alfombrera colarina.

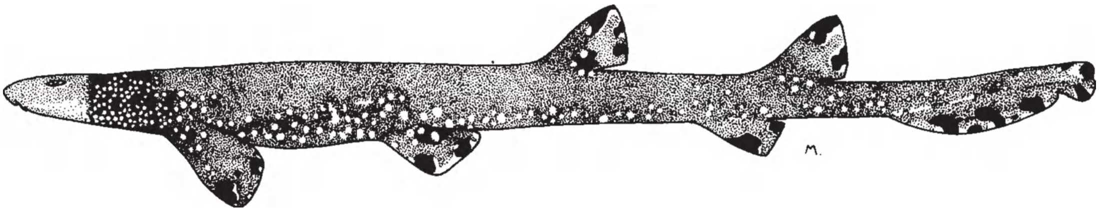
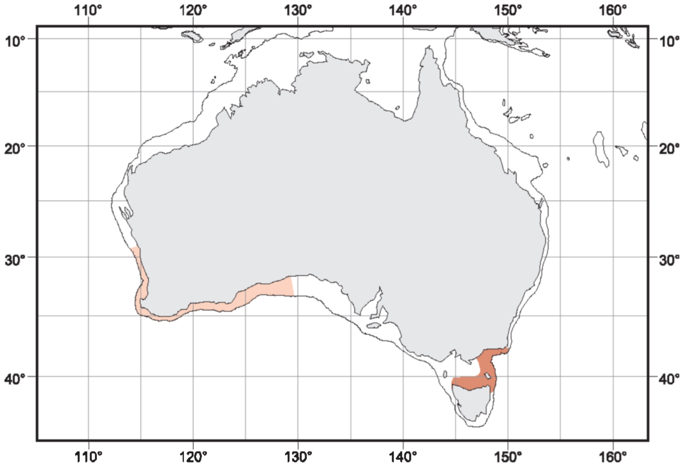


Fig. 103 *Parascyllium variolatum*

Field Marks: The bold, beautiful colour pattern of this shark is unmistakable: a unique, broad, dark, white-spotted collar around the gills, striking black spots or blotches on all fins, dark blotches and dense white spots on body; also, barbels, nasoral and circumnarial grooves present, mouth in front of eyes, two equal-sized, spineless dorsal fins and an anal fin, the first dorsal-fin origin behind the pelvic-fin bases, and the anal-fin origin well in front of the second dorsal-fin origin.

Diagnostic Features: Colour: dark greyish or brown (to chocolate brown) above and below, with six indistinct dark saddles variably present or obscure on trunk and tail; a blackish brown, extremely conspicuous collar marking around the gill region, densely spotted with white like a necklace of pearls; body clouded with irregular dark brown blotches and closely sprinkled with small to large white spots; bold black spots or blotches present on all fins, including prominent blotches on the precaudal fins and black spots alternating with white on the dorsal and ventral web of the caudal fin; discrete dark spots not present on sides of trunk and tail.



Distribution: Western South Pacific: South coast of Australia (Western Australia off Dongara to South Australia, and Victoria off Lakes Entrance, also north coast of Tasmania, but possibly including more than one species, the typical eastern form with type locality Tasmania and an additional western form from Western Australia).

Habitat: A temperate-water bottom shark of the Australian continental shelf at depths from inshore down to about 180 m. Apparently found in a variety of habitats, including sandy bottom, on rocky reefs, in beds of kelp, and in seagrass beds, but details of its ecology are virtually unknown.

Biology: Biology little-known, probably oviparous. Common or unabundant, but nocturnal and seldom seen during the day. Juveniles hide under rocks and bottom debris in shallow water. Coloration may vary considerably, and individuals taken on different bottoms vary in coloration including light spots and dark mottling and saddles, but little is known of the basis of these differences.

Size: Maximum about 91 cm.

Interest to Fisheries and Human Impact: Probably not utilized at present in fisheries. Role in aquarium trade unknown, but an obvious candidate for public display and for private aquaria. Conservation status uncertain.

Local Names: Varied carpet shark, Southern catshark, Southern collared cat shark, Necklace carpet shark, Varied catshark or cat shark, Hémiscylle tacheté.

Remarks: Last and Stevens (1994) noted that "Another white-spotted form occurring off southern Western Australia may be an additional undescribed species."

Literature: McCulloch (1911); Whitley (1940); Fowler (1941); Stead (1963); Compagno (1984); Michael (1993); Last and Stevens (1994).

Parascyllium sp. A Last and Stevens, 1994 Fig. 104

***Parascyllium* sp. A** Last and Stevens, 1994, *Sharks Rays Australia*: 118, pl. 16.

Synonyms: Not named.

Other Combinations: None.

FAO Names: En - Ginger carpet shark; **Fr** - Requin-carpette beige; **Sp** - Alfombrera jengibre.

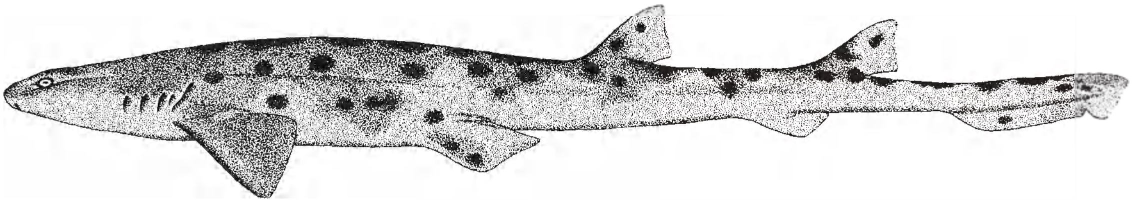
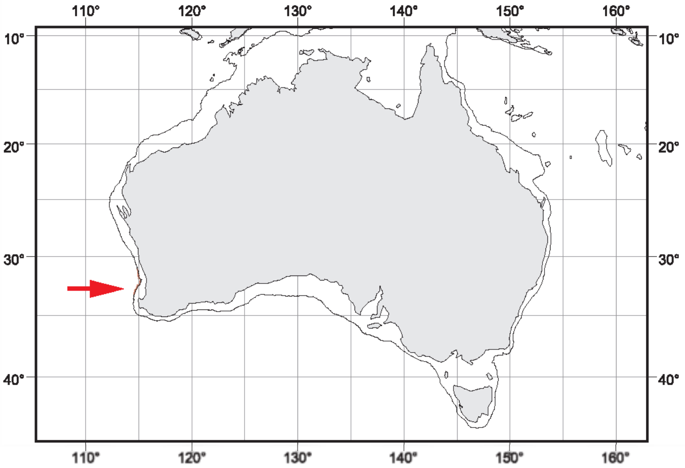


Fig. 104 *Parascyllium* sp. A

Field Marks: Inconspicuous dusky half collar around the gills without spots, five indistinct dusky saddles on back and tail, and sparse, large dark diffuse spots and blotches on the body and fins with fewer than six on the sides of the tail between the dorsal fins; nasal barbels, nasoral and circumnarial grooves present, mouth in front of eyes; two equal-sized, spineless dorsal fins and an anal fin, the first dorsal-fin origin behind the pelvic-fin bases and rear tips, the anal-fin origin well in front of the second dorsal-fin origin.

Diagnostic Features: Colour: pale brownish or greyish above, lighter below, with five inconspicuous saddles on trunk and tail; inconspicuous dusky half collar without spots around the gills; no white spots on body; no bold black spots or blotches on fins; sparse, large dark diffuse spots and blotches on the body and fins, sparse dark spots of sides not in rows, with fewer than six spots on the sides of the tail between the dorsal fins.

Distribution: Southeastern Indian Ocean: Continental slope of Australia (Western Australia between Lancelin and Bunbury).



Habitat: Upper continental slope at 245 to 435 m.

Biology: Virtually unknown.

Size: To at least 79 cm total length.

Interest to Fisheries and Human Impact: Unknown.

Local Names: Ginger carpet shark.

Literature: Last and Stevens (1994).

2.3.2 Family BRACHAELURIDAE

Family: Family Brachaeluridae Compagno, 1973, *J. Linn. Soc. (Zool.)*, 53, suppl. 1: 28. Name only, with the genera ***Brachaelurus*** and ***Heteroscyllium*** assigned to the family; Applegate, 1974, *J. Mar. Biol. Assoc. India*, 14(2): 745.

Type Genus: ***Brachaelurus*** Ogilby, 1907.

Number of Recognized Genera: 2.

Synonyms: Family Brachyaeluridae Eschmeyer and Bailey, 1990: 63; Eschmeyer, 1990: 435. Consistent emendation or error for Brachaeluridae Compagno, 1973 or Applegate, 1974.

FAO Names: En - Blind sharks; **Fr** - Requins aveugles; **Sp** - Tiburones ciegos.

Field Marks: Small sharks with nasoral grooves, perinasal grooves, long barbels, small transverse mouths in front of eyes, symphysial grooves, dorsolateral eyes, large spiracles below and behind eyes, no lateral skin flaps on head, two spineless dorsal fins and an anal fin, the second dorsal-fin origin well ahead of the anal-fin origin, and a short precaudal tail much shorter than the head and body.

Diagnostic Features: Head broad and somewhat flattened, without lateral flaps of skin. Snout broadly rounded. Eyes dorsolaterally situated on head and with strong subocular ridges below them. Eyes without movable upper eyelids but with subocular pockets and ridges below them. Spiracles very large and subequal or larger than eyes, with prominent raised external rims; spiracles somewhat below and behind eyes. Gill slits small, fifth gill slit close to fourth but not overlapping it; internal gill slits without filter screens. Nostrils with very long pointed barbels; circumnarial folds and circumnarial grooves present around outer edges of incurrent apertures. Nasoral grooves long and strongly developed. Mouth small, slightly arched and nearly transverse, subterminal on head. Lower lip not trilobate and without lateral orolabial grooves connecting edge of lip with medial ends of lower labial furrows, but with a longitudinal symphysial groove on chin. Lower labial furrows extending medially nearly to symphysis, but not connected medially by a mental groove or mental flap. Teeth not strongly differentiated in upper and lower jaws, with symphysial teeth not enlarged nor fang-like. Tooth row count 32 to 34/21 to 29. Teeth with a strong medial cusp, a pair of short lateral cusplets, and weak labial root lobes. Teeth orthodont with a central pulp cavity in crowns and no plug of osteodentine. Body cylindrical or moderately depressed, without ridges on sides. Precaudal tail shorter than body. Caudal peduncle without lateral keels or precaudal pits. Pectoral fins moderately large, broad and rounded. Pectoral fins aplesodic and with fin radials not expanded into fin web. Pectoral fin tribasal, propterygium very large and separate from mesopterygium and metapterygium; pectoral-fin radial segments three at most, and with longest distal segments less than 0.3 times the length of longest proximal segments. Pelvic fins about as large as dorsal fins and much larger than anal fin, nearly as large as pectoral fins and with anterior margins 0.5 to 0.7 times the pectoral-fin anterior margins. Claspers poorly known but probably without mesospurs, claws or dactyls. Dorsal fins equal-sized or with second dorsal fin slightly smaller than first. First dorsal-fin origin over pelvic-fin bases, insertion well behind the pelvic-fin rear tips. Anal fin less than half as large as second dorsal fin, with broad base, angular apex, origin about opposite second dorsal-fin midbase or insertion, and insertion separated by a space or narrow notch much less than base length from lower caudal-fin origin. Caudal fin horizontally elongated and not crescentic, weakly heterocercal with its upper lobe at a low angle above the body axis; dorsal caudal-fin margin about a fourth as long as the entire shark. Caudal fin with a strong terminal lobe and subterminal notch but without a ventral lobe, preventral and postventral margins not differentiated and forming a continuous curve. Vertebral centra with well-developed radii. Total vertebral count 117 to 142, monospondylous precaudal count 30 to 40, diplospondylous precaudal count 35 to 50, diplospondylous caudal count 46 to 62, and precaudal count 69 to 90. Cranium narrow and not greatly expanded laterally. Medial rostral cartilage moderately long and not reduced to a low nubbin. Nasal capsules elevated and not greatly depressed or fenestrated, internarial septum high and compressed. Orbits with small foramina for preorbital canals, medial walls not fenestrated around the optic nerve foramina. Supraorbital crests present on cranium but not laterally expanded and pedicellate. Suborbital shelves moderately broad and not greatly reduced. Cranial roof with isolated small frontal and parietal fenestrae but without a continuous fenestra from the anterior fontanelle to the parietal fossa. Basal plate of cranium with a pair of stapediocarotid foramina. Adductor mandibulae muscle of jaws with two divisions. Preorbitalis muscles not extending onto posterodorsal surface of cranium. No anterodorsal palpebral depressor, rostromandibular, rostronuchal or ethmonuchal muscles. Valvular intestine of spiral-ring type with 11 or 12 turns. Development ovoviviparous. Colour pattern of a few broad darker saddles present on back in young but obscure or absent in adults; small white spots present or absent. Size small, with adults between 52 and 122 cm but exceptionally over 1 m total length; young are born at 15 to 18 cm.

Distribution: Blind sharks are known from the western South Pacific, in the coastal waters of Australia from the east coast off New South Wales and Queensland; additional records from Western Australia and Northern Territory need confirmation.

Habitat: These are inshore bottom sharks of temperate and tropical continental coastal waters, ranging in depth from the intertidal down to 137 m. They commonly occur on rocky reefs, in seaweed, or on coral close inshore, sometimes in water only sufficient to cover them.

Biology: These are small sharks that attain a total length of less than 1.3 m, with most individuals less than 80 cm long. Live-bearing (ovoviviparous or aplacental viviparous), with foetal nutrition primarily from the large, yolky eggs; foetuses have large yolk-sacks which are reabsorbed just before birth. Litter size 6 to 8. Known prey of these sharks include small fishes, crustaceans, squid, and sea anemones. At least one of the species is very hardy and can live a long time out of water as well as surviving readily in captivity. The name 'blind shark' stems not from lack of vision but because these sharks close their eyelids when removed from the water.

Local Names: Blind sharks.

Remarks: There are two living and monotypic genera in this family: ***Brachaelurus*** Ogilby, 1907 and ***Heteroscyllium*** Regan, 1908, which are confined to Australian inshore coastal waters. The members of this family were included in the family Orectolobidae or Crossorhinidae until Compagno (1973) and Applegate (1974) placed them in their own family Brachaeluridae, which has been followed by various authors including Compagno (1981b, 1982, 1984, 1988), Cappetta (1986), Eschmeyer (1990, 1998), and Last and Stevens (1994), but not Nelson (1976, 1984), Gubanov, Kondyurin and Myagkov (1986), and Carroll (1986), who retain them in the Orectolobidae.

The systematic status of the genera of Brachaeluridae was uncertain until recently and was confounded by nomenclatural problems and doubts on the validity of the species ***Heteroscyllium colcloughi.*** Ogilby (1907) proposed his new genus ***Brachaelurus*** for ***Chiloscyllium modestum*** Günther, 1871 (equals ***Squalus waddi*** Bloch and Schneider, 1801). ***Brachaelurus*** has been uniformly recognized by subsequent authors. Ogilby (1908) proposed a second new genus, ***Cirriscyllium***, for ***C. modestum*** while transferring ***Brachaelurus*** to his new species ***B. colcloughi***. Regan (1908c) noted that as the two species are apparently generically distinct, ***Cirriscyllium*** was a junior synonym of ***Brachaelurus*** Ogilby, 1907 and that a new generic name, ***Heteroscyllium*** Regan, 1908, was necessary to replace ***Brachaelurus*** sensu Ogilby (1908) for the species ***B. colcloughi.***

Ogilby and McCulloch (1908), in a review of Australian Orectolobidae, adapted Regan's arrangement of ***Heteroscyllium*** as a genus for ***B. colcloughi*** and ***Brachaelurus*** as a genus for ***Chiloscyllium modestum*** (= ***Brachaelurus waddi***). Engelhardt (1913), Ogilby (1916), McCulloch and Whitley (1925), Whitley (1934, 1940), Bigelow and Schroeder (1948), Fowler (1967a), Compagno (1973, 1981b, 1982, 1984), and Applegate (1974) all followed this arrangement. Exceptionally and inexplicably Fowler (1967a) listed ***Hemiscyllium trispeculare*** Richardson, 1843 as a species of ***Brachaelurus*** along with ***B. waddi***.

Garman (1913) ranked ***Heteroscyllium*** as a subgenus for ***B. colcloughi*** within ***Brachaelurus***, which also included ***B. modestus***. Fowler (1929), White (1937), and more recently Last and Stevens (1994) placed ***H. colcloughi*** and ***B. modestum*** or ***B. waddi*** in ***Brachaelurus*** but did not recognize ***Heteroscyllium*** as a genus or subgenus. In contrast Fowler (1941) followed Ogilby (1908) in recognizing ***Brachaelurus*** as a genus based on ***B. colcloughi***, but reduced ***Cirriscyllium*** to a subgenus of ***Brachaelurus*** for inclusion of ***B. waddi***.

Whitley (1940) provided the first published illustrations of ***Heteroscyllium colcloughi*** (lateral view and underside of head) and a short diagnosis and description of the species. According to Whitley (1940), the type and only known specimen of ***H. colcloughi*** was a young male 45.7 cm (1.5 ft) long that was no longer preserved (as noted by Ogilby, 1916) and the illustrations (Whitley, 1940, fig. 77, 78) were from sketches of "the type" by A.R. McCulloch made "some years ago". Whitley apparently overlooked the existence of the second, Queensland Museum syntype of ***H. colcloughi*** (QM I-965, designated as lectotype below) as mentioned by Ogilby (1908, 1916) and Ogilby and McCulloch (1908), and which still exists. It is also unclear from Whitley's account if the sketches of the "type" were made from the specimen that was lost (AFAQ no. 410, see species account of ***H. colcloughi*** below) or from QM I-965.

Unfortunately Whitley's illustrations of the "type" of ***H. colcloughi*** are deceptive, leading Compagno (1984) to suggest that ***Heteroscyllium*** differed from ***Brachaelurus*** by lacking a symphysial groove and by having a much longer caudal fin, smaller spiracles well behind eyes, subterminal nostrils, a more anterior anal-fin origin, and a longer anal-caudal space. Dingerkus (1986) followed Whitley (1934, 1940) in suggesting that only a single specimen of ***H. colcloughi*** existed and stated: "Except for its lack of a chin cleft, descriptions of it fall within the variability of ***Brachaelurus waddi.*** Unless other specimens are collected to confirm its existence, I consider ***Heteroscyllium colcloughi*** to be based on an aberrant specimen of ***Brachaelurus waddi*** and thus synonymize ***Heteroscyllium colcloughi*** (Ogilby) under ***Brachaelurus waddi*** (Bloch et Schneider)".

Apart from the Queensland Museum syntype, an additional smaller specimen of ***Heteroscyllium colcloughi*** is preserved in the collection of the Australian Museum, Sydney (P. Last, pers. comm.). Last and Stevens (1994) noted that both ***H. colcloughi*** and ***B. waddi*** had symphysial grooves and were valid species. They considered ***Heteroscyllium*** a synonym of ***Brachaelurus*** on the suggestion that Compagno (1984) had primarily based the separation of the two genera on the symphysial groove character (which is not correct). They also gave a descriptive account of ***H. colcloughi*** and an accurate illustration presumably based on the Australian Museum specimen.

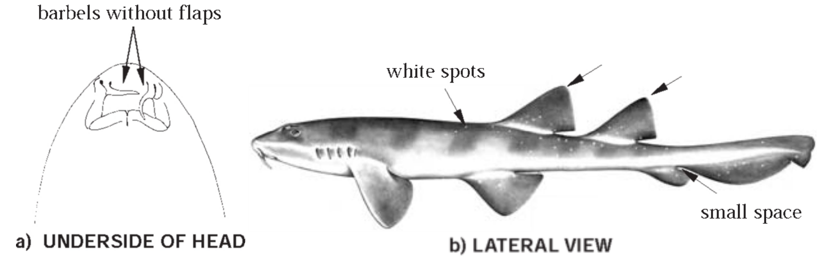
The Queensland Museum has over the past few decades acquired several additional specimens of ***Heteroscyllium colcloughi*** from Moreton Bay near Brisbane, and currently has 13 catalogued lots with all stages from late foetuses to adult females. Several of these specimens were examined by the writer (including the surviving syntype), and compared with specimens of ***Brachaelurus waddi*** during a visit to the Queensland Museum in July 1996. This suggests that a symphysial groove may have been omitted from Whitley's (1940) head sketch of ***H. colcloughi,*** which was otherwise accurate in comparison with specimens of ***H. colcloughi*** (all of which have the symphysial groove present). Also, Whitley's lateral view sketch shows the caudal fin too long and the spiracles are too small and too far from the eyes in comparison with specimens. With spurious characters eliminated, ***H. colcloughi*** can be separated from ***B. waddi*** in its own genus as clearly demonstrated by Ogilby (1908) and as redefined below.

Literature: Ogilby (1907, 1908); Regan (1908a,c); Ogilby and McCulloch (1908); Garman (1913); Whitley (1934, 1940); Fowler (1941); Bigelow and Schroeder (1948); Compagno (1973, 1984); Applegate (1974); Dingerkus (1986); Michael (1993); Last and Stevens (1994).

Key to Genera:

1a. Barbels without expanded posterior flaps; second dorsal fin about as large as first; anal-fin insertion just anterior to lower caudal-fin origin; usually brown above with white spots, no white patches on anterior margins and webs of dorsal fins (Fig. 105) . . . . ***Brachaelurus***

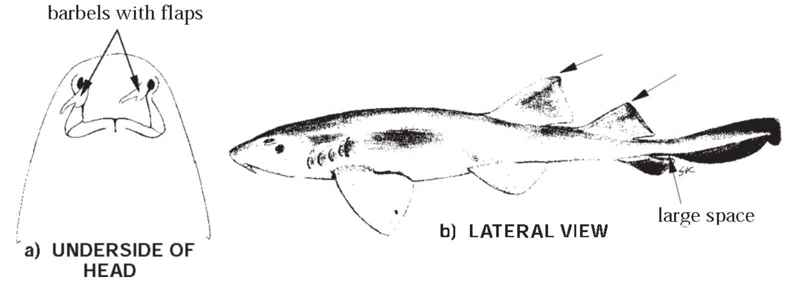
1b. Barbels with expanded posterior flaps at their mid-lengths; second dorsal fin smaller than first; anal-fin insertion separated from lower caudal origin by a space about equal to anal-fin inner margin; usually grey above without white spots, white patches on anterior margins and webs of dorsal fins (Fig. 106) . . . . . . ***Heteroscyllium***



a) UNDERSIDE OF HEAD

b) LATERAL VIEW

Fig. 105 ***Brachaelurus waddi***



a) UNDERSIDE OF HEAD

b) LATERAL VIEW

Fig. 106 ***Heteroscyllium colcloughi***

Brachaelurus Ogilby, 1907

Genus: ***Brachaelurus*** Ogilby, 1907, *Proc. R. Soc. Queensland*, 1906, 20: 27.

Type Species: ***Hemiscyllium modestum*** = ***Chiloscyllium modestum*** Günther, 1871, by original designation.

Number of Recognized Species: 1.

Synonyms: Genus ***Cheloscyllium*** Ramsay, 1880: 97, in part. Name only, apparent error for ***Chiloscyllium*** Müller and Henle, 1837. Genus ***Cirriscyllium*** Ogilby, 1908: 2, 4. Type species: ***Chiloscyllium modestum*** Günther, 1871, by original designation. Unjustified replacement for genus ***Brachaelurus*** Ogilby, 1907.

Field Marks: See species account of ***Brachaelurus waddi***.

Diagnostic Features: Head short and flat in adults, head about 19% of total length, maximum head height about 0.6 times head width; head broadly arched in dorsoventral view; snout very short, prenarial snout about 1.5% and preoral snout about 3.2% of total length; snout bluntly rounded in lateral view, with ventral surface of prenarial snout nearly vertical. Eye small and ovate with length about 1.5% of total length; eyes elevated above level of head. Spiracles horizontally situated and ovate, about opposite rear ends of eyes. Nostrils nearly terminal on snout; nasal barbel without an expanded posterior flap at its midlength. Anal-caudal space virtually obsolete and much less than anal-fin inner margin. Denticles large and rough. First dorsal fin with origin usually slightly posterior to middle of pelvic-fin bases; apex posterior to insertion; free rear tip bluntly angular or rounded. Dorsal fins about equal-sized, with similar height and base length. Second dorsal-fin apex posterior to insertion; rear tip bluntly angular. Anal-fin origin about under second dorsal-fin insertion or under last fourth of second dorsal-fin base; anal-fin free rear tip extends well behind dorsal caudal-fin origin. Total vertebral count 140 to 142, precaudal count 88 to 90, monospondylous precaudal count 39 to 40, diplospondylous precaudal count 49 to 50. **Colour:** background colour of the dorsal surface dark brown, with scattered white spots on fins and body; adults with faint saddles but without white blotches on anterior webs of dorsal fins; young without black blotches on posterior dorsal-fin webs and along caudal base but with dark saddles with very narrow transverse light lines between them.

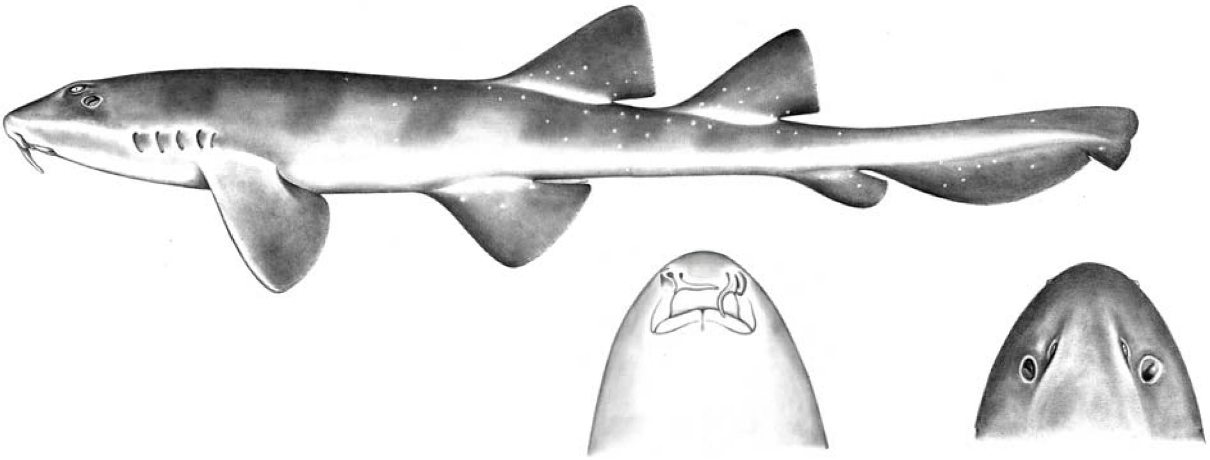
Brachaelurus waddi (Bloch and Schneider, 1801) Fig. 107

Squalus waddi Bloch and Schneider, 1801, *Syst. Ichthyol.*: 130. No type material. Australia?? Whitley, 1934, *Mem. Queensland Mus.* 10(4): 182 considered ***S. waddi*** to be the earliest name for this species, but the description could apply also to ***Chiloscyllium punctatum*** Müller and Henle, 1838. Bloch and Schneider mention an illustration of ***S. waddi*** made by Dr Latham, but unfortunately did not reproduce it in their plates. Whitley (1934) stated: "The type painting was evidently prepared from a specimen collected near Sydney, New South Wales, by Dr Latham, and the description most nearly applies to the 'blind shark', which was later called ***Chiloscyllium modestum*** by Günther and ***C. furvum*** by Ramsay." However, Whitley, 1941, *Fish. Australia* 1: 78, stated that he was unable to find the illustration either in the British Museum (Natural History) or Berlin Museum, and apparently never saw it.

Synonyms: ***Squalus (Scyliorhinus) waddii*** Blainville, 1816: 121 (variant spelling). ***Chiloscyllium modestum*** Günther, 1871: 654, pl. 54. Holotype: British Museum (Natural History), skin of 52 cm (20.5 in) female. ***Cheloscyllium furvum*** Ramsay, 1880: 97. Name only (*nomen nudum*), possibly quoted from a personal communication to him by W. Macleay, genus apparently an error for ***Chiloscyllium*** Müller and Henle, 1837. According to Ramsay (1880): "A new species, closely allied to ***C. modestum*** Günth.". ***Chiloscyllium furvum*** Macleay, 1881a: 364 (description); also Macleay, 1881b: 300 (verbatim copy of earlier work). No type material mentioned, type locality "Port Jackson" [= Sydney Harbour]. ***Chiloscyllium fuscum*** Parker and Haswell, 1897: 135. No type material, Australia, possible error for ***C. furvum***?

Other Combinations: ***Brachaelurus modestum*** (Günther, 1871).

FAO Names: En - Blind shark; **Fr** - Requin aveugle des roches; **Sp** - Tiburón ciego de roca.


UNDERSIDE OF HEAD

DORSAL VIEW OF HEAD

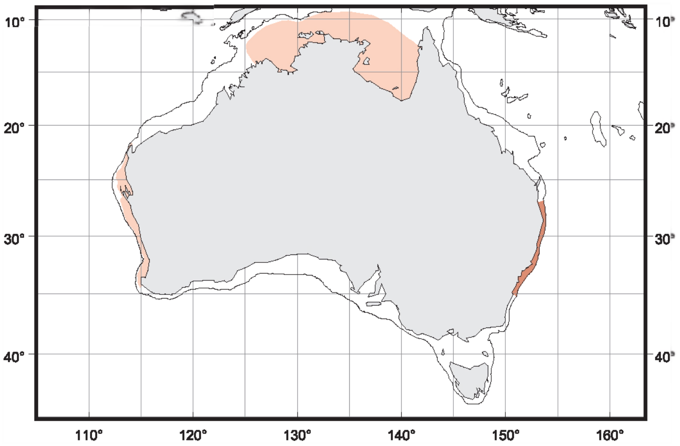
Fig. 107 ***Brachaelurus waddi***

Field Marks: A small stout shark with long tapering barbels, nasoral grooves and circumnarial grooves, very large spiracles, a short mouth ahead of the eyes, a median symphysial groove on the chin, no dermal lobes on sides of head, two equal-sized spineless dorsal fins and an anal fin, the first dorsal-fin origin over the pelvic-fin bases, a short precaudal tail and short caudal fin, and colour blackish to light brown above with or without darker saddles, light yellowish on underside, usually with many small white spots.

Diagnostic Features: See genus ***Brachaelurus*** above.

Distribution: Confined to the western South Pacific off eastern Australia (southern Queensland and New South Wales from Moreton Bay near Brisbane south to Jervis Bay). Records from Western Australia and northern Territory need confirmation.

Habitat: An inshore bottom shark of temperate Australian waters, often close inshore in tidepools that are barely deep enough to cover it and at the surf line but occasionally down to about 73 m and exceptionally to about 137 m. It favours rocky shoreline areas, patches of seaweed and coral reefs. Adults occur in caves and under ledges during the day, while juveniles may be in shallow areas with wave surge in crevices and under ledges.



Biology: A common sluggish shark that is night-active but will take angler's baits during the daytime. Development ovoviviparous, with 7 or 8 young in a litter. Said to breed in summer (November in the Sydney area). Feeds on small reef invertebrates, including crabs, shrimp, cuttlefish, squid and sea anemones, and small fishes; a coralline alga was found in the stomach of one shark. Termed 'blind shark' by anglers because it retracts its eyeballs, which causes its thick eyelids to close, when removed from the water. It can apparently live a long time out of water.

Size: Maximum exceptionally to between 90 and 122 cm, most individuals smaller; an adult male was 62 cm long and an adult female, 66 cm; size at birth 15 to 18 cm.

Interest to Fisheries and Human Impact: A harmless and hardy shark that thrives in aquaria. Taken offshore in bottom trawls but not utilized commercially. Commonly caught by sports anglers with rod-and-reel from shore in rocky areas, off reefs, and in seaweed patches, particularly around Sydney and in southern Queensland. Regarded as a pest by anglers, because it sucks in baited hooks which are hard to remove from its pharynx through its small mouth and strong jaws. It may nip people when provoked. Its flesh is regarded as unpalatable because of an ammoniacal taste that is not readily removed by soaking in seawater. The conservation status of this shark is uncertain.

Local Names: Brown cat-shark, Catshark or Cat shark, Dusky dogfish.

Remarks: Whitley (1934: 182) suggested that ***Squalus waddi*** is the earliest name for the Australian 'blind shark', which Bloch and Schneider described from an illustration of an Australian shark by Dr John Latham. Although there are problems with this interpretation (see species name above) Whitley's substitution of ***waddi*** for ***modestum*** (which had universal use prior to Whitley's note) for this species has been widely followed by subsequent authors.

Literature: Waite (1901); Whitley (1940); Fowler (1941, 1967a); Stead (1963); Grant (1972, 1982); Shiino (1976); Compagno (1984); Dingerkus (1986); Last and Stevens (1994).

Heteroscyllium Regan, 1908

Genus: ***Heteroscyllium*** Regan, 1908c, *Ann. Mag. Nat. Hist.*, (8), 2(11): 455.

Type Species: ***Brachaelurus colcloughi*** Ogilby, 1907, by original designation. Replacement name for genus ***Brachaelurus*** Ogilby, 1908.

Number of Recognized Species: 1.

Synonyms: Genus ***Brachaelurus*** Ogilby, 1908: 2, 3. Type species: ***Brachaelurus colcloughi*** Ogilby, 1908, by original designation. A junior homonym of genus ***Brachaelurus*** Ogilby, 1907.

Field Marks: See ***Heteroscyllium colcloughi*** below.

Diagnostic Features: Head long and slightly flattened in adults, about 22% of total length and with maximum head height 0.7 to 0.8 times head width; head narrowly arched and parabolic in dorsoventral view. Snout moderately long, prenarial snout about 2.5% and preoral snout about 5.4 to 6.0% of total length; snout wedge-shaped in lateral view, with ventral surface of prenarial snout nearly horizontal. Eyes large and elongated-fusiform with length 2.4 to 2.5% of total length in adults; eyes not elevated above level of head. Spiracle rounded, lateral and vertical on head, just behind eyes. Nostrils ventral and well behind snout tip; nasal barbel with an expanded, hooked or rounded posterior flap at its midlength. Anal-caudal space elongated, about equal to anal-fin inner margin. Denticles small and smooth. First dorsal-fin origin usually anterior to middle of pelvic-fin bases; apex anterior to insertion; free rear tip acutely angular. Second dorsal fin noticeably smaller than first and with height and base length less than 0.9 times first dorsal fin. Second dorsal-fin apex anterior to insertion; free rear tip acutely angular. Anal-fin origin about under midbase to second third of second dorsal fin; free rear tip just reaches lower caudal origin. Total vertebral count 117 to 120, precaudal count 69 to 73, monospondylous precaudal count 30 to 35, diplospondylous precaudal count 36 to 39. **Colour:** background colour of the dorsal surface light grey-brown, sometimes golden brown, without white spots on fins and body; adults plain with indistinct saddles and white blotches on anterior webs of dorsal fins; young have conspicuous black blotches on posterior dorsal-fin webs and along base of caudal fin and dark saddles with broad light spaces between them.

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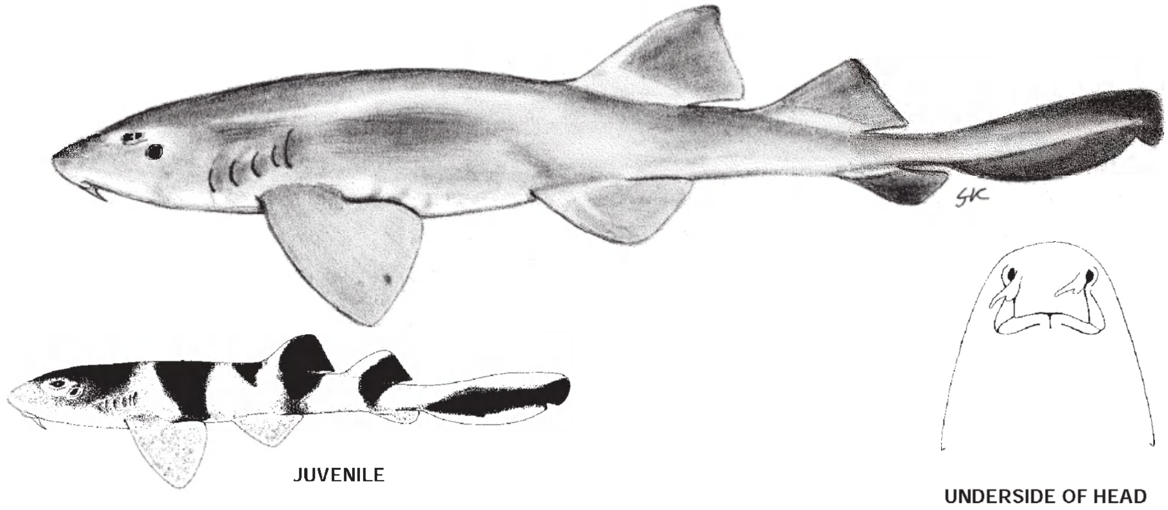
Heteroscyllium colcloughi (Ogilby, 1908) Fig. 108

Brachaelurus colcloughi Ogilby, 1908, *Proc. Roy. Soc. Queensland*, 1907, 21: 4. "Type": Amateur Fisherman's Association of Queensland Museum AFAQ no. 410, an immature male 460 mm TL (extended) according to the original description, or 457 mm TL (extended) according to Ogilby and McCulloch (1908, *J. Proc. Roy. Soc. N.S. Wales*, 42: 285), from Mud Island, Moreton Bay, Queensland, Australia. According to Ogilby (1916, *Mem. Queensland Mus.* 5: 76) this specimen was "accidentally destroyed". J. Johnson (pers. comm.), Queensland Museum, July 31, 1996) noted that the Queensland Museum had made an effort to locate the AFAQ specimens and failed. Ogilby (1908) also noted: "There is a second specimen of about the same size in the State Museum" [Queensland Museum, where J.D. Ogilby was based]. Ogilby and McCulloch (1908) also cite this as: "A second specimen, also a young male of similar size, has been for some years in the Queensland Museum." The description fits QM I-965, a 516 mm adolescent male from Moreton Bay which was examined and measured by the writer and which is labelled "lectotype" in Ogilby's handwriting (J. Johnson, pers. comm.). The two specimens apparently are syntypes because they were both mentioned in the original description. Following Ogilby's apparent wishes on its label, the syntype specimen QM I-965 is designated here as lectotype.

Synonyms: None.

Other Combinations: None.

FAO Names: En - Bluegray carpet shark; **Fr -** Requin aveugle gris-bleu; **Sp -** Tiburón ciego gris.



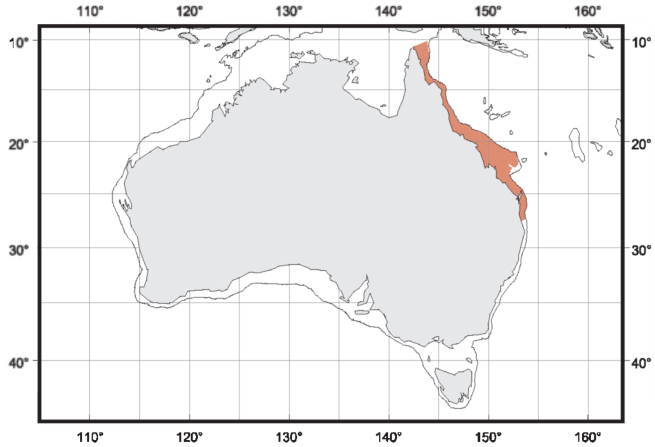
JUVENILE

UNDERSIDE OF HEAD

Fig. 108 *Heteroscyllium colcloughi*

Field Marks: A small stout to slender shark with a pair of long barbels each bearing an expanded, hooked or rounded posterior flap at its midlength, nostrils with nasoral grooves and circumnarial grooves, a short mouth ahead of the eyes, symphysial groove present on the chin, no dermal lobes on sides of head, large spiracles; two spineless dorsal fins and an anal fin, the first dorsal fin larger than the second and with origin over the pelvic-fin bases, a short precaudal tail and caudal fin, and colour greyish above and white below without light spots. Young with conspicuous black and white markings on back, dorsal fins and caudal fin, fading with growth and inconspicuous in adults.

Diagnostic Features: See genus ***Heteroscyllium*** above.



Distribution: Apparently confined to the western South Pacific, off Australia (southern and northeast Queensland). Most records are from Moreton Bay just east of Brisbane, with a few records north or south of it between Gladstone and Coolangatta, and in northeastern Queensland off the York Peninsula and the Great Barrier Reef.

Habitat: A little-known tropical or subtropical, inshore bottom shark of the Queensland continental shelf, most records from shallower than 6 m depth on soft bottom or around wrecks.

Biology: A rare to uncommon species, with biology poorly known. Presumably feeds on benthic invertebrates, but diet not recorded. Ovoviviparous (aplacental viviparous), with litters of six or seven young. Apparently egg-cases are lost early in development, and term or near-term foetuses are not enclosed in hard or soft egg-cases. Near-term foetuses 164 to 168 mm long had relatively large yolk-sacks filled with yolk but these were lost in term foetuses 174 to 186 mm long, suggesting that foetal nutriment is primarily through vitelline yolk. As with ***Brachaelurus waddi*** this species also closes its eyes when removed from the water (J. Johnson, pers. comm.).

Size: Maximum to at least 75.5 cm, pregnant females 65.8 to 75.5 cm, males adolescent at ca. 48.2 to 51.6 cm. Term foetuses 174 to 184 mm, size at birth probably between 17 to18 cm.

Interest to Fisheries and Human Impact: A harmless shark of no interest to fisheries but occasionally caught by sports anglers. It is partly sympatric with ***Brachaelurus waddi*** off southern Queensland and has been confused with it in the past.

By analogy to ***B. waddi*** and because of its inshore benthic habitat this is likely to be a hardy aquarium shark and an attractive exhibit (particularly the boldly barred young). Some of these sharks have been kept in aquaria (J. Stevens, pers. comm.). If this species enters the aquarium trade in any numbers this should be strictly regulated.

Restricted habitat, distribution in areas heavily and increasingly utilized by people, and possibly rarity suggested by few records in suitable habitat in the relatively well-surveyed waters where it occurs makes it inherently vulnerable to depletion. Its distribution, behaviour, ecology, and conservation status need to be studied in detail by diving surveys. Surveys of angler catches and commercial demersal landings need to be made to determine its presence in inshore fisheries. This species has a status of *Vulnerable* in the IUCN 2000 Red List.

Local Names: Colclough's shark or Colcloughs shark, Blue-grey catshark, Blue-grey shark.

Literature: Ogilby (1908, 1916); Ogilby and McCulloch (1908); Garman (1913); McCulloch and Whitley (1925); Whitley (1934, 1940); Fowler (1929, 1941, 1967a); White (1937); Bigelow and Schroeder (1948); Grant (1972, 1982); Compagno (1973, 1981b, 1982, 1984); Applegate (1974); Dingerkus (1986); Last and Stevens (1994); J. Johnson (pers. comm.), P. Last (pers. comm.), J. Stevens (pers. comm.).

2.3.3 Family ORECTOLOBIDAE

Family: Orectolobidae Gill, 1896, *Proc. U.S. Natl. Mus.* 18(1057): 212. Also subfamily Orectolobinae Fowler, 1934, *Proc. Acad. Nat. Sci. Philadelphia*, 85: 238 (Family Orectolobidae).

Type Genus: ***Orectolobus*** Bonaparte, 1834.

Number or Recognized Genera: 3.

Synonyms: Subfamily Crossorhinae Swainson, 1839: 318 (Family Squalidae). Type genus: ***Crossorhinus*** Müller and Henle, 1837.

FAO Names: En - Wobbegongs; **Fr** - Requins-tapis; **Sp** - Tiburones tapiceros.

Field Marks: These are distinctive flattened, variegated sharks, differing from all others (except angel sharks, Squatinidae), having narrow dermal flaps along the sides of the head. Wobbegongs differ from angel sharks in having anal fins and separate cermal lobes among many other differences. Wobbegongs also have long barbels, short, nearly terminal mouths in front of the eyes, nasoral grooves and circumnarial grooves and flaps, symphysial grooves, large spiracles and dorsolateral eyes.

Diagnostic Features: Head very broad and flattened, with unique lateral flaps of skin. Snout truncated. Eyes dorsolaterally situated on head and with strong subocular ridges below them. Eyes without movable upper eyelids but with subocular pockets and ridges. Spiracles very large and larger than eyes, with prominent raised external rims; spiracles somewhat below, behind and lateral to eyes. Gill slits small, fifth gill slit well-separated or close to fourth but not overlapping it; internal gill slits without filter screens. Nostrils with very long pointed or branched barbels, circumnarial folds and circumnarial grooves around outer edges of incurrent apertures. Nasoral grooves short and strongly developed. Mouth large, slightly arched and nearly transverse, and nearly terminal on head. Lower lip not trilobate and without lateral orolabial grooves connecting edge of lip with medial ends of lower labial furrows, but with a longitudinal symphysial groove on chin. Lower labial furrows extending medially nearly to symphysis, but not connected medially by a mental groove or groove and flap. Teeth strongly differentiated in upper and lower jaws, with three rows of fang-like teeth at the upper symphysis and two rows at the lower. Tooth row count 23 to 26/19. Teeth with a strong medial cusp, lateral cusplets variably present or absent, and labial root lobes weak. Teeth orthodont with a central pulp cavity and no plug of osteodentine. Body considerably depressed, without ridges on sides. Precaudal tail shorter than body. Caudal peduncle without lateral keels or precaudal pits. Pectoral fins moderate-sized or very large, broad and rounded. Pectoral fins aplesodic and with fin radials not expanded into fin web. Pectoral propterygium large and separate from mesopterygium and metapterygium; pectoral-fin radial segments three at most, and with longest distal segments about 0.5 times the length of longest proximal segments. Pelvic fins larger than dorsal and anal fins, nearly as large as pectoral fins and with anterior margins 0.6 to 0.8 times the pectoral-fin anterior margins. Claspers without mesospurs, claws or dactyls. Dorsal fins equal-sized, first dorsal-fin origin over or slightly behind the pelvic-fin insertion, insertion far behind the pelvic-fin rear tips. Anal fin about half as large as second dorsal fin or less, with broad base, subangular or narrowly rounded apex, origin about opposite rear third of second dorsal-fin base or its insertion, and insertion separated by a narrow notch much less than base length from lower caudal-fin origin. Caudal fin short and not crescentic, weakly heterocercal with its upper lobe at a low angle above the body axis; dorsal caudal-fin margin less than a fourth as long as the entire shark. Caudal fin with a strong terminal lobe and subterminal notch but without a ventral lobe, preventral and postventral margins not differentiated and forming a continuous curve. Vertebral centra with well-developed radii. Total vertebral count 149 to 158, monospondylous precaudal count 41 to 52, diplospondylous precaudal count 42 to 62, diplospondylous caudal count 49 to 62, and precaudal count 87 to 106. Cranium moderately broad and not greatly expanded laterally. Medial rostral cartilage extremely short and reduced to a low projection. Nasal capsules greatly depressed and with double longitudinal fenestrae, internarial septum compressed but low, not expanded laterally. Orbits with small foramina for preorbital canals, medial walls not fenestrated around the optic nerve foramina. Supraorbital crests present on cranium but not laterally expanded and pedicellate. Suborbital shelves very broad and not reduced. Cranial roof without fenestrae. Basal plate of cranium with separate pairs of stapedial and carotid foramina. Adductor mandibulae muscle of jaws with two divisions. Preorbitalis muscles not extending onto posterodorsal surface of cranium. No anterodorsal palpebral depressor, rostromandibular, rostronuchal or ethmonuchal muscles. Valvular intestine of ring type with 23 to 33 turns. Development ovoviviparous. Size small to large with adults between 60 cm and at least 3 m. Colour pattern highly developed, including dark and light spots, dark saddles, rings and reticulations on back.

Distribution: Wobbegongs are common, largish flattened bottom sharks that are endemic at present to warm-temperate to tropical continental waters of the western Pacific. They are most diverse in Australian and New Guinean waters, but occur northwards to Japan.

Habitat: Wobbegongs occur in inshore and offshore bottom habitats from the intertidal down to at least 110 m. They are often found on rocky and coral reefs or on sandy bottom, where they lurk and are concealed in part by their cryptic coloration and dermal lobes on their heads.

Biology: Wobbegongs are reportedly sluggish fishes, moving little, but can clamber around with their paired fins on the bottom and even climb partway out of the water while moving between tidepools. At least two species may attain a size of 3.2 to 3.7 m. These sharks are ovoviviparous, with large litters of 20 or more young. Wobbegongs are powerful bottom predators with heavy jaws and greatly enlarged, dagger-shaped, extremely sharp teeth in the front of their mouths. They feed on bottom fishes, crabs, lobsters, octopi, and other bottom animals.

Interest to Fisheries and Human Impact: Wobbegongs are utilized for food in Australia and off China, Japan, Malaysia (Sabah) and probably elsewhere where they occur; their colourful skins are also used for leather. Wobbegongs can bite when captured or when provoked or stepped upon, and have inflicted severe lacerations on the limbs of people. There are rare records of large wobbegongs biting off people's feet or killing them, but these need to be verified. Wobbegongs are often difficult to see against the bottom and can be contacted accidentally. These sharks should be treated with respect because of their strong dentition, as with angel sharks (Squatinidae), even though they do not appear to be particularly prone to bite people unless provoked. Michael (1993) thought that these sharks had poor visual acuity and tended to bite at any object that moved near their heads, so that people should avoid placing their limbs near them. Wobbegongs are regularly kept in public aquaria in Australia, Europe, and the United States, and are often viewed by divers on the Great Barrier Reef of Australia and probably off Japan. They have bred in captivity.

Local Names: Wobbegongs, Carpetsharks, Carpet sharks; Kovrovye akuly (Russian).

Remarks: The arrangement of this family follows Compagno (1984), Dingerkus (1986), and Last and Stevens (1994). Although apparently a monophyletic group and the sister taxon of the Brachaeluridae (Dingerkus, 1986; Compagno, 1988), the Orectolobidae requires a detailed morphological and genetic investigation to elucidate the interrelationships of its component taxa. Dingerkus (1986) suggested that the highly derived ***Eucrossorhinus*** was the sister genus of ***Orectolobus***, and both formed the sister taxon of ***Sutorectus***, but this is complicated by ***Orectolobus* sp. A**, which has some characters, including its narrow interdorsal space, slightly lower dorsal fins, and longitudinal rows of small dermal knobs and ridges in young, that suggest that it is intermediate between typical ***Orectolobus*** and the bizarre ***Sutorectus tentaculatus***.

Literature: Ogilby and McCulloch (1908); Regan (1908a); Garman (1913); Whitley (1940); Fowler (1941); Compagno (1984); Dingerkus (1986); Michael (1993); Last and Stevens (1994).

Key to Genera:

1a. Chin with highly branched dermal lobes; dermal lobes on sides of head mostly extensively branched (Fig. 109); body with a reticular pattern of narrow dark lines . . . . ***Eucrossorhinus***

1b. Chin without dermal lobes; dermal lobes on sides of head mostly simple or with a few branches (Fig. 110); colour pattern variable, but without a reticular pattern of narrow dark lines . . . . → ***2***

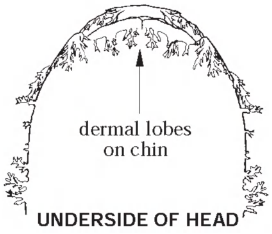


Fig. 109 ***Eucrossorhinus***

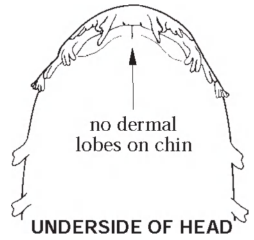


Fig. 110 ***Orectolobus***

2a. Head and body without tubercles or with small ones or inconspicuous dermal ridges in young (lost in adults); dorsal fins high, height at least three-fourths of base length; origin of first dorsal fin behind midbases of pelvic fins (Fig. 111). . . . . . . ***Orectolobus***

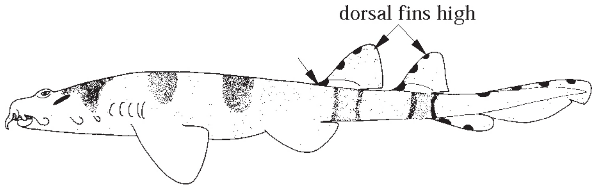


Fig. 111 *Orectolobus*

2b. Head and body covered by large rounded tubercles; dorsal fins long and low, height about half of base length; origin of first dorsal fin anterior to pelvic-fin midbases (Fig. 112) . . . . ***Sutorectus***

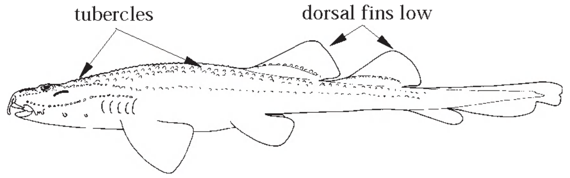


Fig. 112 *Sutorectus*

Eucrossorhinus Regan, 1908

Genus: ***Eucrossorhinus*** Regan, 1908a, *Proc. Zool. Soc. London*, 1908: 357.

Type Species: ***Eucrossorhinus dasypogon*** Regan, 1908, by monotypy, equals ***Crossorhinus dasypogon*** Bleeker, 1867.

Number of Recognized Species: 1.

Synonyms: Genus ***Crossohrinus*** Compagno, 1984: 179. Typographical error for ***Crossorhinus dasypogon*** Bleeker, 1867.

Diagnostic Features: Head very broad, its width slightly greater than its length from snout tip to fifth gill openings. Chin with a bushy beard of highly branched dermal lobes. Dermal lobes of sides and front of head highly branched and numerous, in approximately 24 to 26 pairs, forming a virtually continuous fringe from snout tip to pectoral-fin bases. Nasal barbels branched, with complex multiple lobes. Mouth broad, width about 11% of total length. Head and body without enlarged tubercles on body, except for those above eyes. Trunk very broad, width across pectoral-fin insertions about equal to head length. Precaudal tail rather short, distance from pelvic-fin insertion to lower caudal origin about equal to head length. Interspace between first and second dorsal fins longer than first dorsal-fin inner margin and slightly more than half first dorsal-fin base. Pectoral and pelvic fins very large, distance from pectoral-fin insertions to pelvic-fin origins about equal to pectoral-fin bases and less than pelvic-fin lengths from origins to free rear tips. Dorsal fins high and short, height of first dorsal fin about equal to its base length, length of first dorsal fin base less than pelvic-fin length. Origin of first dorsal fin opposite posterior fourth of pelvic-fin bases. **Colour:** dorsal surface with a reticular pattern of narrow dark lines on a light background, with scattered symmetrical enlarged dark dots at the junction of lines.

Remarks: This genus was originally proposed by Regan (1908a) to separate ***Crossorhinus dasypogon*** Bleeker, 1867 from other wobbegongs primarily because of its supposedly even-spaced gill slits, but he also mentioned that the genus differed from ***Orectolobus*** by having a broader, more depressed head, smaller eyes and wider spiracles. However, Regan (1909) reversed himself and rejected Eucrossorhinus because his new, very similar (and ultimately conspecific) ***Orectolobus ogilbyi*** had the last two gill slits close together.

Ogilby and McCulloch (1908), Fowler (1941), and Stead (1963) did not recognize the genus ***Eucrossorhinus*** but Garman (1913), Whitley (1940), Bigelow and Schroeder (1948), Garrick and Schultz (1963), Compagno (1973, 1984), Applegate (1974), Dingerkus (1986), and Last and Stevens (1994) all retained it. ***Eucrossorhinus*** is morphologically divergent from other wobbegongs, but its phyletic relationships are unclear and require a detailed study of its morphology.

Two species of ***Eucrossorhinus*** have been recognized, ***E. dasypogon*** from Indonesia, and ***E. ogilbyi*** from Torres Straits and Papua-New Guinea. Regan (1909) distinguished the two as follows:

> ***[Eucrossorhinus] ogilbyi***: Gill slits decreasing in size from first to fourth, last larger; last two closer together than rest. Dermal lobes on sides of head in three separate groups. Origin of first dorsal fin well behind middle of total length. Distance between origins of dorsals nearly half that from origin of second dorsal fin to end of tail.
>
> ***[Eucrossorhinus] dasypogon***: First gill slit slightly smaller than rest, which are of equal size and equidistant. Dermal lobes on head in two separate groups. Origin of first dorsal fin in the middle of total length. Distance between origins of dorsals slightly more than one-third that from origin of second dorsal-fin to end of tail.

Fowler (1941) used ***Eucrossorhinus*** as a subgenus of ***Orectolobus***, but placed ***O. dasypogon*** in ***Eucrossorhinus*** and ***Orectolobus ogilbyi*** in the subgenus ***Orectolobus***. Compagno (1984) compared a possible syntype of ***Eucrossorhinus dasypogon*** collected by P. Bleeker from Indonesia (see below) with a larger specimen labelled ***E. ogilbyi*** from northern

Queensland (BMNH 1911.4.1.43, 415 mm female), as well as a much larger specimen labelled ***E. dasypogon*** from New Guinea (Australian Museum, Sydney, AMS I4783, 117 cm adult male). This suggested that the characters supposed to separate the two species did not hold. All specimens had the last two gill openings more closely spaced than the first three, though the New Guinea and Queensland specimens had them slightly closer than the small Indonesian specimen. All three specimens have the first four gill openings about equal in length or with the first slightly smaller; the fifth is slightly smaller than the fourth in the Indonesian specimen, slightly larger in the large New Guinea adult, and about equal to it in the Queensland specimen. In the two smaller specimens the first dorsal-fin origin is actually slightly ahead of the midlength, but slightly behind in the New Guinea adult, suggesting allometric increase in abdominal length with growth. The Indonesian specimen has the distance from the second dorsal-fin origin to the caudal-fin tip 2.7 times the space between the origins of the first and second dorsal fins, the Queensland specimen 2.6 times, and the large New Guinea specimen 2.4 times.

Compagno (1984) synonymized ***E. ogilbyi*** with ***E. dasypogon***, and suggested that the differences listed between the two species in the literature and in the specimens he had examined represented individual and ontogenetic variation in a single species. The specimens were strikingly similar in colour pattern and general morphology, and Compagno indicated that there was nothing in the literature to suggest any significant differences between Australian, Papua-New Guinean and Indonesian ***Eucrossorhinus***. This was accepted by Last and Stevens (1994).

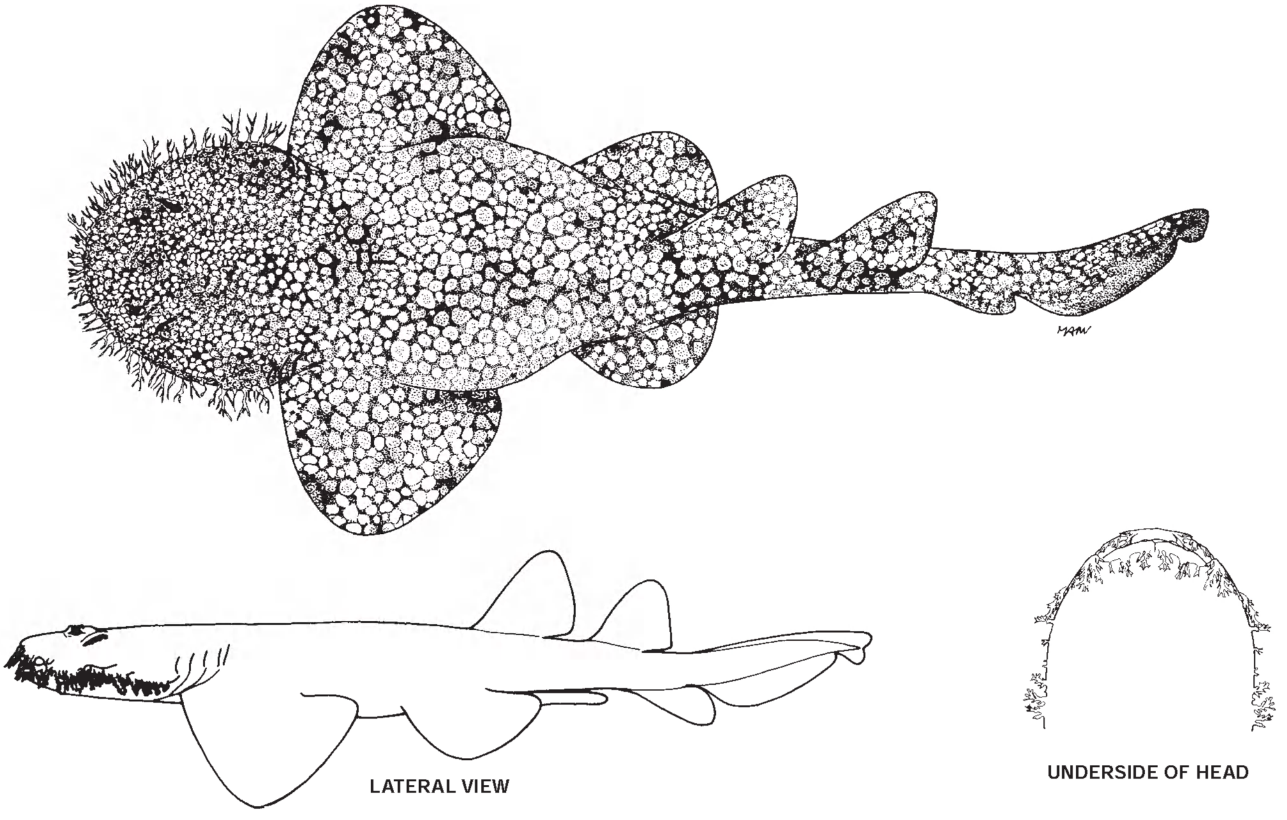
Eucrossorhinus dasypogon (Bleeker, 1867) **Fig. 113**

Crossorhinus dasypogon Bleeker, 1867, *Arch. Neerl. Sci. Nat.* 2: 400, pl. 21, fig. 1. Syntypes: Rikjsmuseum van Natuurlijke Histoire, Leiden, RMNH 7411 (1) Waigiu (Waigeo), RMNH 5118 (1) Aru, Indonesia, according to Eschmeyer (1998, *Cat. Fish.*: CD-ROM). Uncertain status: British Museum (Natural History), BMNH-1867.11.28.209, 215 mm immature male and noted as a syntype by Compagno (1984, *FAO Fish. Syn.* (125), 4 (1): 179) from documentation on the specimen.

Synonyms: ***Orectolobus ogilbyi*** Regan, 1909: 529. New name for ***Orectolobus dasypogon*** Ogilby and McCulloch, 1908: 272, pl. 43, fig. 1. Syntypes: Two specimens from Torres Strait and Samarai, Papua-New Guinea, including one 1 210 mm long, according to Ogilby and McCulloch. Eschmeyer (1998: CD-ROM) identified one of these as Australian Museum, Sydney, AMS I.5405.

Other Combinations: ***Orectolobus dasypogon*** (Bleeker, 1867).

FAO Names: En - Tasselled wobbegong; **Fr** - Requin-tapis barbu; **Sp** - Tapicero barbudo.



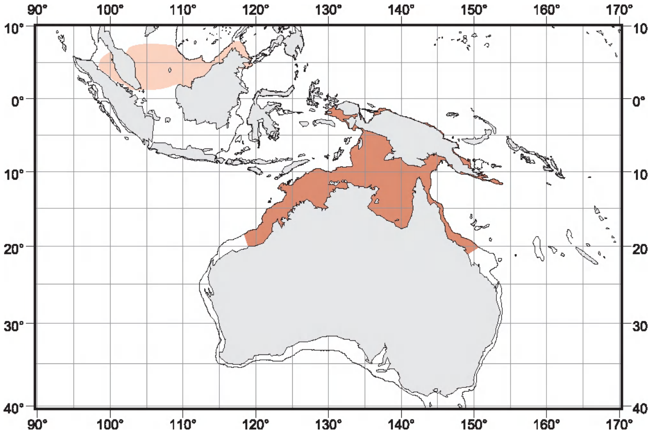
LATERAL VIEW

UNDERSIDE OF HEAD

Fig. 113 *Eucrossorhinus dasypogon*

Field Marks: This squat, broad, angler-like shark is unmistakable, with profuse, highly branched dermal lobes on its head, a beard of similar lobes on its chin, and reticulated colour pattern of narrow dark lines and dark spots at their junctions on a light background. It is also recognizable by having its mouth in front of eyes, a symphysial groove on chin, very broad pectoral and pelvic fins, two spineless dorsal fins and an anal fin, the first dorsal-fin origin opposite the pelvic-fin hindbases, and the anal-fin origin well behind the second dorsal-fin origin.

Diagnostic Features: See genus ***Eucrossorhinus*** above.



Distribution: Western South Pacific: Indonesia (Waigeo, Aru), New Guinea, Malaysia?, northern Australia (northern Queensland, Northern Territory, Western Australia).

Habitat: A little-known inshore and offshore tropical bottom shark, present inshore and on coral reefs, commonly seen on coral heads, and in reef channels and reef faces. Michael (1993) suggested that this species was an obligate coral-reef dweller.

Biology: Commonly seen on the northern Great Barrier Reef; rests on the bottom with its tail curled. This nocturnal species is said to be a faster swimmer than other wobbegongs (Whitley and Pollard, 1980), but its more flattened shape, exquisite camouflage, and bushy dermal flaps suggests the reverse, that it might be more sluggish than other wobbegongs. It is thought to be solitary (Michael, 1993), and individuals are seen resting in caves and under ledges in the day, but may leave their retreats at night to feed. Individuals apparently have a small home range and several retreats within it. Probably ovoviviparous, though reproductive biology is little known. Feeds on bottom fishes and possibly invertebrates, and is known to eat nocturnal teleost fishes such as squirrelfish and soldierfish (Holocentridae) and sweepers (Pempheridae) that share their caves.

Size: Maximum said to be 366 cm but this is uncertain and thought by Last and Stevens (1994) to be incorrect; maximum reliably to 125 cm. Born at about 20 cm; the 215 mm possible syntype in the British Museum (Natural History) is newborn or close to it. Reaches 125 cm; an adult male from New Guinea with calcified claspers and examined by the writer (see above) was only 117 cm long.

Interest to Fisheries and Human Impact: Interest to fisheries uncertain and probably minimal; the tough skin with its handsome reticulated colour pattern is occasionally used for leather.

According to an informant quoted by Whitley (1940), this shark "...attacks and generally kills the natives" in Papua-New Guinea, but this is questionable. This shark no doubt should be treated with respect like other wobbegongs, but its fearsome reputation may be greatly exaggerated and may well evaporate as its biology becomes better known. Divers commonly approach and photograph the tasselled wobbegong during the daytime, without inciting agonistic behaviour, though probably stepping on or near this well-camouflaged shark might cause it to bite at least in self-defence or by possibly mistaking a human foot for prey. Michael (1993) thought that it was more likely to bite people than other wobbegongs, and has bitten divers without provocation several times. It is kept in aquaria in the United States and probably elsewhere and is viewed by ecotouristic divers in Australia. It makes a spectacular subject for display and photography.

The conservation status of this species is uncertain, but should be of concern because of its limited distribution and habitat on reefs, including poorly protected areas outside Australian territorial waters that are subject to habitat destruction from pollution and bad fishing practices such as dynamiting, netting and poisoning reefs.

Local Names: Bearded wobbegong, Ogilby's wobbegong, Tasselled wobbegong.

Literature: Ogilby and McCulloch (1908); Regan (1908a, c, 1909); Garman (1913); Whitley (1940); Fowler (1941); Marshall (1965); Whitley and Pollard (1980); Compagno (1984); Dingerkus (1986); Last and Stevens (1994).

Orectolobus Bonaparte, 1834

Genus: Subgenus ***Orectolobus*** Bonaparte, 1834, *Iconog. Fauna Italica, 3, Pesci, fasc.* 7. (Genus ***Scyllium*** Cuvier, 1816).

Type Species: ***Squalus barbatus*** Gmelin, *in* Linnaeus and Gmelin, 1788, by subsequent restriction of Gill, 1896, *Proc. U. S. Natl. Mus.* 18(1057): 211; a junior synonym of ***Squalus maculatus*** Bonnaterre, 1788.

Number of Recognized Species: 5.

Synonyms: Genus ***Crossorhinus*** Müller and Henle, 1837a: 113. Type species: ***Squalus lobatus*** Bloch and Schneider, 1801, by monotypy. Genus ***Chrossorhinus*** (Müller and Henle) Smith, 1837: 86; Smith, 1838: 73. Type species: ***Squalus lobatus*** Bloch and Schneider, 1801, by monotypy. Error or emendation for ***Crossorhinus*** Müller and Henle, 1837.

Diagnostic Features: Head narrow, its greatest width about equal to or less than distance from snout tip to first gill openings. Chin smooth, without a beard of dermal lobes. Dermal lobes of sides and front of head small, short, unbranched or slightly branched, and in 3 to 10 pairs, forming isolated groups that are broadly separated from one another. Nasal barbels simple and unbranched or with a weak basal branch. Mouth narrow, width about 9% of total length. Dorsal surface of head, body and precaudal tail, and dorsal fin bases smooth or with small inconspicuous tubercles or low longitudinal ridges, not noticeably warty. Trunk moderately broad, width across pectoral-fin insertions considerably less than head length. Precaudal tail rather long, distance from pelvic-fin insertion to lower caudal-fin origin much greater than head length. Pectoral and pelvic fins small and widely spaced from each other, distance from pectoral-fin insertions to pelvic-fin origins at least 1.5 times length of pectoral-fin bases and somewhat greater than pelvic-fin lengths from origins to free rear tips. Interspace between first and second dorsal fins usually slightly longer than first dorsal-fin inner margin but slightly shorter in ***Orectolobus*** **sp. A**, and varying from over half to about a fifth of first dorsal-fin base. Dorsal fins fairly high and short to moderately long, height of first dorsal fin over three-fourths of its base length, length of first dorsal-fin base less than pelvic-fin length from origin to free rear tip. Origin of first dorsal fin behind midbases of pelvic fins. Dorsal surface with a colour pattern of regular or jagged-edged broad dark saddles separated by light areas with dusky blotches, scattered dark spots or semi-reticulated broad lines, or O-shaped light spots on a dark background; no reticulating narrow lines with spots at their junctions, but broad reticulating lines without spots are present in a few species.

Remarks: The present account of this genus follows Ogilby and McCulloch (1908), Regan (1908a), Whitley (1940), Compagno (1984), and Last and Stevens (1994). As with Compagno (1984), the account is regarded as provisional, with some problems including the status of subspecies in ***Orectolobus ornatus.*** Also, in Western Australian waters there is a distinct, undescribed species of wobbegong, that is very abundant and resembles ***O. ornatus*** as well as ***Sutorectus tentaculatus*** (B. Hutchins, pers. comm.). It is termed ***Orectolobus*** **sp. A** by Last and Stevens (1994) and in the present account, and is being described by P. Last, B. Hutchins, and the writer. There is also a record of a member of this genus from Sabah, Borneo (Fowler et al., 1999), based on a dried specimen of ***Orectolobus*** that is of uncertain placement in the genus. A wobbegong from Japan illustrated by Nakaya and Shirai (1984, pl. 8, fig. B) is identified as ***O. ornatus*** but may be an undescribed species. Its coloration of broad black rings and reticulations on a yellowish background and reduced saddles is very different from the Australian ***O. ornatus*** and unlike any other wobbegong.

Key to Species:

1a. Nasal barbels not branched (Fig. 114); dermal lobes of head very broad-based, only 2 or 3 in front of eyes; colour pattern simple, with a few dark spots, dusky mottling, and three large dark, light-edged rounded saddles on back anterior to first dorsal fin . . . . ***Orectolobus wardi***

1b. Nasal barbels branched (Fig. 115); dermal lobes narrower-based and more numerous, four or more in front of eyes; colour pattern with elaborate variegated spots and saddles . . . . → ***2***

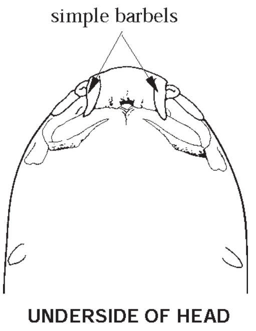


Fig. 114 ***Orectolobus wardi***

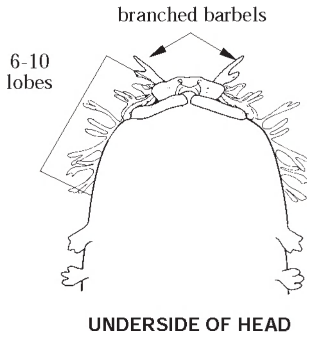


Fig. 115 ***Orectolobus maculatus***

2a. About 6 to 10 dermal lobes below and in front of eyes; back dark, with white O-shaped spots and white blotches obscuring darker saddles (Figs 115 and 116) . . . . ***Orectolobus maculatus***

2b. About 4 to 6 dermal lobes below and in front of eyes; back with dark colour variegated with light blotches and prominent saddle markings . . . . → ***3***

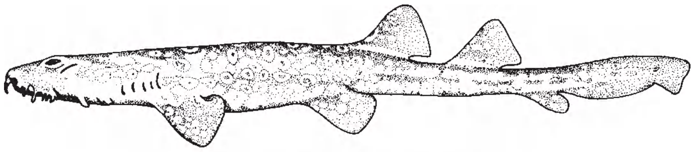


Fig. 116 ***Orectolobus maculatus***

3a. About four dermal lobes below and in front of eyes; dermal lobes behind spiracle unbranched and slender; interdorsal space slightly shorter than inner margin of first dorsal fin (Fig. 117) . . . . ***Orectolobus sp. A***

3b. About 5 or 6 dermal lobes below and in front of eyes; dermal lobes behind spiracle branched, or if unbranched very broad; interdorsal space slightly longer than inner margin of first dorsal fin (Fig. 118) . . . . → ***4***

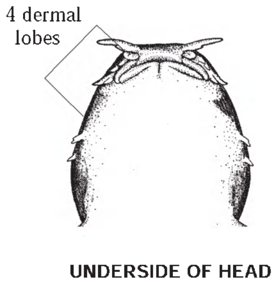


Fig. 117 *Orectolobus* sp. A

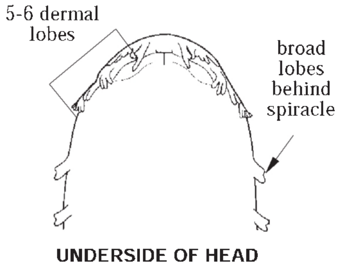


Fig. 118 *Orectolobus ornatus*

4a. Back with light areas between dark saddles marked with broad reticulated dark lines; borders of saddles dark but not conspicuously black-edged (Fig. 119) . . . . ***Orectolobus japonicus***

4b. Back with light areas between dark saddles marked with dark, light centred blotches and spots, not reticulated lines; saddles with conspicuous black borders (Fig. 120) . . . . ***Orectolobus ornatus***

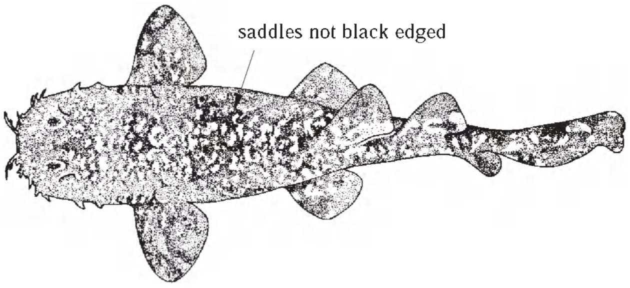


Fig. 119 *Orectolobus japonicus*

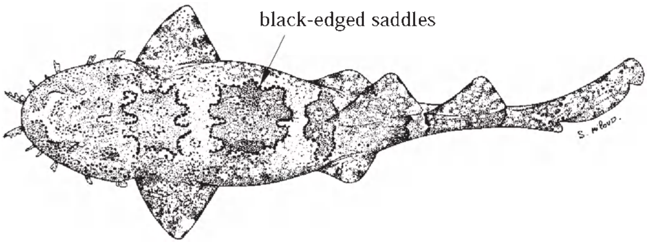


Fig. 120 *Orectolobus ornatus*

Orectolobus japonicus Regan, 1906

Fig. 121

Orectolobus japonicus Regan, 1906b, *Ann. Mag. Nat. Hist.* (7), 18(108): 435. Syntypes: British Museum (Natural History), BMNH 1862.11.1.18 and BMNH 1862.11.1.90 according to Eschmeyer (1998, *Cat. Fish.*: CD-ROM), two females, 1 000 and 780 mm TL, Japan.

Synonyms: None.

Other Combinations: ***Crossorhinus*** or ***Orectolobus barbatus*** (not Gmelin, 1788), ***Crossorhinus lobatus*** (not Bloch and Schneider, 1801).

FAO Names: En - Japanese wobbegong; **Fr** - Requin-tapis moustache; **Sp** - Tapicero japonés.

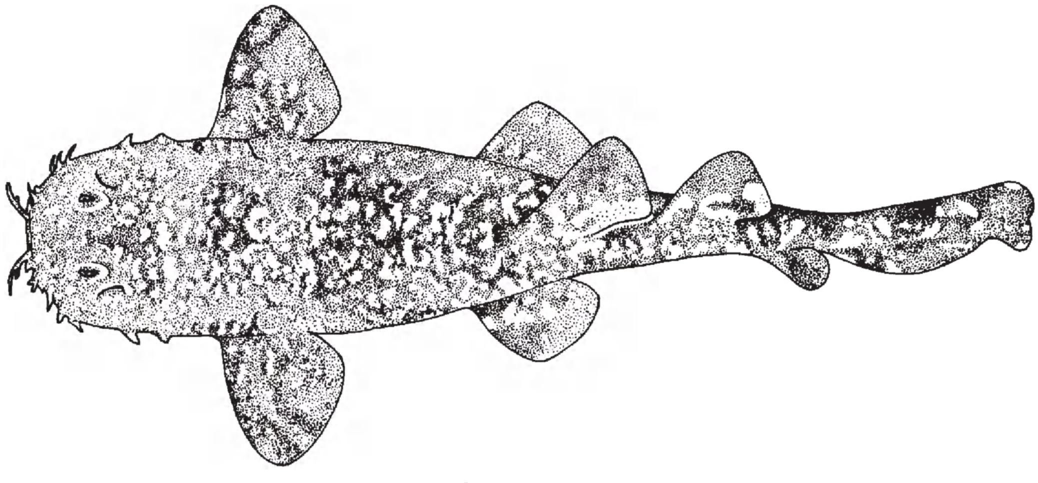


Fig. 121 *Orectolobus japonicus*

Field Marks: Flattened benthic sharks with dermal lobes on sides of head, symphysial groove on chin, very conspicuous variegated colour pattern of broad dark dorsal saddles with light spots and corrugated edges, interspaced with light areas with dark broad reticular lines; also, mouth in front of eyes, long, basally branched nasal barbels, nasoral grooves and circumnarial grooves, two rows of enlarged fang-like teeth in upper jaw and three in lower jaw; first dorsal-fin origin over pelvic-fin bases.

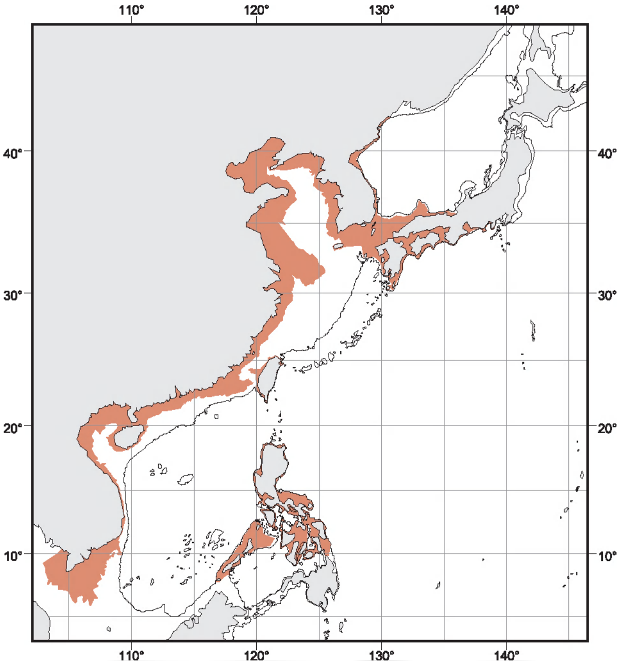
Diagnostic Features: Nasal barbels with a few branches. Five dermal lobes below and in front of eye on each side of head; dermal lobes behind spiracles branched and broad. No dermal tubercles or ridges on back. Interspace between dorsal fins longer than inner margin of first dorsal fin, about half first dorsal-fin base. Origin of first dorsal fin behind midbases of pelvic fins. First dorsal-fin height about equal to base length. **Colour:** colour pattern highly variegated and conspicuous, dorsal surface of body with conspicuous broad, dark rectangular saddles with deeply corrugated margins, dotted with light spots and not ocellate in appearance; interspaces between saddles light, with numerous broad reticulated lines.

Distribution: Western North Pacific: off Japan, Korea, China, Taiwan (Province of China), Viet Nam, and Philippines.

Habitat: A little-known temperate to tropical inshore bottom shark, found on rocky and coral reefs.

Biology: A nocturnal shark, rarely observed by divers. Ovoviviparous, with litters of up to 20 to 23 young. In captivity in an aquarium in Okinawa, Japan, gives birth in spring (March through May), and has been observed in courtship. The male grabs the female in the gill area while mating with her. The gestation period is about a year. Eats primarily benthic fish, including lizardfishes (Synodontidae), cutlassfish (Trichiuridae), horse mackerel and other jacks (Carangidae), goatfishes (Mullidae), groupers (Serranidae), tilefishes (Malacanthidae), sea robins (Triglidae), whiting (Sillaginidae), parrotfishes (Scaridae), sea bream (Sparidae), croakers (Sciaenidae), also skates (Rajidae), shark egg-cases, cephalopods, and shrimp.

Size: Maximum uncertain, reaches at least 107 cm. Size at birth 21 to 23 cm; a male was mature at 103 cm; adult females that gave birth in captivity were 101 to 107 cm.



Interest to Fisheries and Human Impact: Interest to fisheries probably limited, caught in set nets in Japan and used for human consumption; also taken in China, Taiwan (Province of China), Korea and Viet Nam. Conservation status uncertain. Probably viewed by ecotouristic divers in Japan, and kept in aquaria in Japan and the United States.

Local Names: Japanese carpet shark, Carpet shark, Bearded shark, Japanese bearded shark, Fringe shark, Kirinotobuka, Oose or Ôse (Japan).

Literature: Ogilby and McCulloch (1908); Regan (1908a); Garman (1913); Fowler (1941); Herre (1953); Lindberg and Legeza (1959); Fourmanoir and Nhu-Nhung (1965); Matsubara (1955); Chen (1963); Masuda, Araga and Yoshino (1975); Uchida (1982); Compagno (1984); Nakaya and Shirai (1984); Uchida, Toda and Kamei (1990); Michael (1993).

Orectolobus maculatus (Bonnaterre, 1788)

Fig. 122

Squalus maculatus Bonnaterre, 1788, *Tabl. Encyclop. Method. Trois Reg. Nat., Ichthyol., Paris*: 8. No type material? Type locality: "La mer du sud".

Synonyms: ***Squalus barbatus*** Gmelin, *in* Linnaeus and Gmelin, 1788: 1493. New Holland. On 'barbu' of Broussonet, 1780, *Mem. Acad. Sci. Paris*, 657, no. 7, New Holland. No types known according to Eschmeyer (1998: CD-ROM). ***Squalus lobatus*** Bloch and Schneider, 1801: 137. On the 'Watt's Shark' of Phillip, 1789: 285, pl. 53. Sydney Cove, Port Jackson, New South Wales, Australia. No types known according to Eschmeyer (1998: CD-ROM). ***Squalus appendiculatus*** Shaw and Nodder, 1806: pl. 737. Antarctic seas. On the 'Watt's Shark' of Phillip, 1789: 285, pl. 53. Sydney Cove, Port Jackson, New South Wales, Australia. No types known according to Eschmeyer (1998: CD-ROM).

Other Combinations: ***Crossorhinus***, ***Orectolobus***, ***Scyllium***, ***Chiloscyllium***, or ***Scyliorhinus barbatus*** (Gmelin, 1788), ***Chrossorhinus*** or ***Crossorhinus lobatus*** (Bloch and Schneider, 1801).

FAO Names: En - Spotted wobbegong; **Fr** - Requin-tapis tacheté; **Sp** - Tapicero manchado.

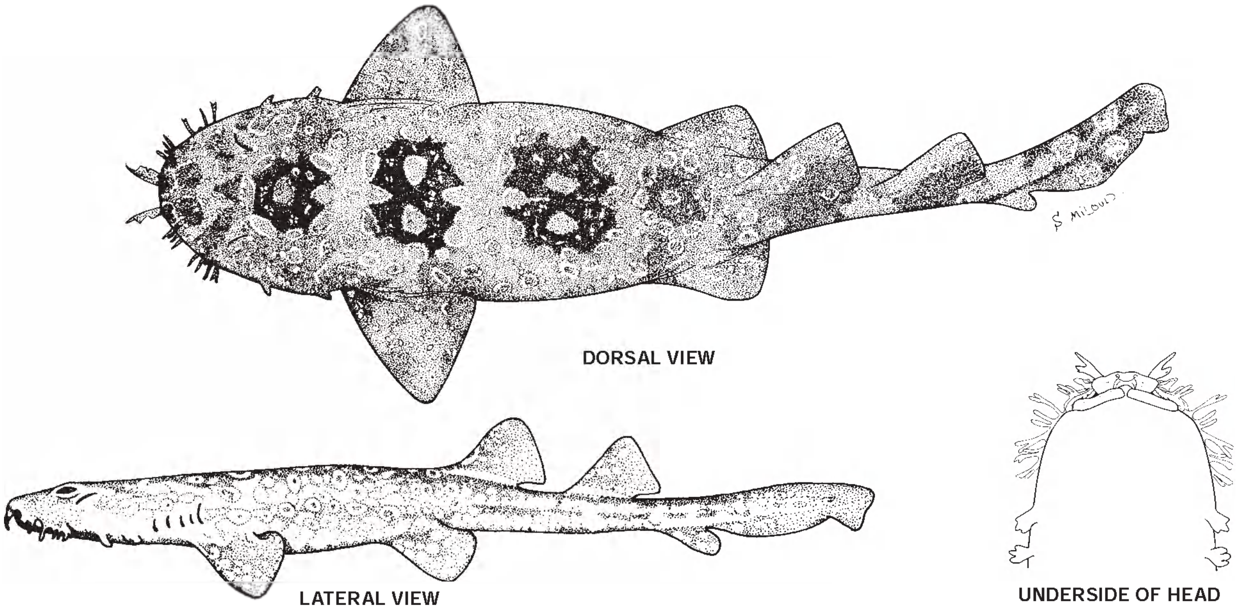
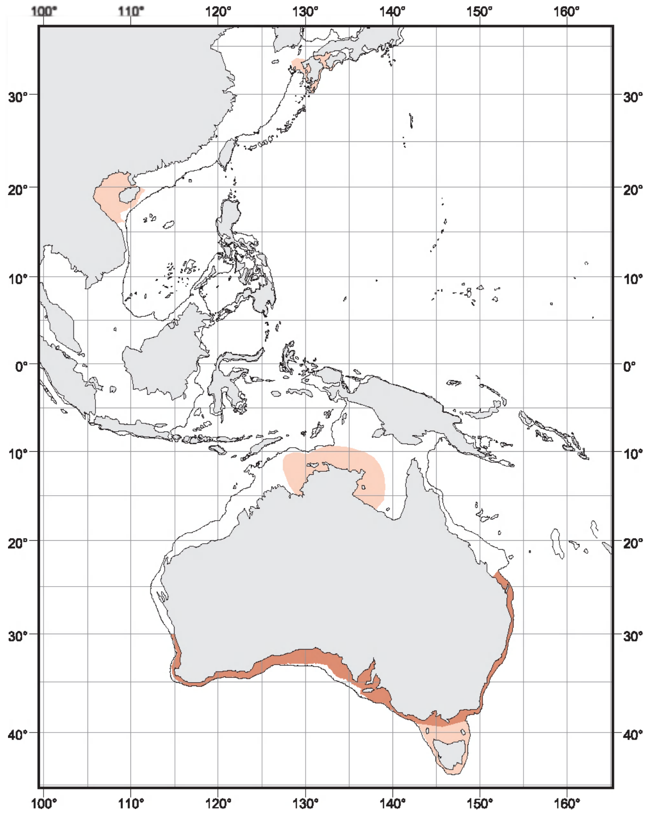


Fig. 122 ***Orectolobus maculatus***

Field Marks: Flattened benthic sharks with dermal lobes on sides of head, symphysial groove on chin; a rather sombre, variegated colour pattern of dark back with obscure darker dorsal saddles and densely covered with prominent light O-shaped spots; also, mouth in front of eyes, long, basally branched nasal barbels, nasoral grooves and circumnarial grooves, two rows of enlarged fang-like teeth in upper jaw and three in lower jaw; first dorsal-fin origin over pelvic-fin bases.

Diagnostic Features: Nasal barbels with a few basal branches. Six to ten dermal lobes below and in front of eye on each side of head; dermal lobes behind spiracles branched and broad. No dermal tubercles or ridges on back. Interspace between dorsal fins longer than inner margin of first dorsal fin, about half length of dorsal-fin base. Origin of first dorsal fin over about last third of pelvic-fin base. First dorsal-fin height about equal to base length. **Colour:** colour pattern variegated but more sombre and less contrasting than most other wobbegongs except ***O. wardi***, dorsal surface of body dark with somewhat obscure, broad, darker rectangular saddles with deeply corrugated margins separated by lighter areas, the entire dorsal surface densely spotted with large, O-shaped, light markings; saddles not ocellate in appearance; interspaces between saddles without broad reticulated lines.



Distribution: Western Pacific: South coast of Australia (Western Australia, South Australia, Victoria, New South Wales and southern Queensland, Tasmanian records probably invalid, possibly not Northern Territory). Records from Japan and the South China Sea need confirmation.

Habitat: An abundant, temperate to tropical, inshore to offshore bottom shark of the continental shelves of the western Pacific, occurring in the intertidal down to at least 110 m, commonly on coral and rocky reefs, in coastal bays, in estuaries, in seagrass beds, under piers, and on sandy bottom. It may occur in water barely deep enough to cover it, and has been seen climbing over ridges between tidepools, with its back out of water. Juveniles occur on low reefs, in seagrass beds, and in estuaries. It sometimes makes short trips well above the bottom.

Biology: This shark apparently is sluggish and inactive and is often found motionless on the bottom, at least during the day when it is presumably resting. It often is found in caves, under overhangs on rocky reefs, in channels, and in shipwrecks during the day. It is well camouflaged by its colour pattern and dermal flaps on rough bottom but is rather conspicuous on sand. This species (and wobbegongs in general) has not been studied to the extent of some nurse sharks (Ginglymostomatidae), but site specificity may be a feature of its behaviour as with nurse sharks: anecdotal accounts suggest that individuals may return to the same site repeatedly. It may occur singly but also occurs in aggregations of a dozen or more. It is said to be nocturnal, and may swim and clamber about the bottom at night looking for food as nurse sharks do. It is not known how important their camouflage patterns are for feeding in this and other wobbegongs. It is uncertain if wobbegongs take a substantial amount of prey that simply blunders into proximity while they sit on the bottom (as shown in a recent video), or if they do so by active prowling and stalking at night. Wobbegongs in the Sydney area, presumably this common species, were observed to slowly sneak up to a bait at night from a considerable distance, as if stalking potential prey like a cat, but this may not be the case with live, uninjured prey.

Ovoviviparous, with large numbers of young per litter; one female had 37. There are anecdotal accounts that male wobbegongs from the Sydney area (and presumably this species, which is abundant there) kept in aquaria fight vigorously among themselves while courting females, and that females are bitten by males in the gill region during courtship and one clasper is inserted; in captivity, these wobbegongs copulated in July. A wild male wobbegong was said to be attracted to a female kept in a wired enclosure open to the sea and tried to enter the enclosure during the breeding season; the implication is that the female gave off an attractive stimulus, presumably a chemical pheromone but possibly some other signal.

The spotted wobbegong feeds on bottom invertebrates, including crabs, lobsters and octopuses, bony fishes including sea bass (Serranidae), scorpionfishes (Scorpaenidae) and luderick (Kyphosidae), other nonbatoid sharks including conspecifics, and rays (batoids). Prey items may blunder right up to the mouth of a lurking wobbegong, and even nibble on its tentacles, before being caught and eaten. Apparently the short broad mouth and large broad pharynx of this and other wobbegongs aid them in sucking in prey. Video footage suggests that prey is suddenly sucked into the mouth as the pharynx expands, much as in angel sharks, but the prey is taken in front of the wobbegong rather than above it as in angel sharks (Squatinidae). The powerful jaws and big, modified anterior teeth in the symphysial region of this and other wobbegongs, with one median and two lateral rows of teeth in the lower jaw that interdigitate with two rows of enlarged lateral teeth in the upper jaw, form an effective trap to impale and kill their prey.

Size: Maximum about 320 cm, but with most individuals smaller, up to 150 to 180 cm. Size at birth about 21 cm. Adult males may mature at about 60 cm long.

Interest to Fisheries and Human Impact: Interest to fisheries limited, utilized for human consumption and for leather; the meat is apparently excellent eating and the skin of this and other wobbegongs is tough and makes an excellent, decorative leather with its handsome patterning. Spotted wobbegongs are commonly caught as bycatch in trawls, beach seines, trammel nets, in lobster pots and traps, and are fished with line gear (droplines) off New South Wales. Some are taken by divers with spears. These sharks are regarded as a pest by lobster fishers, because they are adept at wedging themselves into lobster pots, to eat the catch and bait.

Much has been made of the danger of this and other wobbegongs to people, often to the exclusion of everything else of their life history. This species has been known to bite people that step on it or put their feet near its mouth, and can and will bite when molested or provoked, as when speared or caught by line or nets. These sharks can inflict severe lacerations, and there is one report of a fisher losing his foot to a spotted wobbegong that was disturbed in a rock pool. At least for this species, inflicting fatalities on people is virtually unknown and requires verification in other wobbegongs. The strong jaws and jaw musculature, and (unlike nurse sharks) large and effective impaling teeth of these wobbegongs, coupled with their tendency to hold on after biting, makes them a minor hazard to unwary explorers of tide-pools, fishermen and divers, but the sharks otherwise appear to be relatively unaggressive and sluggish when unprovoked, as when a diver views them underwater. However, placing one's limb near the head of a wobbegong may be inviting trouble, as the shark may bite either from mistaking the limb as a smaller prey item, or in response to being cornered. Several unprovoked and provoked bite incidents on people (including some on divers near the bottom and well above it) by Australian wobbegongs (probably including this species), and even a few cases of wobbegongs biting boats, have been reported in the literature, but it is often difficult to determine which species was involved or what the precise circumstances were that led to the incident. Wobbegongs of all sizes, but especially larger individuals, should be treated with due respect.

This species is displayed in large public aquaria in Europe, the United States, and probably Australia and is viewed by divers in Australia.

Local Names: Wobbegong, Carpet shark, Kumohada-oose or Kumohada-ôse (Japan).

Remarks: Extra-Australian records for this species require confirmation according to Last and Stevens (1998) and in the writer's estimation.

Literature: Ogilby and McCulloch (1908); Garman (1913); Whitley (1940); Fowler (1941); Matsubara (1955); Chen (1963); Garrick and Schultz (1963); Stead (1963); Marshall (1965); Grant (1972); Compagno (1984); Nakaya and Shirai (1984); Michael (1993); Last and Stevens (1994).

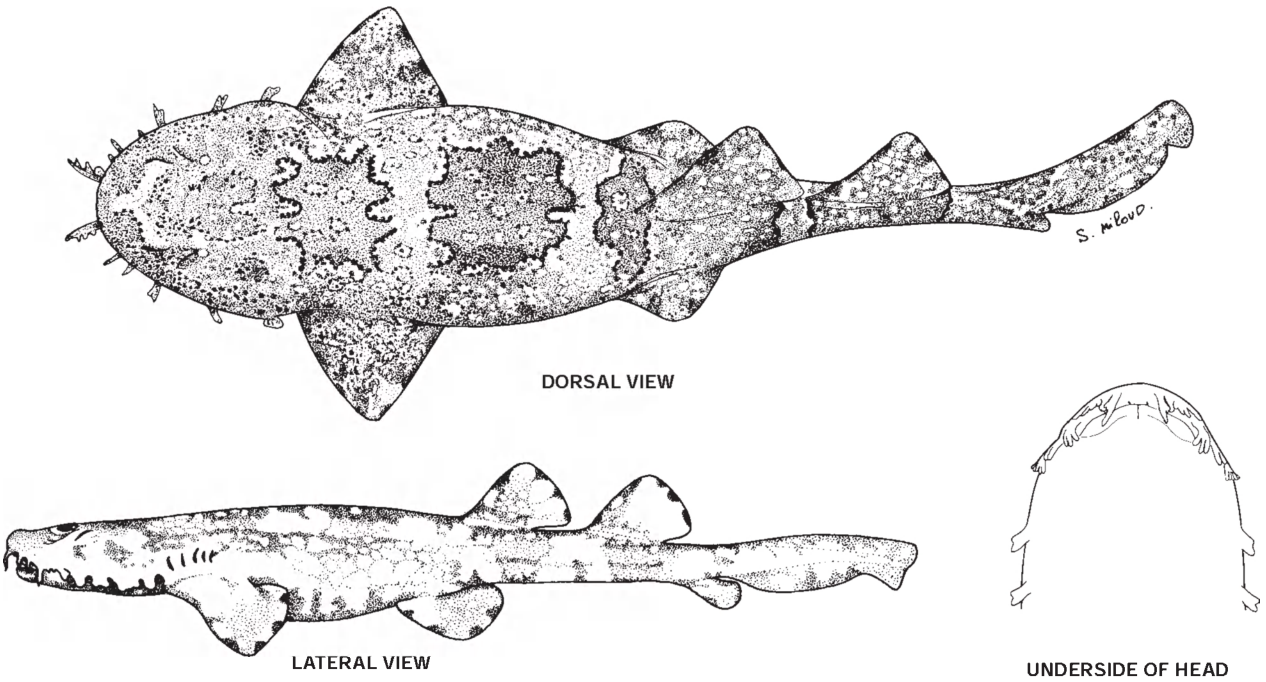
Orectolobus ornatus (De Vis, 1883) **Fig. 123**

Crossorhinus ornatus De Vis, 1883, *Proc. Linn. Soc. New South Wales* (1884), 8(2): 289, Mar. 28, 1883. Holotype: Type specimens not mentioned by De Vis but the holotype is Queensland Museum, QM I.164 (dry mount) according to Eschmeyer (1998, *Cat. Fish.*: CD-ROM), type locality, "Moreton Bay, etc.", Queensland.

Synonyms: ***Orectolobus devisi*** Ogilby, 1916: 181. Unnecessary replacement name for ***Crossorhinus ornatus*** De Vis, 1883, presumed by Ogilby to be preoccupied by Bonaparte's (1834) inclusion of ***Scyllium ornatum*** Gray, 1832 (= ***Chiloscyllium plagiosum***) in his new genus ***Orectolobus***. Holotype: Queensland Museum, QM I.164 (dry mount) according to Eschmeyer (1998: CD-ROM). ***Orectolobus ornatus halei*** Whitley, 1940: 81, figs 70-71. Holotype: South Australian Museum, Adelaide, SAMA 2 883 mm TL female (cast), not found in 1997 according to Eschmeyer (1998: CD-ROM), St. Vincent Gulf, South Australia.

Other Combinations: ***Crossorhinus barbatus*** (not Gmelin, 1788).

FAO Names: En - Ornate wobbegong; **Fr** - Requin-tapis paste; **Sp** - Tapicero ornamentado.



DORSAL VIEW

LATERAL VIEW

UNDERSIDE OF HEAD

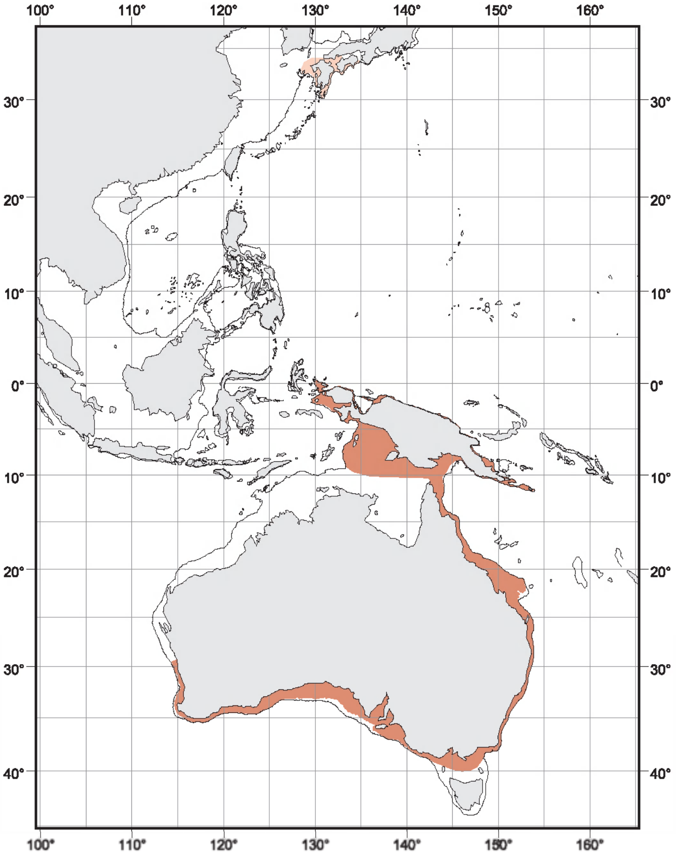
Fig. 123 ***Orectolobus ornatus***

Field Marks: Flattened benthic sharks with dermal lobes on sides of head, symphysial groove on chin; a strongly contrasting, variegated colour pattern of conspicuous broad dark, dorsal saddles with light spots and conspicuous black, corrugated edges, interspaced with lighter areas and conspicuous dark, light-centred spots; also, mouth in front of eyes, long, basally branched nasal barbels, nasoral grooves and circumnarial grooves, two rows of enlarged fang-like teeth in upper jaw and three in lower jaw; first dorsal-fin origin over pelvic-fin bases.

Diagnostic Features: Nasal barbels with a few branches. Five dermal lobes below and in front of eye on each side of head; dermal lobes behind spiracles unbranched or weakly branched and broad. No dermal tubercles or ridges on back. Interspace between dorsal fins longer than inner margin of first dorsal fin, about half first dorsal-fin base. Origin of first dorsal fin over about last third of pelvic-fin base. First dorsal-fin height about equal to base length. **Colour:** colour pattern very conspicuous and highly variegated, dorsal surface of body with conspicuous broad, dark rectangular saddles with deeply corrugated, prominent black-edged margins, dotted with light spots and not ocellate in appearance; interspaces between saddles light, with numerous broad light-centred dark blotches.

Distribution: Western Pacific: ?Japan, Indonesia, New Guinea, and tropical and warm-temperate Australia (Queensland, New South Wales, Victoria, South Australia, south coast of Western Australia; absent from Tasmania, northern Western Australia and Northern Territory).

Habitat: A common inshore bottom shark of continental waters, found in bays, on alga-covered rocky areas and coral reefs on the coast and around offshore islands, in lagoons, on reef flats and faces, and in reef channels. Favours clearer water than does the spotted wobbegong. Occurs frim the intertidal to at least 100 m depth.



Biology: This is a nocturnal shark, that rests on the bottom during the day in caves, under ledges on reefs, and in trenches, and prowls on its reef habitat at night. It is observed singly and often in aggregations during the day, sometimes with several animals piled on top of one another. Ovoviviparous, with litter of at least 12 young. Feeds on bony fishes, sharks, rays, cephalopods, and crustaceans.

Size: Maximum about 288 cm. Size at birth about 20 cm. Normally maturing at about 175 cm but a Queensland male was mature at 63 cm (suggesting the possibility of more than one species included under this taxon).

Interest to Fisheries and Human Impact: Interest to fisheries limited, fished as bycatch of commercial shark fisheries off Western Australia and taken by dropline off New South Wales. Flesh marketed but of little commercial value at present. Skin very tough and attractively patterned, and occasionally used for making a good leather. Said to bite waders and fishers in tidepools and occasionally biting divers. Michael (1993) suggests that large males of this species may be more aggressive during the breeding season. Sometimes they may swim off the bottom and approach a nearby diver, possibly as an agonistic response. This species is kept in public aquaria in the United States and probably Australia. Conservation status uncertain, but of concern in places outside Australian territorial waters where it is found in places subjected to habitat degradation and uncontrolled fisheries.

Local Names: Gulf wobbegong, Banded wobbegong, Carpet shark, Karakusa-ôse (Japan).

Remarks: Whitley (1940) proposed a subspecies, ***O. ornatus halei***, for the ornate wobbegongs from South Australia, separable from ***O. o. ornatus*** of more northeastern waters by differences in its colour pattern and in the dermal flaps of the head. It remains to be seen at what level these apparent differences can be recognized.

Extra-Australian records for this species (Masuda, Araga and Yoshino, 1975; Nakaya and Shirai, 1984, for Japan) require confirmation (Last and Stevens, 1994; see also discussion above).

Literature: Ogilby and McCulloch (1908); Garman (1913); Whitley (1940); Stead (1963); Marshall (1965); Grant (1972); Masuda et al. (1975); Compagno (1984); Nakaya and Shirai (1984); Michael (1993); Last and Stevens (1994).

Orectolobus wardi Whitley, 1939

Fig. 124

Orectolobus wardi Whitley, 1939, *Rec. Australian Mus.*, 20: 264. Holotype: Australian Museum, Sydney, AMS-IA-7784, Cape Keith, Melville Island, northern Australia.

Synonyms: None.

Other Combinations: None.

FAO Names: En - Northern wobbegong; **Fr** - Requin-tapis savetier; **Sp** - Tapicero zapatilla.

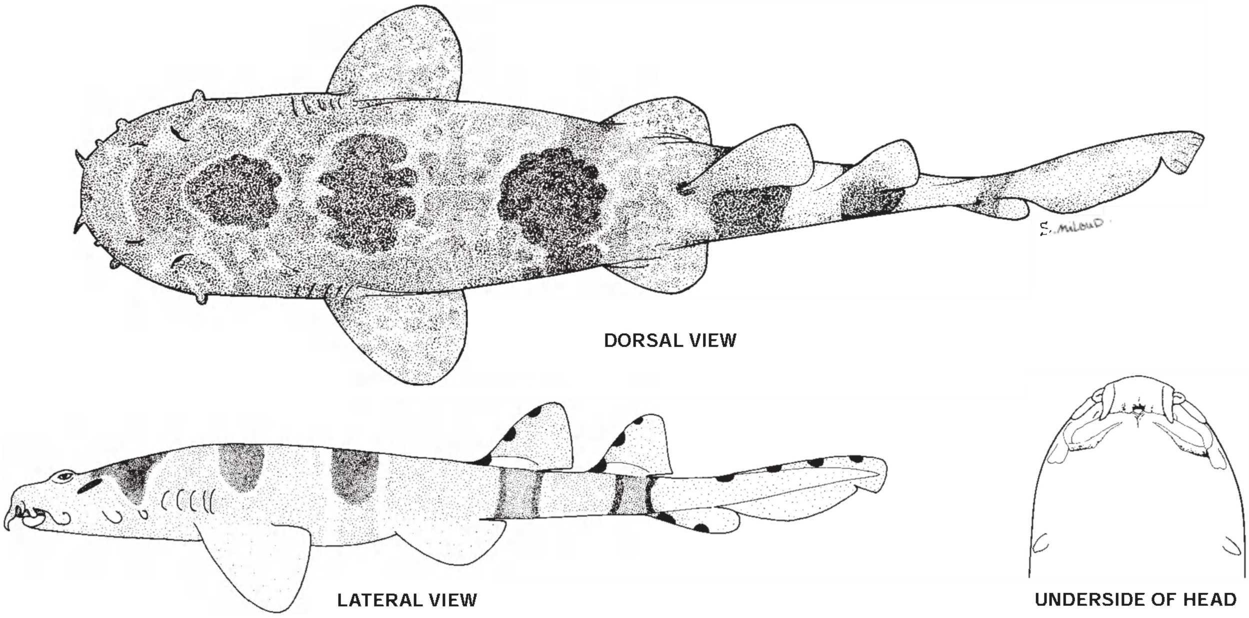
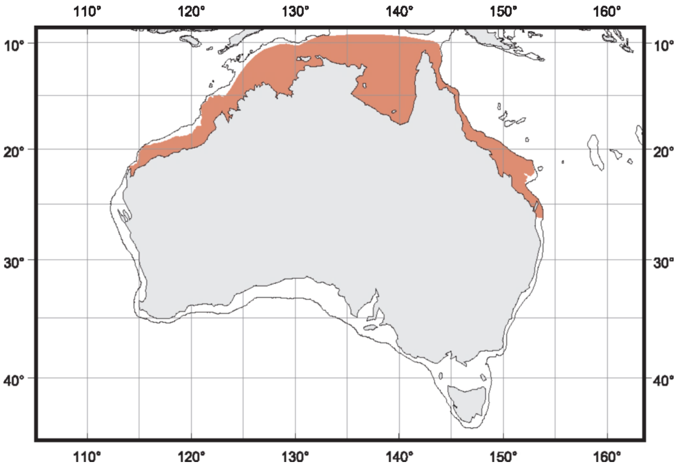


Fig. 124 *Orectolobus wardi*

Field Marks: Flattened benthic sharks with dermal lobes on sides of head, symphysial groove on chin, variegated but rather sombre colour pattern of rounded, ocellate dark dorsal saddles with entire edging and light margins, interspaced with broad dusky areas without spots or reticular lines; also, mouth in front of eyes, long, basally branched nasal barbels, nasoral grooves and circumnarial grooves, two rows of enlarged fang-like teeth in upper jaw and three in lower jaw.

Diagnostic Features: Nasal barbels without branches. Two dermal lobes below and in front of eye on each side of head; dermal lobes behind spiracles unbranched and broad. No dermal tubercles or ridges on back. Interspace between dorsal fins longer than inner margin of first dorsal fin, about half first dorsal-fin base. Origin of first dorsal fin over about last fourth of pelvic-fin base. First dorsal-fin height about equal to base length. **Colour:** colour pattern variegated but dull and sombre compared to most other wobbegongs, dorsal surface of body with small, rounded, ocellate, light-edged saddle marks with entire margins, separated from each other by broad, dusky spaces without spots or broad reticulated lines.



Distribution: Western South Pacific: Confined to Australian waters (Queensland, Northern Territory and Western Australia).

Habitat: A little-known but possibly common tropical inshore bottom shark of the Australian northern continental shelf. Occurs on shallow-water reefs in water less than 3 m deep, often in turbid areas.

Biology: A nocturnal shark, inactive during the day, sometimes seen with its head under a ledge. Probably ovoviviparous. Presumably feeds on bottom invertebrates and fishes, but diet unrecorded.

Size: Maximum to at least 63 cm and possibly 100 cm; a 45 cm male was mature.

Interest to Fisheries and Human Impact: Interest to fisheries none at present. Conservation status unknown.

Local Names: Northern wobbegong, North Australian wobbegong.

Literature: Whitley (1939, 1940); Marshall (1965); Compagno (1984); Michael (1993); Last and Stevens (1994).

click for next page

click for previous page

Orectolobus sp. A Last and Stevens, 1994

Fig. 125

***Orectolobus* sp. A** Last and Stevens, 1994, *Sharks Rays Australia*: 128, pl. 26.

Synonyms: None.

Other Combinations: None.

FAO Names: En - Western wobbegong; **Fr** - Requin-tapis sombre; **Sp** - Tapicero occidental.

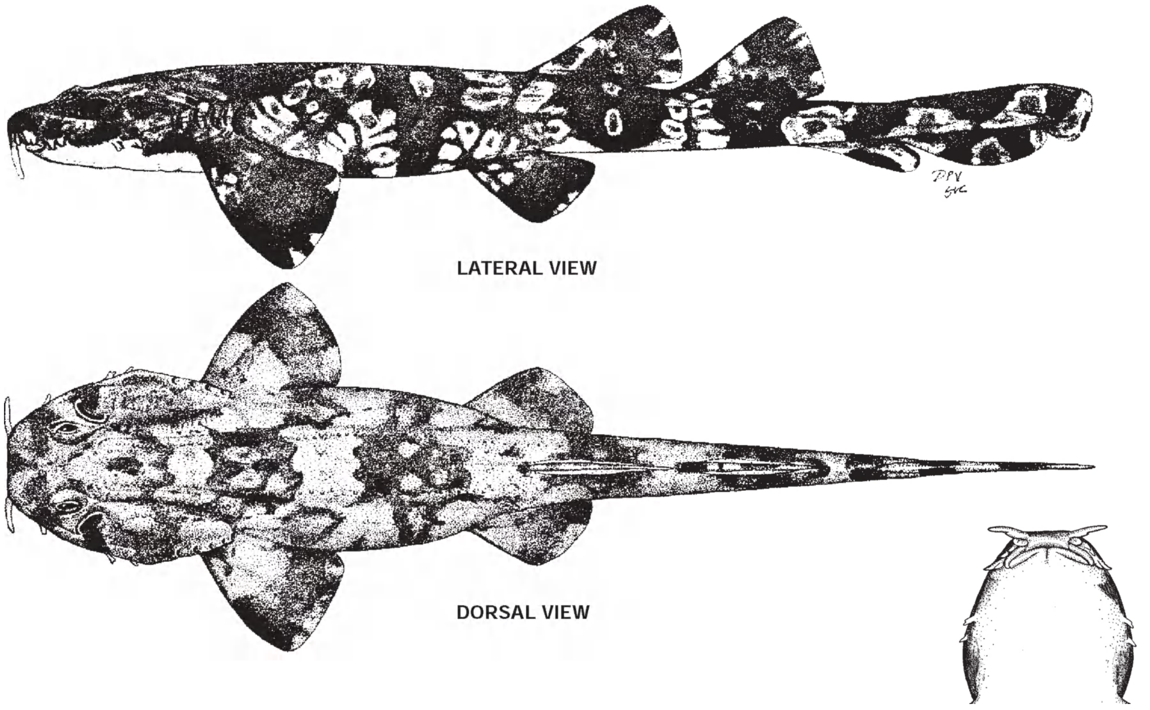
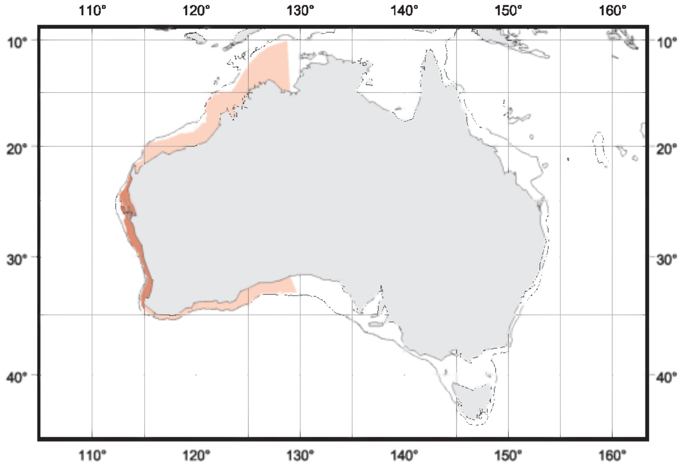


Fig. 125 *Orectolobus* sp. A

Field Marks: Flattened benthic sharks with dermal lobes on sides of head, symphysial groove on chin; a strongly contrasting, variegated colour pattern of conspicuous broad dark, dorsal saddles with light spots and deeply corrugated edges but without conspicuous black margins, interspaced with lighter areas and conspicuous light, dark-centred spots but without numerous light O-shaped rings; also, mouth in front of eyes, long, basally branched nasal barbels, nasoral grooves and circumnarial grooves, two rows of enlarged fang-like teeth in upper jaw and three in lower jaw; first dorsal-fin origin over rear half of pelvic-fin bases.

Diagnostic Features: Nasal barbels with one small branch. Four dermal lobes below and in front of eye on each side of head; dermal lobes behind spiracles unbranched or weakly branched and slender. Low dermal tubercles or ridges present on back in young, lost in adults. Interdorsal space somewhat shorter than inner margin of first dorsal fin, about one-fourth of first dorsal-fin base. Origin of first dorsal fin over about last third of pelvic-fin base. First dorsal-fin height about three-fourths of base length. **Colour:** colour pattern very conspicuous and highly variegated, dorsal surface of body with conspicuous broad, dark rectangular saddles with deeply corrugated margins, not black-edged, dotted with light spots but without numerous O-shaped light rings; saddles not ocellate in appearance; interspaces between saddles light, with numerous broad dark blotches.

Distribution: Eastern Indian Ocean, Australia (temperate west coast of Western Australia from Cape Leeuwin to Coral Bay, but possibly not extending into more southern waters or into tropical Western Australia).



Habitat: Inshore on the continental shelf of Western Australia, on reefs and in seagrass. Depths unreported, but probably in water from the intertidal to less than 100 m.

Biology: Poorly known. Ovoviviparous, presumably feeds on invertebrates and small fish.

Size: Maximum about 200 cm. Size at birth about 22 cm; an 85 cm male was mature.

Interest to Fisheries and Human Impact: Interest to fisheries minimal, taken as a bycatch in small quantities by the Western Australian shark fishery and used for human consumption. Viewed by divers off Western Australia. Conservation status uncertain but should be monitored because of its limited geographic range and presumably limited bathymetric range.

Remarks: See remarks above in the family account on similarities of this species to ***Sutorectus tentaculatus***.

Literature: Compagno (1984); Michael (1993); Last and Stevens (1994).

Sutorectus Whitley, 1939

Genus: ***Sutorectus*** Whitley, 1939, *Australian Zool.*, 9(3): 228.

Type Species: ***Crossorhinus tentaculatus*** Peters, 1864, by original designation.

Number of Recognized Species: 1.

Synonyms: None.

Diagnostic Features: Head rather narrow, its greatest width slightly less than distance from snout tip to first gill openings. Chin smooth, without a beard of dermal lobes. Dermal lobes of sides and front of head small, short, unbranched, and forming isolated groups that are broadly separated from one another, in 4 to 6 pairs. Nasal barbels simple and unbranched. Mouth narrow, width about 9% of total length. Dorsal surface of head, body and precaudal tail, and dorsal-fin bases, with rows of large, conspicuous dermal tubercles, resembling warts. Trunk moderately broad, width across pectoral-fin insertions considerably less than head length. Precaudal tail rather long, distance from pelvic-fin insertion to lower caudal-fin origin much greater than head length. Pectoral and pelvic fins small and widely spaced from each other, distance from pectoral-fin insertions to pelvic-fin origins about twice length of pectoral-fin bases and somewhat greater than pelvic-fin lengths from origins to free rear tips. Interspace between first and second dorsal fins much shorter than first dorsal-fin inner margin and less than a fifth of first dorsal-fin base. Dorsal fins low and long, height of first dorsal fin about half its base length, length of first dorsal-fin base greater than pelvic-fin length from origin to free rear tip. Origin of first dorsal fin in front of midbases of pelvic fins. **Colour:** dorsal surface with a colour pattern of jagged-edged broad dark saddles and scattered dark spots on a light background, no reticulating narrow lines with spots at their junctions.

Remarks: Whitley (1939) proposed the genus ***Sutorectus*** on the simple nasal barbels, tuberculate back, and narrower interdorsal space of the type and only species, ***S. tentaculatus*** (Peters, 1864). This genus was recognized by Whitley (1940), Bigelow and Schroeder (1948), Whitley and Pollard (1980), Compagno (1984), Dingerkus (1986), and Last and Stevens (1994), but was considered a synonym of ***Orectolobus*** by Stead (1963) and Applegate (1974). The writer was inclined to support Applegate's classification (Compagno, 1973) prior to examining specimens of ***Sutorectus tentaculatus***, but found additional characters by which this species may be distinguished from typical ***Orectolobus***. As noted above (see remarks under family), ***Orectolobus* sp. A**. approaches ***S. tentaculatus*** in certain features of its morphology.

Sutorectus tentaculatus (Peters, 1864)

Fig. 126

Crossorhinus tentaculatus Peters, 1864, *Monatsb. Akad. Wiss. Berlin*: 123. Syntypes: Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin, ZMB 5073, a 750 mm female, and ZMB 5264, a 430 mm female (alcohol), according to Paepke and Schmidt (1988, *Mitt. Zool. Mus. Berlin*, 64(1): 163) and Eschmeyer (1998, *Cat. Fish.*: CD-ROM), from Adelaide, South Australia.

Synonyms: None.

Other Combinations: ***Orectolobus tentaculatus*** (Peters, 1864).

FAO Names: En - Cobbler wobbegong; **Fr** - Requin-tapis cordonnier; **Sp** - Tapicero zapatudo.

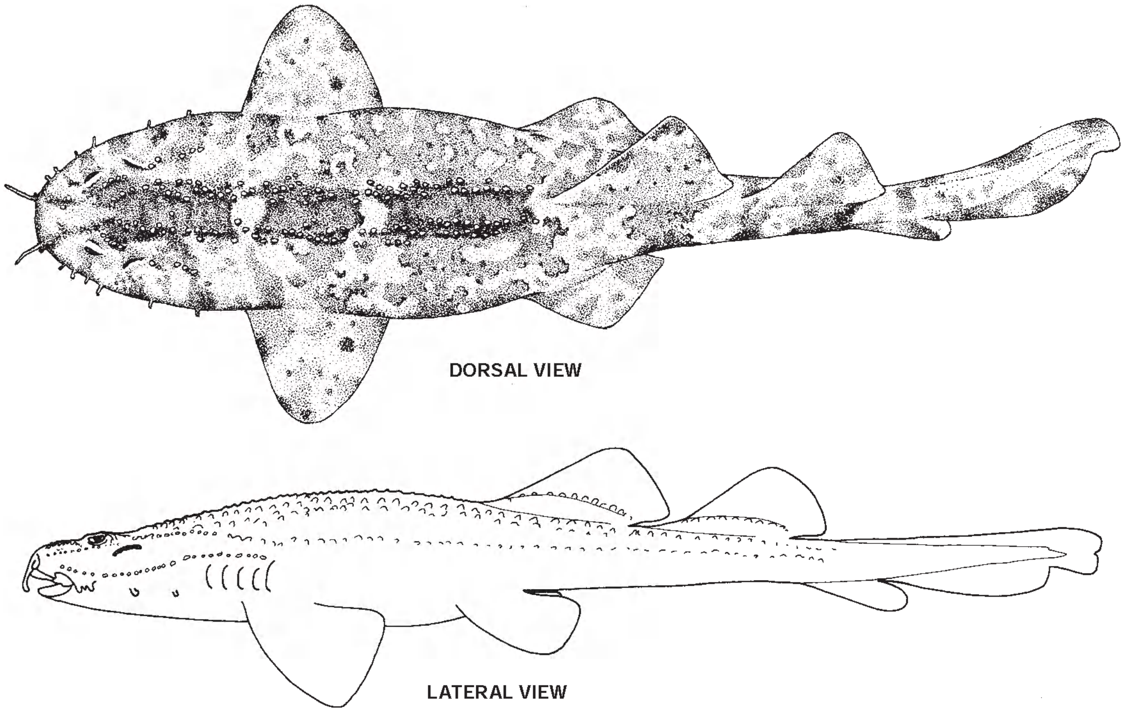
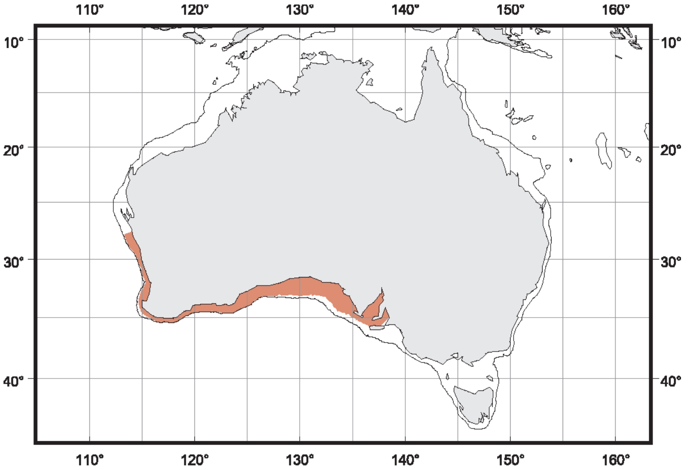


Fig. 126 ***Sutorectus tentaculatus***

Field Marks: A rather slender wobbegong, less flattened than most; with a few slender dermal lobes on sides of head, simple, unbranched nasal barbels, symphysial groove on chin; conspicuous warty tubercles in rows on the dorsal surface of the body and dorsal fin bases; dorsal fins very low and long, with heights half their base lengths, first dorsal-fin origin in front of pelvic-fin midbases; striking variegated colour pattern of broad dark, dorsal saddles with jagged, corrugated edges, interspaced with light areas with irregular dark spots; also, mouth in front of eyes, nasoral grooves and circumnarial grooves present, two rows of enlarged fang-like teeth in upper jaw and three in lower jaw.

Diagnostic Features: See genus ***Sutorectus*** above.

Distribution: Western South Pacific: Confined to Australian waters (west coast of temperate Western Australia from Houtman Abrolhos southeast to Adelaide, South Australia).



Habitat: A little-known but probably common inshore bottom shark of temperate continental waters, on rocky and coral reefs, and in seaweeds. Depths not recorded.

Biology: Biology almost unknown. Presumably ovoviviparous and preying on bottom invertebrates and fishes.

Size: Maximum recorded 92 cm. Size at birth about 22 cm; near full-term young, still with sizeable yolk sacs, were 18 cm long. Males mature at about 65 cm. Said to grow as large as the spotted wobbegong (***Orectolobus maculatus***) according to Stead (1963), but possibly by confusion with ***Orectolobus ornatus*** or some other large wobbegong.

Interest to Fisheries and Human Impact: Interest to fisheries none at present. Conservation status uncertain but needs to be monitored because of its limited range.

Local Names: Cobbler carpet shark, Cobbler shark.

Literature: Ogilby and McCulloch (1908); Garman (1913); Whitley (1940); Fowler (1941); Stead (1963); Compagno (1984); Last and Stevens (1994).

2.3.4 Family HEMISCYLLIIDAE

Family: Subfamily Hemiscylliinae Gill, 1862b, *Ann. Lyceum Nat. Hist. New York*, 7(32): 407, 408 (Family Scylliorhinoidae Gill, 1862). Also subfamily Hemiscylliinae Fowler, 1934, *Proc. Acad. Nat. Sci. Philadelphia*, 85: 238 (Family Orectolobidae).

Type Genus: ***Hemiscyllium*** Müller and Henle, *in* Smith, 1837.

Number of Recognized Genera: 2.

Synonyms: Subfamily Chiloscylliinae Gill, 1862b: 407, 408 (Family Scylliorhinoidae Gill, 1862). Type genus: ***Chiloscyllium*** Müller and Henle, 1837. Family Cheiloscyllium Hasse, 1879: 54. Type genus: ***Cheiloscyllium*** Hasse, 1879, = ***Chiloscyllium*** Müller and Henle, 1837. Family Hemiscylliidae Whitley, 1940: 68. Independently proposed as a separate family. Type genus: ***Hemiscyllium*** Müller and Henle, *in* Smith, 1837:86.

FAO Names: En - Bamboo sharks, Longtailed carpet sharks; **Fr** - Requins-chabot; **Sp** - Bamboas.

Field Marks: Small, slender sharks with nasoral grooves, perinasal grooves, short barbels, small transverse mouths in front of eyes, dorsolateral eyes, large spiracles below eyes, no lateral skin flaps on head; two spineless dorsal fins, the second dorsal-fin origin well ahead of the anal-fin origin, a long, low, keel-like rounded anal fin separated from the lower caudal origin by a narrow notch, and a long precaudal tail much greater than the head and body length.

Diagnostic Features: Head narrow to moderately broad and cylindrical to somewhat flattened, without lateral flaps of skin. Snout broadly to narrowly rounded or slightly pointed. Eyes dorsolaterally situated on head and with strong subocular ridges below them. Eyes without movable upper eyelids or subocular pockets. Spiracles large and subequal in size or somewhat larger than eyes, without prominent raised external rims; spiracles somewhat below and behind eyes. Gill slits small, fifth gill slit overlapping fourth; internal gill slits without filter screens. Nostrils with short pointed barbels, circumnarial folds and circumnarial grooves present around outer edges of incurrent apertures. Nasoral grooves long and strongly developed. Mouth small, nearly transverse, and subterminal on head. Lower lip not trilobate and without lateral orolabial grooves connecting edge of lip with medial ends of lower labial furrows, without a longitudinal symphysial groove on chin. Lower labial furrows extending medially nearly to symphysis and connected medially by a mental groove or groove and flap. Teeth not strongly differentiated in upper and lower jaws, with symphysial teeth not enlarged nor fang-like. Tooth row count 26 to 35/21 to 32. Teeth with a strong medial cusp, with or without a pair of short lateral cusplets, and with weak labial root lobes. Teeth orthodont with a central pulp cavity and no plug of osteodentine. Body cylindrical or slightly depressed, with or without ridges on sides. Precaudal tail longer than body. Caudal peduncle without lateral keels or precaudal pits. Pectoral fins small, broad and rounded. Pectoral fins aplesodic and with fin radials not expanded into fin web. Pectoral propterygium large and separate from mesopterygium and metapterygium or fused with mesopterygium; pectoral-fin radial segments three at most, and with longest distal segments 0.3 to 0.4 times the length of longest proximal segments. Pelvic fins somewhat smaller or about as large as dorsal fins and subequal to or much larger than anal fin, nearly as large or as large as pectoral fins and with anterior margins 0.6 to about 1.1 times pectoral-fin anterior margins. Claspers without mesospurs, claws or dactyls. Dorsal fins equal-sized. First dorsal-fin origin varying from over pelvic-fin bases to behind them, insertion well behind the pelvic-fin rear tips. Anal fin somewhat smaller than second dorsal fin, with broad base, broadly rounded keel-like apex, origin behind second dorsal-fin insertion, and insertion separated by a narrow notch much less than base length from lower caudal-fin origin. Caudal fin horizontally elongated and not crescentic, weakly heterocercal with its upper lobe hardly elevated above the body axis; dorsal caudal-fin margin less than a fifth as long as the entire shark. Caudal fin with a strong terminal lobe and subterminal notch but without a ventral lobe, preventral and postventral margins not differentiated and forming a continuous curve. Vertebral centra with well-developed radii but no annuli. Total vertebral count 151 to 192, monospondylous precaudal count 32 to 41, diplospondylous precaudal count 57 to 90, diplospondylous caudal count 55 to 72, and precaudal count 89 to 129. Cranium narrow and not greatly expanded laterally. Medial rostral cartilage moderately long and not reduced to a low nubbin. Nasal capsules elevated and not greatly depressed or fenestrated, internarial septum high and compressed. Orbits with small foramina for preorbital canals, medial walls not fenestrated around the optic nerve foramina. Supraorbital crests present on cranium but not laterally expanded nor pedicellate. Suborbital shelves moderately broad and not greatly reduced. Cranial roof unfenestrated, with isolated frontoparietal fenestrae, or with a continuous fenestra from the anterior fontanelle to the parietal fossa. Basal plate of cranium with separate pairs of carotid and stapedial foramina. Adductor mandibulae muscles of jaws with two or three divisions. Preorbitalis muscles extending onto posterodorsal surface of cranium. No anterodorsal palpebral depressor, rostromandibular, rostronuchal or ethmonuchal muscles. Valvular intestine of ring type with 12 to 20 turns. Development oviparous, eggs laid in elliptical egg capsules. Size small with adults between about 43 and 107 cm total length with most below 1 m; young may hatch at about 9 to 17 cm. Colour pattern of dark saddles and bars and dark or light spots present, or colour plain.

Distribution: Bamboo sharks are small inshore bottom sharks of continental waters of the Indo-West Pacific, ranging from Madagascar in the west to Japan, Philippines, and the Australian region in the east. One genus (***Hemiscyllium***) is centred on Australia, New Guinea and the Indo-Australian Archipelago, in the western Pacific (with an apparent outlier in the Seychelles), but the second (***Chiloscyllium***) is wide-ranging over the entire range of the family.

Habitat: Bamboo sharks commonly occur in the intertidal, in tidepools on rocky or coral reefs close inshore, sometimes in water sufficient only to cover them, and on soft bottoms inshore and offshore in open and enclosed bays.

Biology: Bamboo sharks are common to abundant and frequently kept in captivity, but their biology is poorly known at best. They have slender trunks and tails and strong, muscular, leg-like paired fins ideal for clambering on reefs and in crevices. These sharks are small, mostly less than 1 m maximum length. Michael (1993) suggested that the large epaulette spots seen on ***Hemiscyllium*** species may serve as eyespots to intimidate predators approaching them from above. At least some and probably all of the species are oviparous, depositing eggs on the bottom in oval egg cases. Colour patterns of the young are often strikingly different and bolder than adults and suggest different habitat preferences or habits. Food of these sharks is little known, but includes small bottom fishes, cephalopods, shelled molluscs, and crustaceans.

Interest to Fisheries and Human Impact: ***Hemiscyllium*** species are little-utilized for fisheries apart from the aquarium trade, but ***Chiloscyllium*** species are commonly caught in small-scale artisanal and commercial fisheries and by bottom trawlers in the western Pacific and East-Central Indian Ocean. In some countries such as Thailand large catches of ***Chiloscyllium*** are occasionally landed. Longtailed carpet sharks are ideal for aquaria, because they are small, often colourful and pleasingly marked, very hardy and can live over a decade in captivity and reproduce there. Several of the species figure in the aquarium trade and are displayed in captivity in public aquaria worldwide. Despite their importance to fisheries and the aquarium trade the conservation status of longtailed carpet sharks is poorly known, and they may be threatened by overfishing, bad fisheries practices and habitat modification, including the alteration and destruction of coral reefs. Some of the species are rare, have limited geographic, bathymetric, and habitat distributions, and live in poorly known and poorly-protected areas. There is an urgent need for investigations on the biology and conservation status of these sharks, particularly those that figure heavily in fisheries and those rarities that live in threatened and restricted habitats.

Remarks: The arrangement of this family follows Garman (1913), Whitley (1940, 1967), Fowler (1941), Compagno (1984), Dingerkus (1986), Last and Stevens (1994), and especially the comprehensive review and revision of the family by Dingerkus and DeFino (1983).

Literature: Müller and Henle (1838d); Bleeker (1852); Dumeril (1853, 1865); Günther (1870); Regan (1908a); Smith (1913); Garman (1913); Whitley (1940, 1967); Stead (1963); Fowler (1941, 1967a); Compagno (1973, 1984, 1988); Applegate (1984); Dingerkus and DeFino (1983); Dingerkus (1986); Michael (1993); Last and Stevens (1994).

Key to Genera:

1a. Nostrils subterminal on snout; preoral snout long, mouth closer to eyes than snout tip; eyes and supraorbital ridges hardly elevated; no black hood on head or large dark spot or spots on sides of body above pectoral fins (Fig. 127a and b) . . . . ***Chiloscyllium***

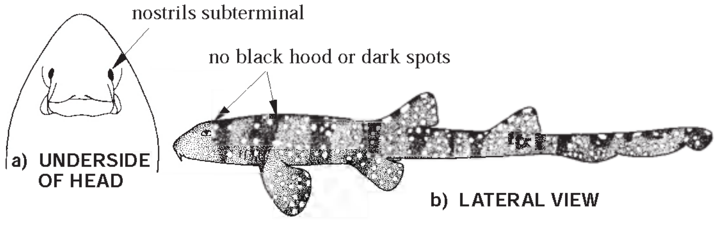


Fig. 127 *Chiloscyllium*

1b. Nostrils terminal on snout; preoral snout short, mouth closer to snout tip than eyes; eyes and supraorbital ridges prominently elevated; a large dark spot or spots on sides of body above pectoral fins, or a black hood on head (Fig. 128a and b) . . ***Hemiscyllium***

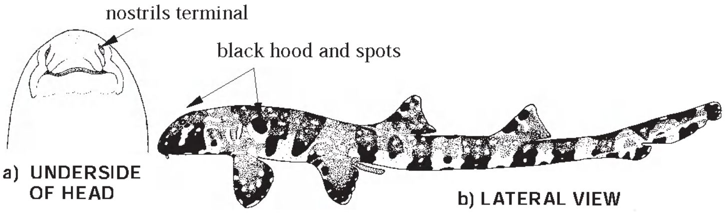


Fig. 128 *Hemiscyllium*

Chiloscyllium Müller and Henle, 1837

Genus: ***Chiloscyllium*** Müller and Henle, 1837a, *Ber. K. preuss. Akad. wiss. Berlin*, 2: 112; Müller and Henle, 1837b, *Arch. Naturg.* 3: 395 (no species mentioned); Müller and Henle, *in* Smith, 1837, *Proc. Zool. Soc. London*, 5: 85 (one species, ***Scyllium plagiosum*** Bennett, 1830); Müller and Henle, 1838a, *Mag. Nat. Hist., new ser.*, 2: 34; Müller and Henle, 1838b, *L'Institut*, 6: 64; Müller and Henle, 1838c, *Arch. Naturg.* 4: 83 (no species mentioned); Müller and Henle, 1838d, *Syst. Beschr. Plagiost.*, pt. 1: 17 (five species, no type allocation).

Type Species: ***Scyllium plagiosum*** Bennett, 1830, by subsequent monotypy of Müller and Henle, *in* Smith, 1837, *Proc. Zool. Soc. London*, pt.5: 85; also by subsequent designation of Gill, 1862b, *Ann. Lyceum Nat. Hist. New York*, 7(32): 408, as "***Chiloscyllium plagiosum*** Mül. and Henle".

Number of Recognized Species: 7.

Synonyms: Genus ***Chyloscyllium*** Dumeril, 1853: 125. Apparent error for ***Chiloscyllium*** Müller and Henle, 1837. Genus ***Cheiloscyllium*** Hasse, 1879: 51, 55 (name only); Hasse, 1882: 276. Probable emendation of ***Chiloscyllium*** Müller and Henle, 1837, as Hasse consistently used ***Cheiloscyllium*** in his work. Genus ***Synchismus*** Gill, 1862b: 407, 408. Type species: ***Chiloscyllium tuberculatum*** Müller and Henle, 1838, by original designation, a junior synonym of ***Squalus indicus*** Gmelin, *in* Linnaeus and Gmelin, 1788.

Diagnostic Features: Snout relatively long, preoral length over 3% of total length. Eyes and supraorbital ridges hardly elevated. Nostrils subterminal on snout and well separated from snout tip. Nasal barbels moderately elongated, length over 1.3% of total length. Mouth slightly closer to eyes than snout tip. Lower labial folds usually connected across chin by a dermal fold. Pregill length more than 13.3% of total length. Preanal tail from vent to anal-fin origin usually less than 38% of total length. Pectoral and pelvic fins relatively thin, not heavily muscular. Pectoral-fin skeleton with propterygium separate from mesopterygium. Total vertebral count usually between 135 and 180. Colour pattern without a black hood on head or large dark spot or spots on sides of body above pectoral fins.

Local Names: Bamboo sharks, Lip sharks.

Remarks: The arrangement of this genus follows Dingerkus and DeFino (1983) and Compagno (1984). *Nomina dubia* possibly referable to ***Chiloscyllium*** include: ***Squalus (Scyliorhinus) lambarda*** Blainville, 1816: 121 (*nomen nudum*). Fowler (1941: 90), suggested that this species was a possible synonym of ***Chiloscyllium indicum*** Gmelin, *in* Linnaeus and Gmelin, 1788. ***Squalus (Scyliorhinus) russellianus*** Blainville, 1816: 121 (*nomen nudum*). Assumed by Fowler (1941: 86), to be based on the "Bokee Sorrah" of Russell (1803: 10, pl. 16), and a possible synonym of ***Chiloscyllium punctatum*** Müller and Henle, 1838. ***Squalus (Scyliorhinus) unicolor*** Blainville, 1816: 121 (*nomen nudum*). Fowler (1941: 88) suggested that this species was a possible synonym of ***Chiloscyllium griseum*** Müller and Henle, 1838. ***Squalus (Scyliorhinus) variegatus*** Blainville, 1816: 121 (*nomen nudum*). Fowler (1941: 90) suggested that this species was a possible synonym of ***Chiloscyllium indicum*** Gmelin, *in* Linnaeus and Gmelin, 1788.

Key to Species:

1a. Body and tail very slender; anal-fin origin far behind free rear tip of second dorsal fin, anal-fin length from origin to free rear tip subequal to length of hypural caudal lobe from lower caudal origin to subterminal notch; colour pattern with numerous small dark spots, bars, and saddles on a light background (Fig. 129) . . . . . ***Chiloscyllium indicum***

1b. Body and tail moderately slender to relatively stout; anal-fin origin below or close behind free rear tip of second dorsal fin, length of anal fin considerably shorter than hypural caudal lobe; colour pattern varying from plain to barred and spotted but without numerous small dark spots and bars (Fig. 130) . . . . → ***2***

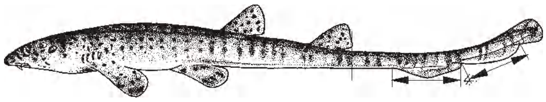


Fig. 129 *Chiloscyllium indicum*

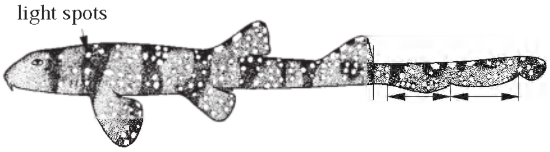


Fig. 130 *Chiloscyllium plagiosum*

2a. Lateral ridges present on trunk; background colour of the dorsal surface of body dark with numerous light spots. (Fig. 130) . . . ***Chiloscyllium plagiosum***

2b. Lateral ridges absent from trunk; background colour of the dorsal surface of body light, uniform or with scattered dark spots or dusky bands . . . . . . → ***3***

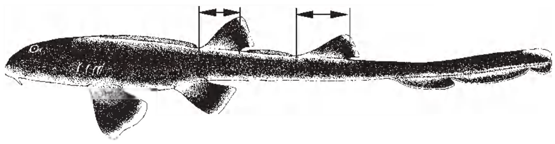


Fig. 131 *Chiloscyllium arabicum*

3a. Second dorsal fin usually with a longer base than the first dorsal fin (Fig. 131); juveniles uniform in coloration, except for spotted fins . . ***Chiloscyllum arabicum***

3b. First dorsal fin base usually longer than the second dorsal fin base (Fig. 132); juveniles, where known, with bars and spots on body . . . . → ***4***

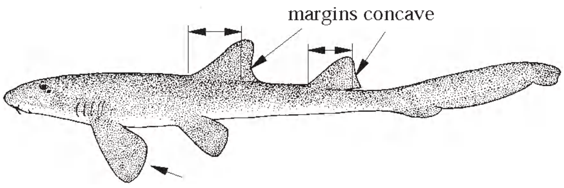


Fig. 132 *Chiloscyllium punctatum*

4a. Posterior margins of first and second dorsal fins distinctly concave, free rear tips projecting; origin of first dorsal fin far forward, over anterior half of pelvic-fin bases (Fig. 132) . . . . . ***Chiloscyllium punctatum***

4b. Posterior margins of first and second dorsal fins distinctly straight or convex, free rear tips not projecting; origin of first dorsal fin over or behind midlengths of pelvic-fin bases (Fig. 133) . . . .→ ***5***

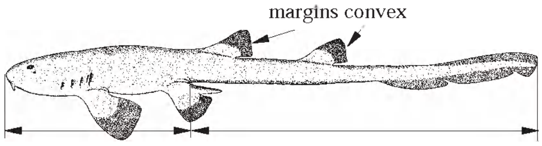


Fig. 133 *Chiloscyllium burmensis*

5a. Eyes small, less than 1.25% of total length; distance from vent to tail tip more than 67% of total length; prepectoral length less than 15.8% of total length; snout to vent length less than 31% of total length (Fig. 133) . . . . ***Chiloscyllium burmensis***

5b. Eyes large, more than 1.25% of total length; distance from vent to tail tip less than 67% of total length; prepectoral length more than 15.8% of total length; snout to vent length more than 31% of total length (Fig. 134) . . . .→ ***6***

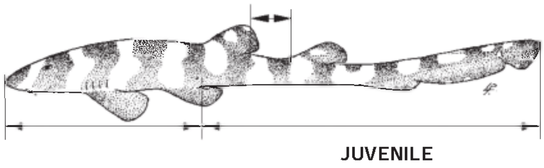


Fig. 134 *Chiloscyllium griseum*

6a. Interdorsal space usually more than 9.3% of total length; first dorsal fin height more than 6.6% of total length; second dorsal fin height usually more than 5.8% of total length; saddle-markings of juveniles without black edging (Fig. 134) . . . . ***Chiloscyllium griseum***

6b. Interdorsal space usually less than 9.3% of total length; first dorsal fin height less than 6.6% of total length; second dorsal fin height usually less than 5.8% of total length; saddle-markings of juveniles with black edging (Fig. 135). . ***Chiloscyllium hasselti***

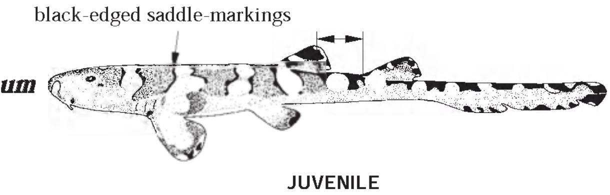


Fig. 135 *Chiloscyllium hasselti*

Chiloscyllium arabicum Gubanov, 1980

Fig. 136

Chiloscyllium arabicum Gubanov, *in* Gubanov and Schleib, 1980, *Sharks Arabian Gulf*: 14, figs 6-7, pl. Type material? Persian Gulf.

Synonyms: ***Chiloscyllium confusum*** Dingerkus and DeFino, 1983: 9, figs 2, 4-7, 51, 57, 61-64. Holotype: American Museum of Natural History, AMNH-44126, 408 mm TL subadult male, 18.5 km (10 mi) offshore of Calicut (Kozhikode), Kerala, India.

Other Combinations: None.

FAO Names: En - Arabian carpet shark; **Fr** - Requin-chabot camot; **Sp** - Bamboa arábiga.

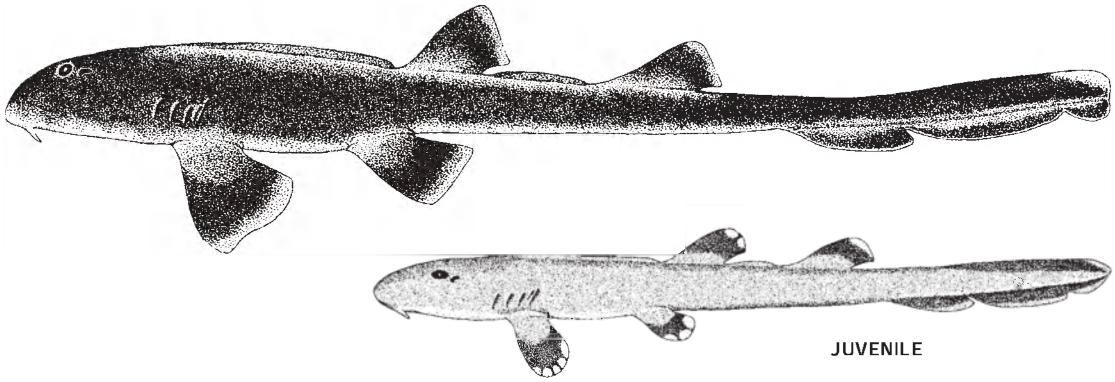
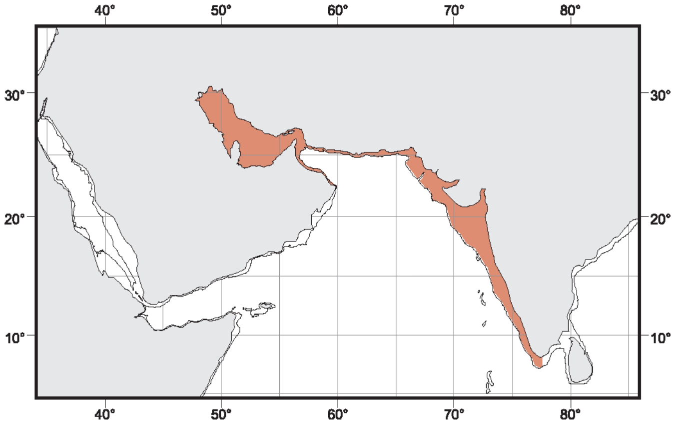


Fig. 136 *Chiloscyllium arabicum*

Field Marks: Mouth well in front of eyes; spineless dorsal fins far posterior on tail, greatly elongated thick precaudal tail, long and low anal fin just anterior to caudal fin, prominent predorsal and interdorsal ridges on back, dorsal fins with nearly straight posterior margins, first dorsal-fin origin opposite or just behind pelvic-fin insertions, second dorsal fin usually with a longer base than first; no colour pattern in young and adults.

Diagnostic Features: Prepectoral length 16.1 to 19.6% of total length. Snout fairly thick and rounded anteriorly. Eyes moderately large, lengths 1.4 to 1.8% of total length. Body and tail moderately slender. Lateral ridges absent from trunk but interdorsal and predorsal ridges prominent. Interdorsal space fairly long, nearly or over twice first dorsal-fin base and 8.7 to 14.5% of total length. Snout to vent length 33.1 to 36.3% of total length; distance from vent to tail tip 61.0 to 67.6% of total length. Dorsal fins large and subangular, subequal to or larger than pelvic fins, and without concave posterior margins and projecting free rear tips. First dorsal-fin origin over or behind rear halves of pelvic-fin bases, first dorsal-fin base usually slightly shorter than second dorsal-fin base (rarely about equal), first dorsal-fin height 4.3 to 8.4% of total length. Second dorsal-fin height 4.2 to 7.1% of total length. Origin of anal fin somewhat behind free rear tip of second dorsal fin, anal-fin length from origin to free rear tip somewhat less than hypural caudal lobe from lower caudal origin to subterminal notch, anal-fin base less than six times anal-fin height. Total vertebral count between 141 and 175 (mean = 158.2, n = 23). Intestinal valve count unknown. **Colour:** colour pattern absent in adults, juveniles with light spots on fins but otherwise unmarked.

Distribution: Western Indian Ocean: India, Pakistan, and the Persian Gulf between Iran and the Arabian Peninsula (including Saudi Arabia and Kuwait).



Habitat: Found on coral reefs, lagoons, rocky shores, and mangrove estuaries, depths from 3 to 100 m.

Biology: A common inshore to offshore bottom shark in the Persian Gulf, especially during the summer. Biology sketchily known. Feeds on squid (Loliginidae), shelled molluscs (Gastropoda?), crustaceans, and snake eels (Ophichthidae). It has reproduced in aquaria, and the male grabs the pectoral fin of the female while mating. Lays up to four egg-cases on coral reefs, with hatching after 70 to 80 days.

Size: Maximum total length about 70 cm. Freeliving at 101 mm, size at hatching uncertain; matures between 45 and 54 cm long; an adult male 58 cm.

Interest to Fisheries and Human Impact: Interest to fisheries minimal at present, apparently little utilized in the Persian Gulf (Gubanov and Schleib, 1980) but probably is used in Pakistan and India. The conservation status of this species is uncertain; an immediate question is whether the Gulf War had an adverse effect on populations of this shark and other Gulf species.

Local Names: Arabian bamboo shark, Confusing bamboo shark.

Remarks: This species was first described by Gubanov and Schleib (1980) but Dingerkus and DeFino (1983) described it as a separate species, ***Chiloscyllium confusum***, without mention of ***C. arabicum.*** Compagno (1984) provisionally recognized ***C. arabicum*** but noted that it was apparently very close to ***C. punctatum***. Dingerkus and DeFino's account clearly establishes this species as being separable from ***C. punctatum***.

Literature: Kuronuma and Abe (1972); Gubanov and Schleib (1980); Dingerkus and DeFino (1983); Compagno (1984, and unpub. data); Michael (1993); Dibelius (1993).

Chiloscyllium burmensis Dingerkus and DeFino, 1983 Fig. 137

Chiloscyllium burmensis Dingerkus and DeFino, 1983, *Bull. American Mus. Nat. Hist.* 176(1): 9, figs 3, 7, 59-60. Holotype: US National Museum of Natural History, USNM-202672, 575 (569) mm TL adult male, 15° 04′ N, 95° 51′ E, off Rangoon, Burma, 29 to 33 m. Status of holotype and additional data from Howe and Springer (1993, *Smiths. Contr. Zool.* [540]: 5).

Synonyms: None.

Other Combinations: None.

FAO Names: En - Burmese bamboo shark; **Fr** - Requin-chabot birman; **Sp** - Bamboa birmana.

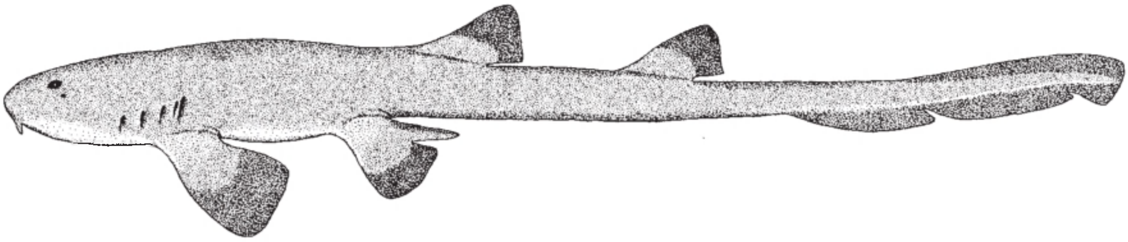


Fig. 137 *Chiloscyllium burmensis*

Field Marks: Mouth well in front of eyes, eyes very small; spineless dorsal fins far posterior on tail, greatly elongated thick precaudal tail, long and low anal fin just anterior to caudal fin, no lateral ridges on trunk, dorsal fins with straight rear margins, first dorsal-fin origin about opposite pelvic-fin insertions; no colour pattern in adults.

Diagnostic Features: Prepectoral length 15.7% of total length. Snout fairly thick and rounded anteriorly. Eyes small, length 1.2% of total length. Body and tail slender. No lateral ridges on trunk, and predorsal and interdorsal ridges not prominent. Interdorsal space fairly long, nearly twice first dorsal-fin base and 11.1% of total length. Snout to vent length 30.8% of total length; distance from vent to tail tip 67.3% of total length. Dorsal fins small and rounded-angular, subequal in size to pelvic fins, and without concave posterior margins and projecting free rear tips. First dorsal-fin origin slightly behind pelvic-fin insertions, first dorsal-fin base slightly longer than second dorsal-fin base, first dorsal-fin height 6.3% of total length. Second dorsal-fin height 5.2% of total length. Origin of anal fin somewhat behind free rear tip of second dorsal-fin, anal-fin length from origin to free rear tip slightly less than hypural caudal lobe from lower caudal origin to subterminal notch, anal-fin base more than six times anal-fin height. Total vertebral count 176. Intestinal valve count unknown. **Colour:** colour pattern absent in adult male, juvenile colour pattern unknown.

Distribution: Northern Indian Ocean: Burma (Myanmar).

Habitat: Unknown, collected off Rangoon (Yangon), Burma, presumably inshore and off the Irrawaddy River delta.

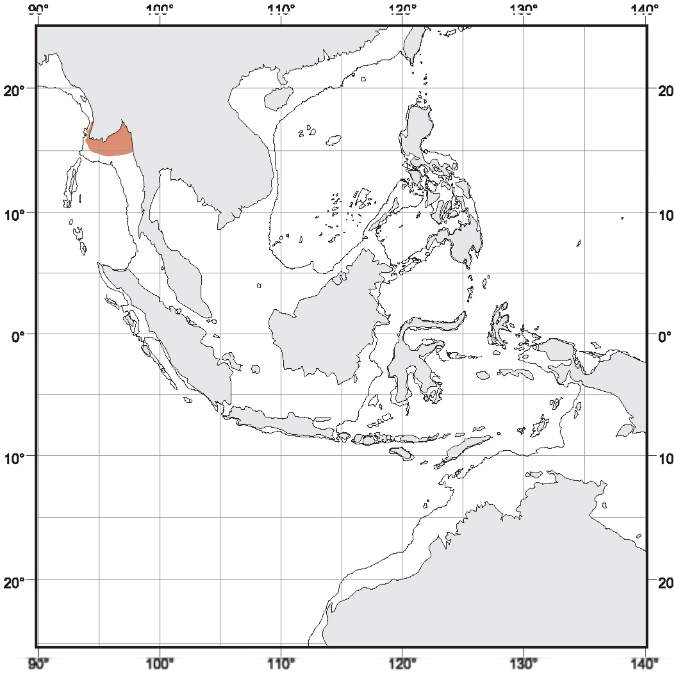
Biology: Biology virtually unknown. Eats small bony fishes.

Size: The holotype and only known specimen is a 57 cm adult male.

Interest to Fisheries and Human Impact: Unknown, but presumably utilized in local fisheries. Conservation status unknown.

Remarks: Characterization of this species from Dingerkus and DeFino (1983).

Literature: Dingerkus and DeFino (1983).



Chiloscyllium griseum Müller and Henle, 1838 Fig. 138

Chiloscyllium griseum Müller and Henle, 1838d, *Syst. Beschr. Plagiost.*, pt. 1: 19. Syntypes: "Ein Exemplar aus Malabar durch Dussumier; 6 Exemplare von Pondichery durch Belanger, in Weingeist, in Paris. Indien, Japan". Lectotype: Museum National d'Histoire Naturelle, Paris, MNHN-1010, 374 mm immature male, Malabar, Kerala, India, designated by Dingerkus and DeFino, 1983, *Bull. American Mus. Nat. Hist.* 176(1): 12.

Synonyms: None.

Other Combinations: ***Hemiscyllium griseum*** (Müller and Henle, 1838).

FAO Names: En - Grey bamboo shark; **Fr** - Requin-chabot gris; **Sp** - Bamboa gris.

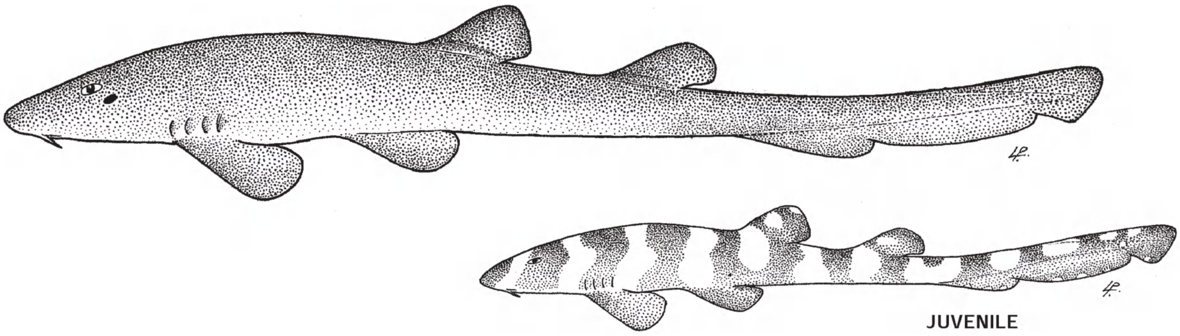


Fig. 138 ***Chiloscyllium griseum***

Field Marks: Mouth well in front of eyes; spineless dorsal fins far posterior on tail, greatly elongated thick precaudal tail, long and low anal fin just anterior to caudal fin, no lateral ridges on trunk, dorsal fins with straight or convex posterior margins, first dorsal-fin origin about opposite rear halves of pelvic-fin bases; often no colour pattern in adults, but young with transverse dark bands that lack black edging.

Diagnostic Features: Prepectoral length 16.5 to 19.5% of total length. Snout rounded anteriorly. Eyes moderately large, lengths 1.3 to 2.2% of total length. Body and tail fairly stout. No lateral ridges on trunk and predorsal and interdorsal ridges not prominent. Interdorsal space fairly short, slightly greater than first dorsal-fin base and 8.7 to 11.5% of total length. Snout to vent length 34.5 to 38.3% of total length; distance from vent to tail tip 58.1 to 64.4% of total length. Dorsal fins fairly large and rounded, subequal to or larger than pelvic fins, and without concave posterior margins and projecting free rear tips. First dorsal-fin origin over rear halves of pelvic-fin bases, first dorsal-fin base slightly longer than second dorsal-fin base, first dorsal-fin height 6.2 to 8.2% of total length. Second dorsal-fin height 7.4 to 9.1% of total length. Origin of anal fin slightly behind free rear tip of second dorsal fin, anal-fin length from origin to free rear tip slightly less than hypural caudal lobe from lower caudal-fin origin to subterminal notch, anal-fin base less than six times anal-fin height. Total vertebral count from 156 to 170 (mean = 161.7, n = 14). Intestinal valve count 15 to 19 (n = 2). **Colour:** colour pattern absent in adults but young with prominent dark saddle-marks without black edging.

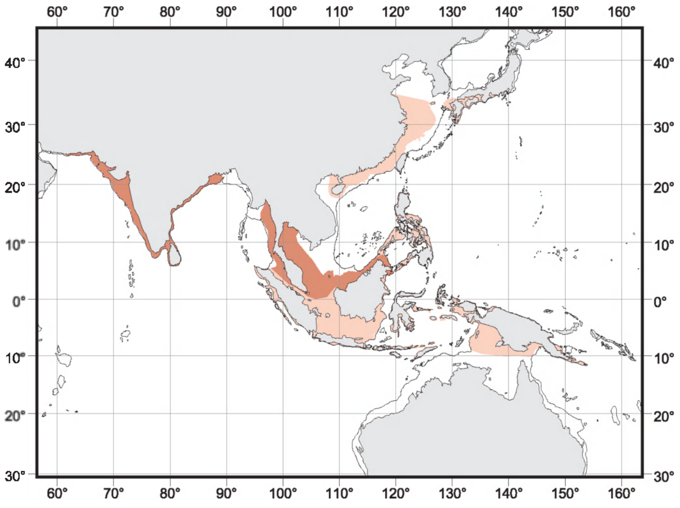
Distribution: Indo-West Pacific: Pakistan, India, Sri Lanka, Malaysia, Thailand; nominal from Indonesia, China, Japan, Philippines, and Papua New Guinea but possibly based in part on ***C. hasselti.***

Habitat: An inshore bottom shark, on rocks and in lagoons. Depths 5 to 80 m.

Biology: Common where it occurs. Oviparous, deposits eggs in small oval egg cases on the bottom. Probably feeds mainly on invertebrates.

Size: Maximum total length at least 77 cm. Freeliving individuals down to at least 12.2 cm, size at hatching uncertain; males maturing between 45 and 55 cm.

Interest to Fisheries and Human Impact: Regularly taken in inshore fisheries off Pakistan, India and Thailand, and utilized for human food. Kept in public aquaria in the United States. Conservation status uncertain.



Local Names: Blackbanded bamboo shark; Ikan tjutjot, Ikan tjutjot pisang (Malaysia, Indonesia); Bambak gorbeh (Iran, possibly not this species); Blackbanded catshark, Catshark, Cat shark; Shimazame (Japan).

Remarks: This species was described as new by Müller and Henle without mention of the earlier ***Scyllium griseum*** van Hasselt, 1823. Fowler (1941) considered van Hasselt's species as lacking a description. Compagno (1984) listed it as a tentative *nomen nudum*, and noted that quite likely Müller and Henle based their name ***Chiloscyllium griseum*** on the earlier ***Scyllium griseum***, as they were apparently aware of van Hasselt's work in Java. Dingerkus and DeFino (1983) considered van Hasselt's species as valid and separable from Müller and Henle's ***Chiloscyllium griseum*** although a *nomen nudum* and not available as such, and so resurrected the earliest valid name based on it, ***C. hasselti*** Bleeker, 1852 (see below).

Literature: Garman (1913); Fowler (1941); Herre (1953); Gubanov and Schleib (1980); Dingerkus and DeFino (1983); Compagno (1984); Nakaya and Shirai (1984); Dibelius (1993); D. Didier (pers. comm.).

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Chiloscyllium hasselti Bleeker, 1852

Fig. 139

Chiloscyllium hasselti Bleeker, 1852, *Verh. Batav. Genoots. Kunst. Wet.* 24: 14. Syntypes: Five specimens, 480 to 590 mm, off Java, Sumatra, and Moluccas, in British Museum (Natural History) and Rikjsmuseum van Natuurlijke Histoire, Leiden. Lectotype: British Museum (Natural History), BMNH-1867.11.28.196, 594 mm TL male, Moluccas, designated by Dingerkus and DeFino, 1983, *Bull. American Mus. Nat. Hist.* 176(1): 17.

Synonyms: ***Scylia griseum*** van Hasselt, 1823: 315 (*nomen nudum*); also ***Scyllium griseum*** van Hasselt, 1824: 89, cf. Dingerkus and DeFino (1983: 17). ***Chiloscyllium obscurum*** Gray, 1851: 35 (*nomen nudum*). Holotype: British Museum (Natural History), BMNH-1845.6.22.122, 487 mm TL, Indonesia. ***Chiloscyllium indicum*** var. ***obscura*** Günther, 1870: 413 (new combination); also Ogilby, 1888: 8 (new combination), *cf.* Dingerkus and DeFino (1983: 17). ***Chiloscyllium dolganovi*** Kharin, 1987: 367?, fig. 5 (original in Russian), also Kharin, 1987: 67, fig. 5 (English translation). Holotype: Zoological Institute, Leningrad, ZIL-46984, 9° 12′ N, 104° 34′ E, Viet Nam, 12 m.

Other Combinations: None.

FAO Names: En - Indonesian bamboo shark; **Fr** - Requin-chabot indonésien; **Sp** - Bamboa indonesa.

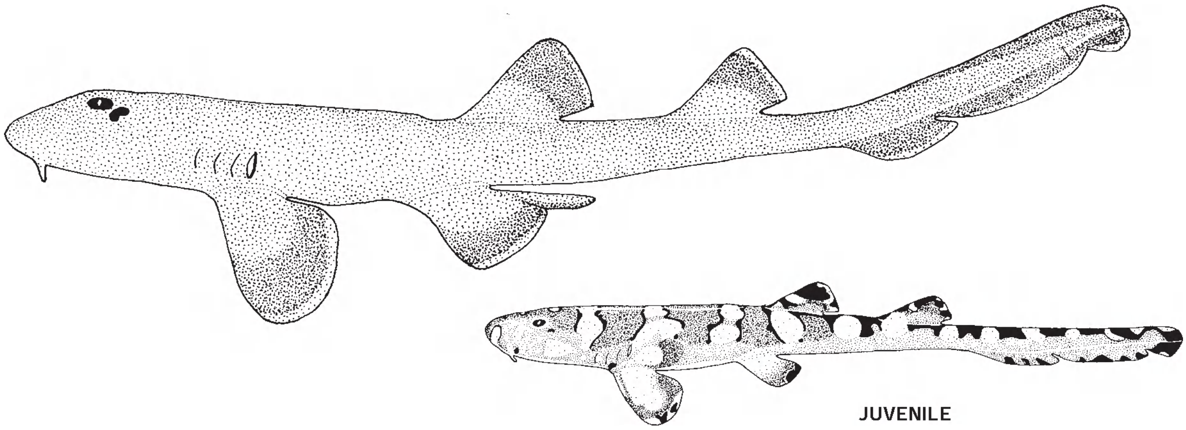
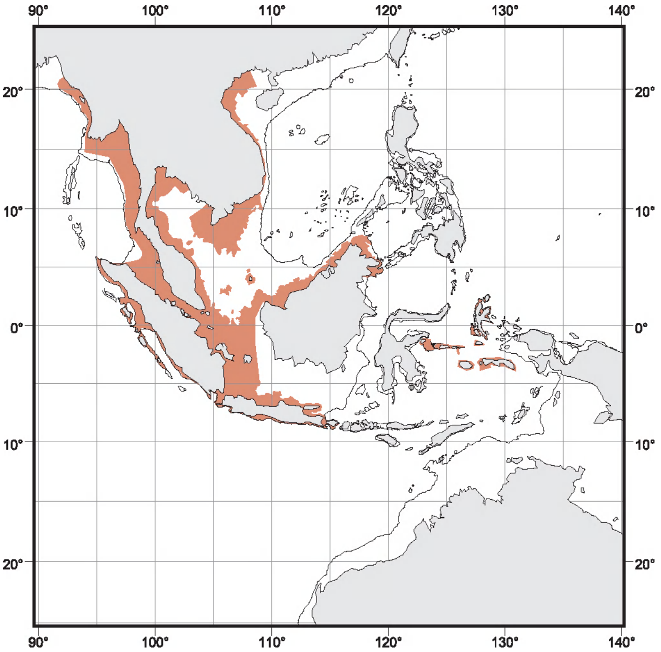


Fig. 139 *Chiloscyllium hasselti*

Field Marks: Mouth well in front of eyes; spineless dorsal fins far posterior on tail, greatly elongated thick precaudal tail, long and low anal fin just anterior to caudal fin, no lateral ridges on trunk, dorsal fins with straight or convex posterior margins, first dorsal-fin origin about opposite rear halves of pelvic-fin bases; often no colour pattern in adults, but young with transverse dark bands that have prominent black edging.

Diagnostic Features: Prepectoral length 16.5 to 20.3% of total length. Snout rounded anteriorly. Eyes moderately large, lengths 1.5 to 2.4% of total length. Body and tail fairly stout. No lateral ridges on trunk and predorsal and interdorsal ridges not prominent. Interdorsal space fairly short, slightly greater than first dorsal-fin base and 6.6 to 11.1% of total length. Snout to vent length 33.2 to 37.7% of total length; distance from vent to tail tip 58.9 to 64.3% of total length. Dorsal fins fairly large and rounded, subequal in size to pelvic fins, and without concave posterior margins and projecting free rear tips. First dorsal-fin origin over rear halves of pelvic-fin bases, first dorsal-fin base slightly longer than second dorsal-fin base, first dorsal-fin height 4.8 to 8.1% of total length. Second dorsal-fin height 7.4 to 9.1% of total length. Origin of anal fin slightly behind free rear tip of second dorsal fin, anal-fin length from origin to free rear tip less than hypural caudal lobe from lower caudal-fin origin to subterminal notch, anal-fin base less than six times anal-fin height. Total vertebral count between 156 and 175 (mean = 166.1, n = 11). Intestinal valve count 15 (n = 1). **Colour:** colour pattern absent in adults except for dusky fins, but young with prominent saddle marks consisting of broad dusky patches with conspicuous black edging and separated by light areas and blackish spots and black or dusky blotches on all fins.

Distribution: Indo-West Pacific: Burma, Thailand, Malaysia, Singapore, Indonesia (Sumatra, Java, between Celebes and New Guinea), Borneo (Sarawak), Viet Nam.



Habitat: Probably mostly close inshore, depth to 12 m.

Biology: Oviparous, eggs hatching in about December. Eggs attached to benthic marine plants.

Size: Maximum total length at least 61 cm. Size at hatching between 94 and 120 mm. Males maturing between 44 and 54 cm, and adult males 54 to at least 59 cm.

Interest to Fisheries and Human Impact: Fished in Singapore, Thailand, and probably wherever else it occurs. Conservation status uncertain.

Remarks: I follow Dingerkus and DeFino (1983) in recognizing this species, and tentatively synonymize ***Chiloscyllium dolganovi*** Kharin (1987) from Viet Nam with it. The latter species agrees with ***C. hasselti*** rather than ***C. griseum*** in its low dorsal fins and short interdorsal space. Among other ***Chiloscyllium*** with plain or nearly plain adults, the holotype of ***C. dolganovi*** agrees with ***C. hasselti*** and differs from ***C. burmensis*** in its larger eyes, differs from ***C. arabicum*** in its shorter second dorsal fin and low interdorsal ridges, and differs from ***C. punctatum*** in lacking concave posterior margins and produced free rear tips on its dorsal fins.

Literature: Dingerkus and DeFino (1983); Kharin (1987); Cook and Compagno (1994).

Chiloscyllium indicum (Gmelin, 1788)

Fig. 140

Squalus indicus Gmelin, *in* Linnaeus and Gmelin, 1788, *Syst. Nat., ed. 13, Pisces* 1(3): 1503. Holotype: British Museum (Natural History), BMNH-1853.11.12.205, 274 mm TL female (dried skin), "Oceano Indico", Gronow collection. Eastern Indian Ocean. Status confirmed by Dingerkus and DeFino, 1983, *Bull. American Mus. Nat. Hist.* 176(1): 22.

Synonyms: [?***Squalus***] ***colax*** Meuschen, 1781: (no pagination). Meuschen's Index to Gronovius' *Zoophylacium* was rejected by the International Commission on Zoological Nomenclature (1950: 504) as being nonbinomial. Holotype: British Museum (Natural History), BMNH-1853.11.12.205, 274 mm TL female (dried skin), "Oceano Indico", Gronow collection. Status confirmed by Dingerkus and DeFino (1983: 22). ***Squalus tuberculatus*** Bloch and Schneider, 1801: 137. Based on "Le Squale dentele" of Lacépède, 1798: 281, pl. 11, fig. 1, no locality. Syntypes: British Museum (Natural History), BMNH-1853.11.12.205, 274 mm TL female (dried skin), "Oceano Indico", Gronow collection (status confirmed by Dingerkus and DeFino, 1983: 22); ?BMNH-1845.7.3.143, 419 mm, Cape Sea, South Africa (locality doubtful). Also ***Squalus (Scyliorhinus) tuberculatus*** Blainville, 1816: 121 (*nomen nudum*), and ***Chiloscyllium tuberculatus*** Müller and Henle, 1838d: 20. ***Squalus gronovianus*** Shaw, 1804: 353 (on Gronow's ***Squalus caudatus***; see Gronow, *in* Gray, 1854: 8). Holotype: British Museum (Natural History), BMNH-1853.11.12.205, 274 mm TL female (dried skin), "Oceano Indico", Gronow collection. Status confirmed by Dingerkus and DeFino (1983: 22). ?***Squalus (Scyliorhinus) dentatus*** Blainville, 1816: 121, (*nomen nudum*), possibly based on "Le Squale dentele" of Lacépède, 1798: 281, pl. 11, fig. 1, no locality, according to Fowler (1941: 90). ***Chiloscyllium phymatodes*** Bleeker, 1852: 21. Holotype: Probably Rikjsmuseum van Natuurlijke Histoire, Leiden, RMNH-7406, one of two, 410 mm female, Semarang, Java, according to Dingerkus and DeFino (1983: 22). ***Squalus caudatus*** Gronow, *in* Gray, 1854: 8. Holotype: British Museum (Natural History), BMNH-1853.11.12.205, 274 mm TL female (dried skin), "Oceano Indico", Gronow collection. Status confirmed by Dingerkus and DeFino (1983: 22). ***Chiloscyllium colax*** Whitley, 1939: 228. Also ***Hemiscyllium colax*** Fowler, 1941: 89. Revival of [?***Squalus***] ***colax*** Meuschen, 1781.

Other Combinations: ***Hemiscyllium indicum*** (Gmelin, *in* Linnaeus and Gmelin, 1788).

FAO Names: En - Slender bamboo shark; **Fr** - Requin-chabot élégant; **Sp** - Bamboa elegante.

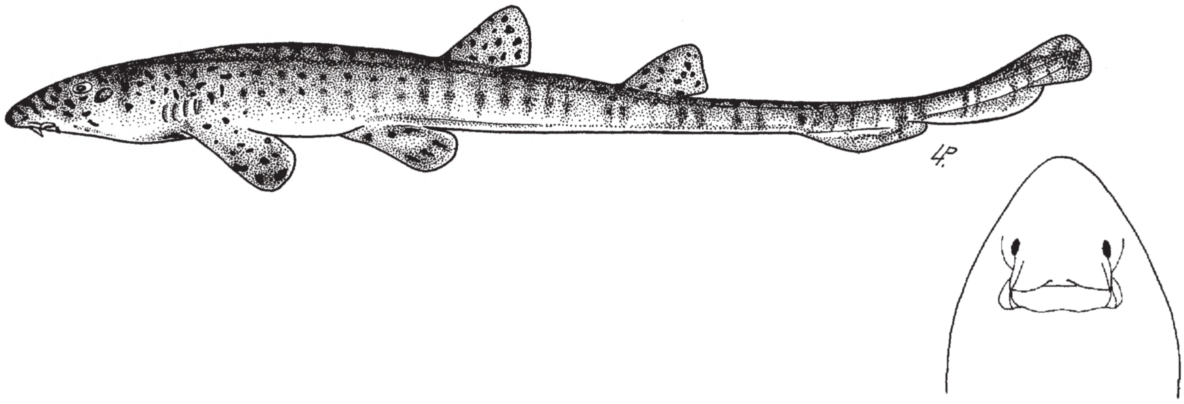


Fig. 140 ***Chiloscyllium indicum***

Field Marks: Mouth well in front of eyes; spineless dorsal fins far posterior on tail, greatly elongated slender precaudal tail, long and low anal fin just anterior to caudal fin, lateral ridges on trunk, dorsal fins with straight or convex posterior margins, first dorsal-fin origin opposite or just behind pelvic-fin insertions; colour pattern of numerous small dark spots, saddles, and dashes.

Diagnostic Features: Prepectoral length 15.2 to 18.0% of total length. Snout narrowly rounded anteriorly. Eyes moderately large, lengths 1.4 to 1.9% of total length. Body and tail very slender. A lateral ridge present on each side of trunk, and strong predorsal and interdorsal ridges on midline of back. Interdorsal space fairly long, nearly twice first dorsal-fin base and 10 to 12% of total length. Snout to vent length 32.4 to 35.1% of total length; distance from vent to tail tip 62.3 to 67.0% of total length. Dorsal fins small and rounded, subequal to or smaller than pelvic fins, and without concave posterior margins and projecting free rear tips. First dorsal-fin origin over or behind pelvic-fin insertions, first dorsal-fin base slightly longer than second dorsal-fin base, first dorsal-fin height 3.9 to 5.4% of total length. Second dorsal-fin height 3.9 to 5.1% of total length. Origin of anal fin far behind free rear tip of second dorsal fin, anal-fin length from origin to free rear tip about equal to or greater than hypural caudal lobe from lower caudal-fin origin to subterminal notch, anal-fin base over six times anal-fin height. Total vertebral count between 166 and 170 (mean = 167.0, n = 4). Intestinal valve count 14 to 15 (n = 6). **Colour:** colour pattern of numerous dark brown or blackish spots, dashes and bars on light brown background present in juveniles and adults; saddle-markings or bars of young without prominent black edging.

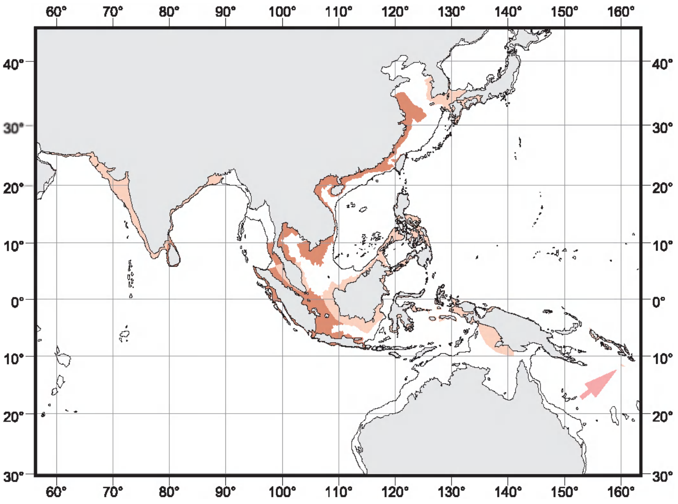
Distribution: Indo-West Pacific: Possibly Arabian Sea and India, Sri Lanka, Singapore, Thailand, ?Malaysia, Indonesia, Viet Nam, Taiwan Island (Province of China), China, ?Republic of Korea, ?Japan, ?Philippines, ?Solomon Islands.

Habitat: A common but little-known inshore bottom shark. It possibly may occur in fresh water in the lower reaches of the Perak River in peninsular Malaysia.

Biology: Oviparous.

Size: Maximum total length about 65 cm; freeliving individual 13 cm but size at hatching unknown; males maturing between 39 and 42 cm and reaching at least 54 cm; adult female 43 cm.

Interest to Fisheries and Human Impact: Interest to fisheries considerable. Regularly taken in inshore fisheries in India, Sri Lanka and Thailand, and utilized for human food. Conservation status unknown.



Local Names: Ridgebacked bamboo shark, Slender bamboo shark, Ridge back shark (Sri Lanka); Corungun sorrah, Karikkan schura (Tamil); Ettee (Malabar, India); Bokee sorrah, Ra sorrah (Telugi); Poos hee (Baluchistan); Balavala (Marathi); Nga man ing-myong (Burma); Ca cha beo, Ca nham, Ca cheo beo (Viet Nam); Yu tokele, Yu belangkas, Yu bodoh, Ikan tjutjot kumbang, Ikan tjutjot tekeh (Malaysia); Chalarm gope or Frog shark, Chalarm hin or Stone shark (Thailand); Kau kang sha or Time teller shark (China); Ridgeback catshark, Catshark, Nurse shark, Tenjikuzame (Japan).

Remarks: Whitley (1939) proposed that ***Squalus colax*** Meuschen, 1781 was the earliest name for this species. However, Meuschen's work (1781) indicates that although ***colax*** apparently refers to the Gronow species later named ***Squalus indicus***, it was never proposed in the binomial form ***Squalus colax*** but simply listed as ***colax***. Apparently ***colax*** is not available for this species.

Dingerkus and DeFino (1983) listed specimens from South Africa, Indonesia (Java; Semarang-Riau Archipelago; Bintan Island; Bangka Island; Muntok), Malaysia (Penang Island), Thailand (Gulf of Thailand), Singapore, and China, and did not verify the wider distribution accorded this species by previous writers. They mentioned a stuffed specimen from "Cape Seas, South Africa" collected by Dr Andrew Smith (British Museum [Natural History], BMNH-1845.7.3.143, 419 mm), but no ***Chiloscyllium*** have been collected off southern Africa despite extensive collecting over the past two centuries. The specimen might have been a waif, but it is more likely to have been procured in India or the Far East and shipped to South Africa.

Literature: Garman (1913); Smith (1913); Fowler (1941); Herre (1953); Taniuchi (1979); Gubanov and Schleib (1980); Dingerkus and DeFino (1983); Compagno (1984); Nakaya and Shirai (1984).

Chiloscyllium plagiosum (Bennett, 1830)

Fig. 141

Scyllium plagiosum Bennett, 1830, *Fishes, in* S. Raffles, 1830, *Mem. Life Pub. Serv. Sir Thomas Stamford Raffles*, London: 694. Holotype: British Museum (Natural History), probably lost, Sumatra. Neotype: California Academy of Sciences, CAS-36046, 503 mm TL adult male, 5° 58′ S, 106° 48′ E, Java Sea, Indonesia, designated by Dingerkus and DeFino, 1983, *Bull. American Mus. Nat. Hist.*, 176(1): 24. Also ***Chiloscyllium indicum*** var. ***plagiosa*** Günther, 1870, *Cat. Fish. British Mus.*, 8: 412; and ***Chiloscyllium indicum*** var. ***plagiosum*** Ogilby, 1888, *Cat. Fish. coll. Aust. Mus. Pt. 1, Recent Palaeichthyan Fishes*, White, Sydney: 8 (new combination), *cf.* Dingerkus and DeFino, 1983, *Bull. American Mus. Nat. Hist.*, 176(1): 23.

Synonyms: ***Scyllium ornatum*** Gray, 1830, pl. 98, fig. 2. Name and illustration only. Holotype: British Museum (Natural History), BMNH-1982.2.26.1, 653 mm TL skin, China Seas. Status of holotype confirmed by Dingerkus and DeFino (1983: 24). ?***Scyllium plagiosum*** var. ***interruptum*** Bleeker, 1852: 18. Types: None known according to Eschmeyer (1998: CD-ROM), type locality Batavia (Jakarta) and Semarang (Samarang), Java, Indonesia. ***Chiloscyllium margaritiferum*** Bleeker, 1863: 243. Also ***Chiloscyllium indicum*** var. ***margaritifera*** Günther, 1870: 412. Holotype (both species): Rikjsmuseum van Natuurlijke Histoire, Leiden, RMNH-7404, 250 mm immature male, Obi Island, Moluccas, Indonesia. Status of holotype confirmed by Dingerkus and DeFino (1983: 24). ?***Chiloscyllium caerulopunctatum*** Pellegrin, 1914: 230. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN-14-9, 670 mm TL female, Fort Dauphin [Taolanaro], Madagascar. Status of holotype confirmed by Bass, D'Aubrey and Kistnasamy (1975c: 49, fig. 23); and Dingerkus and DeFino (1983: 24).

Other Combinations: ***Hemiscyllium plagiosum*** (Bennett, 1830).

FAO Names: En - Whitespotted bamboo shark; **Fr** - Requin-chabot á taches blanches; **Sp** - Bamboa punteada.

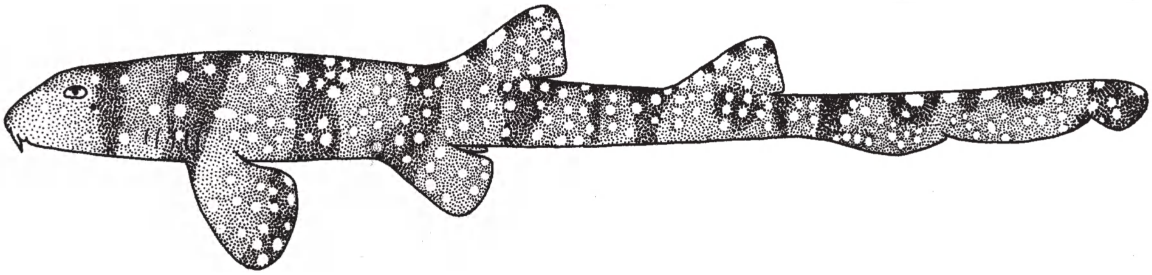


Fig. 141 ***Chiloscylium plagiosum***

Field Marks: Mouth well in front of eyes; spineless dorsal fins far posterior on tail, greatly elongated thick precaudal tail, long and low anal fin just anterior to caudal fin, lateral ridges on trunk, dorsal fins with straight or convex posterior margins, first dorsal-fin origin opposite or just behind pelvic-fin insertions; colour pattern of numerous white or bluish spots and dark spots, dark bands and saddles on a light background.

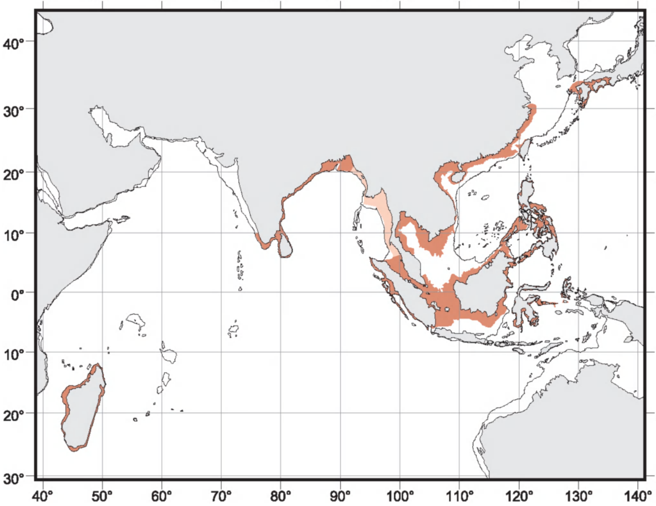
Diagnostic Features: Prepectoral length 15.0 to 19.4% of total length. Snout rounded or truncated anteriorly. Eyes moderately large, lengths 1.4 to 2.2% of total length. Body and tail fairly stout. A lateral ridge present on each side of trunk, and strong predorsal and interdorsal ridges present on midline of back. Interdorsal space short, slightly greater or less than first dorsal-fin base and 9.3 to 11.6% of total length. Snout to vent length 31.1 to 35.1% of total length; distance from vent to tail tip 61.8 to 67.1% of total length. Dorsal fins moderately large and rounded or angular, subequal to or larger than pelvic fins, and without concave posterior margins and projecting free rear tips. First dorsal-fin origin varying from slightly anterior to slightly behind pelvic-fin insertions, first dorsal-fin base slightly longer than second dorsal-fin base, first dorsal-fin height 5.4 to 7.3% of total length. Second dorsal-fin height 4.7 to 6.8% of total length. Origin of anal fin somewhat behind free rear tip of second dorsal fin, anal-fin length from origin to free rear tip somewhat less than hypural caudal lobe from lower caudal-fin origin to subterminal notch, anal-fin base less than six times anal-fin height. Total vertebral count between 161 and 185 (mean = 173.9, n = 8). Intestinal valve count 16 to 17 (n = 2). **Colour:** a prominent pattern of numerous white spots on a dark brown background in juveniles and adults, with small dark spots and darker brown or blackish transverse bands or saddles that are not conspicuously edged with black.

Distribution: Indo-West Pacific: Madagascar, India, Sri Lanka, Malaysia (Sandakan, Sarawak, Borneo), Singapore, Thailand, Indonesia (Obi Island, Moluccas; Manado, Celebes; Sumatra), Viet Nam, China, including Taiwan Island (Province of China), Japan, and Philippines.

Habitat: A little-known inshore bottom shark. Occurs on reefs in the tropics.

Biology: Common but biology poorly known. Nocturnal, rests in reef crevices during the day, but feeds at night. Oviparous. Eats bony fishes and crustaceans.

Size: Maximum total length 95 cm; possible hatchlings or free-living specimens 9.8 to 12.5 cm; adolescent males up to 64 cm, adult males 50 to 83 cm; an adult female 95 cm.



Interest to Fisheries and Human Impact: Interest to fisheries considerable. Regularly taken in inshore fisheries in India, Thailand, China, and utilized for human consumption. Marketed in Madagascar, for human consumption. A particularly handsome and popular aquarium species, kept in public aquaria in Europe and the United States. Conservation status uncertain.

Local Names: Whitespotted bamboo shark, Cat shark; Bluespotted bamboo shark, Requin-chabot à taches bleues, Bamboa estrellada; Ikan tjutjot matjan (Malaysia, Indonesia); Chalarm hin or Stone shark, Chalarm seour or Tiger shark, Chalarm lye or Striped shark (Thailand); Pan chu sha or Striped bamboo shark, Ta sha (China); Whitespotted cat shark, Catshark, Shiroboshi-tenjiku (Japan).

Remarks: There is a question as to whether ***Chiloscyllium caerulopunctatum*** Pellegrin, 1914, known from a single specimen from Madagascar, is a valid species or a synonym of the wide-ranging but disjunct ***C. plagiosum*** from the northern Indian Ocean east to Japan and Philippines. Fowler (1941) synonymized ***C. caerulopunctatum*** with ***C. plagiosum,*** but Bass, D'Aubrey and Kistnasamy (1975c) retained it as a valid species without comparing it with ***C. plagiosum*** or other ***Chiloscyllium*** species. After comparing the redescription of the holotype of ***C. caerulopunctatum*** in Bass, D'Aubrey and Kistnasamy (1975c) with specimens of ***C. plagiosum*** Compagno (1984) tentatively recognized this species as being valid, because it seemed to differ from ***C. plagiosum*** in having larger dorsal fins, a shorter blunter snout, possibly wider mouth, and a different coloration, with smaller blue rather than white spots and lighter ground colour. Dingerkus and DeFino (1983), in a comprehensive review of the genus, synonymized ***C. caerulopunctatum*** with ***C. plagiosum*** without comment. I follow their synonymy here tentatively and with some reluctance, but suggest that a multivariate comparison of specimens of Madagascar "***C. caerulopunctatum***" with ***C. plagiosum*** from elsewhere (including comparison of vertebral and intestinal valve count as well as morphometrics) is required to resolve the issue. M.-L. Bauchot and G. Bianchi, pers. comm. to Compagno (1984) and Bauchot and Bianchi (1984) noted the presence of ***C. caerulopunctatum*** in fish markets in Madagascar, confirming Pellegrin's initial record.

Dingerkus and DeFino (1993) mentioned a stuffed specimen of ***Chiloscyllium plagiosum*** from "Cape Seas, South Africa" collected by Dr A. Smith (British Museum [Natural History] BMNH-1845.7.3.140, 745 mm), but extensive collecting over the past two centuries did not reveal the presence of any ***Chiloscyllium*** in South Africa. As with Smith's specimen of ***C. indicum*** from "Cape Seas" the specimen of ***C. plagiosum*** might have been a waif from the northern Indian Ocean (or Madagascar), but it is possible that the specimen was procured in India or the Far East and shipped to South Africa.

Literature: Garman (1913); Pellegrin (1914); Fowler (1941); Herre (1953); Chen (1963); Bessednov (1969); Bass, D'Aubrey and Kistnasamy (1975c); Gubanov and Schleib (1980); Dingerkus and DeFino (1983); Compagno (1984); Nakaya and Shirai (1984); Bauchot and Bianchi (1984); Michael (1993); Cook and Compagno (1994); M.-L. Bauchot and G. Bianchi, (pers. comm.).

Chiloscyllium punctatum Müller and Henle, 1838 — Fig. 142

Chiloscyllium punctatum Müller and Henle, 1838d, *Syst. Beschr. Plagiost.*, pt. 1: 18, pl. 3, 4 (pls 4 labelled as ***C. griseum***). Holotype: Rikjsmuseum van Natuurlijke Histoire, Leiden, probably lost, Java. Neotype: American Museum of Natural History, AMNH-38153, 352 mm TL female, Batavia (Djakarta), Java, Indonesia, designated by Dingerkus and DeFino, 1983, *Bull. American Mus. Nat. Hist.*, 176(1): 30. Fowler, 1941, *Bull. U. S. Natl. Mus.*, (100) 13: 85 gave an earlier reference to this species as "***Scyllium punctatum*** van Hasselt, Algemein Konst., Letterbode, May 1823, p.__", but this could not be confirmed. Müller and Henle, 1838d, *Syst. Beschr. Plagiost.*, pt. 1: 18, list "***Scyllium punctatum***. Kuhl et v. Hasselt" under their new ***Chiloscyllium punctatum***.

Synonyms: None.

Other Combinations: ***Hemiscyllium punctatum*** (Müller and Henle, 1838).

FAO Names: En - Brownbanded bamboo shark; **Fr** - Requin-chabot bambou; **Sp** - Bamboa estriada.

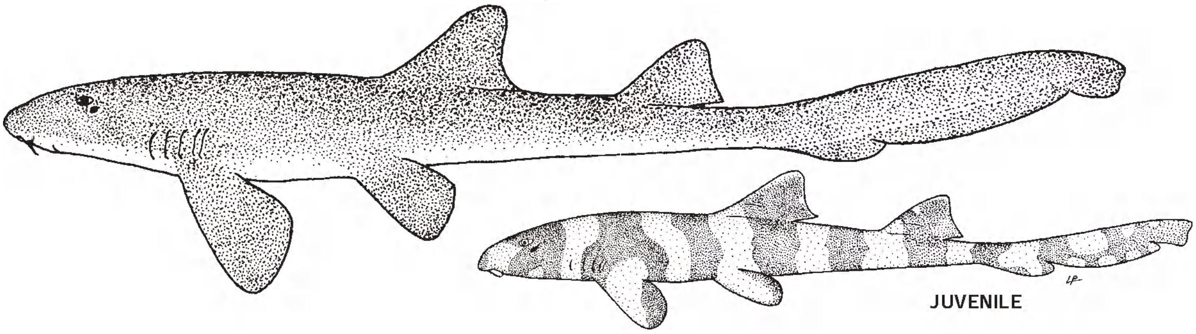
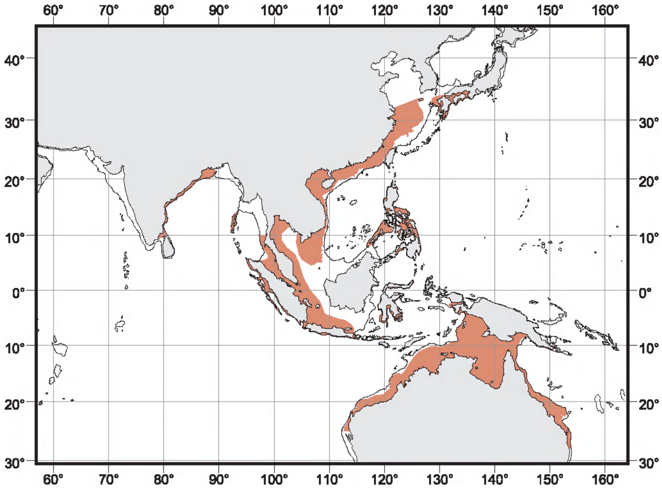


Fig. 142 *Chiloscyllium punctatum*

Field Marks: Mouth well in front of eyes; spineless dorsal fins far posterior on tail, greatly elongated thick precaudal tail, long and low anal fin just anterior to caudal fin, no lateral ridges on trunk, dorsal fins with concave posterior margins and elongated free rear tips, first dorsal-fin origin opposite anterior halves of pelvic-fin bases; usually no colour pattern in adults but young with bold dark transverse bands and a few dark spots.

Diagnostic Features: Prepectoral length 16.2 to 18.4% of total length. Snout rounded anteriorly. Eyes moderately large, lengths 1.5 to 2.4% of total length. Body and tail moderately slender. No lateral ridges on trunk, and predorsal and interdorsal ridges not prominent. Interdorsal space fairly short, slightly greater than first dorsal-fin base and 9.1 to 12.7% of total length. Snout to vent length 32.7 to 35.8% of total length; distance from vent to tail tip 61.1 to 64.4% of total length. Dorsal fins large and angular, larger than pelvic fins, and with concave posterior margins and prominently projecting free rear tips. First dorsal-fin origin varying from slightly anterior to pelvic-fin origins to over anterior halves of pelvic-fin bases, first dorsal-fin base longer than second dorsal-fin base, first dorsal-fin height 6.8 to 9.9% of total length. Second dorsal-fin height 6.4 to 8.4% of total length. Origin of anal fin somewhat behind free rear tip of second dorsal fin, anal-fin length from origin to free rear tip less than hypural caudal lobe from lower caudal-fin origin to subterminal notch, anal-fin base less than six times anal-fin height. Total vertebral count between 136 and 170 (mean = 154.7, n = 6). Intestinal valve count 20 (n = 4). **Colour:** light brown in adults, usually without a colour pattern, but young with broad dark transverse bars and usually a scattering of small blackish spots, bars not prominently edged with black.

Distribution: Indo-West Pacific: India (east coast, Andaman Islands), Malaysia, Singapore, Thailand, Indonesia (Java, Sumatra, Sulawesi, Komodo), Viet Nam, China, Taiwan (Province of China), Japan, Philippines, south coast of New Guinea (Papua-New Guinea and Irian Jaya, Indonesia), north coast of Australia (Northern Territory, Western Australia, Queensland).



Habitat: An inshore bottom shark found on coral reefs, often in tidepools, on tidal flats, and on reef faces, but probably also present on soft bottom offshore. Found in the intertidal down to at least 85 m.

Biology: A common shark but not often seen; young hide in crevices at the bases of coral heads, and adults under table corals. Very tenacious of life, can survive out of water for a long period (half a day). Oviparous, eggs deposited in rounded egg cases about 11 by 5 cm. Feeds on bottom invertebrates and possibly small fishes, but biology little-known despite its abundance in some parts of its range. Gills sometimes infested by larval isopods (*praniza*-larvae of the isopod ***Gnathia***).

Size: Maximum total length about 105 cm; hatchlings about 13 to 17 cm; adult males about 68 to 76 cm; an adult female 62.9 cm.

Interest to Fisheries and Human Impact: Regularly taken in inshore fisheries in India, Thailand, probably Singapore, Malaysia, and Philippines, and utilized for human food. It was seen in large numbers by the writer in the fish market at Samut Sakon, near Bangkok, Thailand, in 1993. In Australia it is taken in beach seines and on hook-and-line and is said to prefer squid bait; it is little utilized but regarded as good eating. It may nip divers if provoked. It also is taken in the aquarium trade and displayed in numerous public aquaria in Australia, Canada, Mexico, Europe, and the United States; breeds in captivity. The live young are particularly handsome, with brilliant black and whitish bands on the body and fins. Conservation status uncertain.

Local Names: Brownbanded bamboo shark, Gray carpet shark, Brown-banded catshark or Cat shark, Brownbanded catshark, Spotted catshark, Brown-banded bamboo shark, Brownspotted catshark, Inuzame (Japan).

Remarks: Müller and Henle (1839) listed "***Scyllium punctatum*** Kuhl and van Hasselt" under their ***Chiloscyllium punctatum***, but I was unable to examine Kuhl and van Hasselt's account of their species and so could not determine if ***Scyllium punctatum*** as proposed by Kuhl and van Hasselt was a valid species and not a *nomen nudum*. As per Dingerkus and DeFino (1983) and Compagno (1984), Müller and Henle's account is retained as the first valid description of this species. Fowler (1967a:103) termed this species ***Chiloscyllium russellianum***, because the ***Squalus (Scyliorhinus) russellianus*** of Blainville (1816) was "assumed as based on Bokee sorah Russell, F. of Coromandel I 1803, 10 pl. 16. Vizagapatam, India". However, Fowler (1941) had previously hesitated to replace the extensively-used ***C. punctatum*** with Blainville's *nomen nudum.*

Literature: Garman (1913); Smith (1913); Whitley (1940); Herre (1953); Stead (1963); Marshall (1964); Gubanov and Schleib (1980); Whitley and Pollard (1980); Dingerkus and DeFino (1983); Compagno (1984); Nakaya and Shirai (1984); Michael (1993); Last and Stevens (1994); Cook and Compagno (1994).

Hemiscyllium Müller and Henle, 1837

Genus: ***Hemiscyllium*** Müller and Henle, *in* Smith, 1837, *Proc. Zool. Soc. London*, 5: 86 (name only, with one species, "***Squalus ocellatus*** Bloch", equals ***Squalus ocellatus*** Bonnaterre, 1788); Müller and Henle, 1838a, *Mag. Nat. Hist., new ser.*, 2: 34 (definition, no species); Müller and Henle, 1838c, *Arch. Naturg.*, 4: 83 (definition, one species, ***Squalus ocellatus***); Müller and Henle, 1838d, *Syst. Beschr. Plagiost.*, pt. 1: 16 (definition, one species, ***Hemiscyllium ocellatum***).

Type Species: ***Squalus ocellatus*** Bloch and Schneider, 1801, by monotypy, equals ***S. ocellatus*** Bonnaterre, 1788; also by subsequent designation of Gill, 1862b, *Ann. Lyceum Nat. Hist. New York*, 7(32): 408, as "***Hemiscyllium ocellatum*** Mül. and Henle".

Number of Recognized Species: 5 or possibly 6.

Synonyms: None.

Diagnostic Features: Snout relatively short, preoral length less than 3% of total length. Eyes and supraorbital ridges well elevated. Nostrils virtually terminal on snout tip. Nasal barbels very short, length less than 1.3% of total length. Mouth slightly closer to snout tip than to eyes. Lower labial folds not connected across chin by a dermal fold. Pregill length less than 13.3% of total length. Preanal tail from vent to anal-fin origin usually more than 38% of total length. Pectoral and pelvic fins thick and heavily muscular. Pectoral-fin skeleton with propterygium fused to mesopterygium. Total vertebral count usually more than 180 centra and up to 195. Colour pattern with large black or dusky epaulette spots on shoulders above pectoral fin, sometimes partially merged with dark shoulder-saddle.

Local Names: Epaulette sharks, Speckled cat sharks, Yu tadek (Malaysia).

Remarks: The arrangement of this genus follows Whitley (1940, 1967), Fowler (1941), Compagno (1984) and the revision by Dingerkus and DeFino (1983). Data published in Dingerkus and DeFino suggests that ***Hemiscyllium*** species cannot be readily distinguished by vertebral count, morphometrics or differences in fin and body shape but are easily distinguishable by coloration. Coloration does, however, vary with growth as in ***Chiloscyllium***, and changes in colour pattern can be dramatic. Two of the five described species are known only from adults and subadults (***H. strahani*** and ***H. trispeculare***), and the juvenile colour pattern remains to be described for them.

Dingerkus and DeFino (1983: 54, fig. 37) reported a juvenile ***Hemiscyllium*** (USNM-123025, 148 mm female) from Amsterdam Island, Irian Jaya, New Guinea, Indonesia, that is of uncertain identity. It is distinguished by broad dark transverse stripes on a white background, a partial dark hood covering the region of the eyes and spiracles but not the snout, and a large black saddle blotch extending from the gills to the back and flank just behind the pectoral fins. It could be an undescribed species as it does not agree with the juvenile colour patterns of ***H. freycineti***, ***H. hallstromi*** or ***H. ocellatum***. Alternatively, it may represent the juvenile colour pattern of ***H. strahani*** (or, much less likely, ***H. trispeculare***). In either case the colour change with growth would be more extreme than those of other members of the genus. Resolution of the problem awaits further collections of ***Hemiscyllium*** from New Guinea.

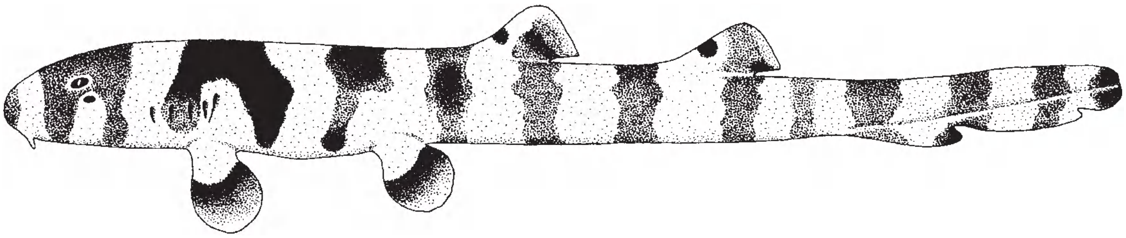


Fig. 143 ***Hemiscyllium* sp.**

There is an outlier record of a ***Hemiscyllium*** from Seychelles (Dibelius, 1993: 15, as the "Seychelles bamboo shark", ***H.*** cf. ***ocellatum***; and Dibelius, pers. comm.), of an adult male specimen photographed by a diver (Norbert Wu) and far west of any other records of the genus. This has no black hood-marking and has a few scattered small to large dark spots on the preorbital snout, no white spots, large and small scattered black spots on the head, body and tail, a large conspicuous black epaulette spot with a light margin, smaller black spots around the epaulette-spot, numerous large spots on the pectoral and pelvic fins, and spots and possibly dark bands on the underside of the tail. It matches ***H. freycineti*** and ***H. trispeculare*** in the key below by having spots on the preorbital snout, but does not quite agree with either of them in coloration. It is closest in coloration to ***H. freycineti*** but differs in having a more prominent epaulette spot and spots and banding on the underside of the tail. It also resembles ***H. hallstromi*** and differs from ***H. ocellatum*** in having mostly large dark spots on its body, but differs from both in its spotted preorbital snout, spotted pectoral fins and spotted and banded tail. It is said to reach about 100 cm and was photographed at a depth of 20 to 30 m on coral branches (Dibelius, 1993). The record probably represents an undescribed species of ***Hemiscyllium*** but its status needs to be confirmed by collection and deposition of material in a museum collection.

Key to Species:

1a. Prebranchial head and snout with an abrupt black hood or mask, black spots and bands on the underside of the head; black epaulette spots of shoulder partially merged with black shoulder saddle; body and fins with numerous, conspicuous small to large white spots (Fig. 144) . . . . ***Hemiscyllium strahani***

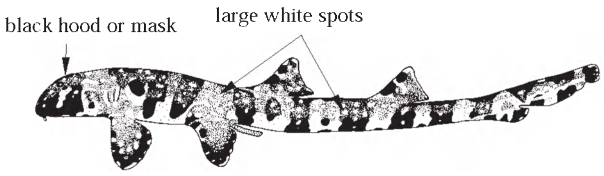


Fig. 144 ***Hemiscyllium strahani***

1b. Head and snout light to dusky, without a black hood, underside of head uniformly light; black epaulette spots of shoulder strongly marked; white spots inconspicuous or absent on fins and body . . . . → ***2***

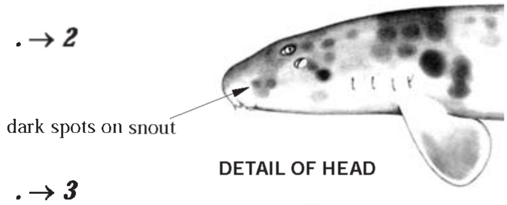


Fig. 145

2a. Preorbital snout with numerous dark spots (Fig. 145) . . . . → ***3***

2b. Preorbital snout uniformly light, without spots (Fig. 146) . . . . → ***4***

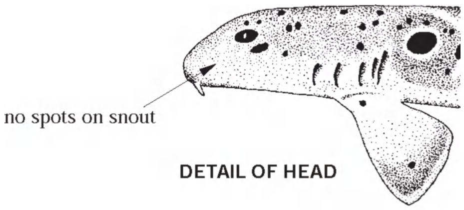


Fig. 146

3a. Dark spots on preorbital snout mostly less than half eye length, body and fins covered with numerous small and large dark spots that form a reticular network of light background colour between them; black epaulette spot of shoulder large, in the form of a conspicuous white-ringed ocellus with a central large black spot and two curved black marks surrounding the posterior half of the spot (Fig. 147) . . . . ***Hemiscyllium trispeculare***

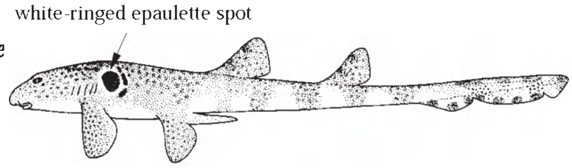


Fig. 147 ***Hemiscyllium trispeculare***

3b. Dark spots on preorbital snout mostly subequal to eye length, dark spots on body and fins mostly large and sparse, not forming a reticular network of light background colour; black epaulette spots of shoulder small to moderately large, not in the form of a conspicuous white-ringed ocellus, dark ocellar spot without curved black marks surrounding its posterior half (Fig. 148) . . . . ***Hemiscyllium freycineti***

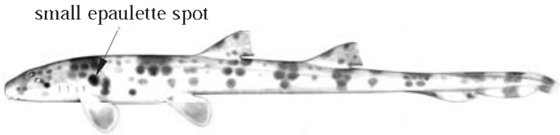


Fig. 148 ***Hemiscyllium freycineti***

4a. All spots on body distinctly smaller than epaulette spot; epaulette spot not surrounded by large black spots (Fig. 149) . . . . ***Hemiscyllium ocellatum***

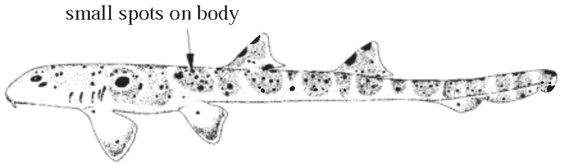


Fig. 149 ***Hemiscyllium ocellatum***

4b. Some body spots subequal to or larger than epaulette spot; epaulette spot surrounded by large black spots (Fig. 150) . . . . ***Hemiscyllium hallstromi***

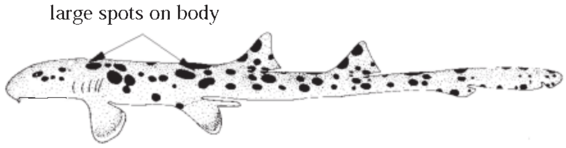


Fig. 150 ***Hemiscyllium hallstromi***

Hemiscyllium freycineti (Cuvier, 1824)

Fig. 151

Scyllium freycineti Cuvier, *in* Quoy and Gaimard, 1824, *Zoologie*, Poissons, *in* L. de Freycinet, *Voyage aut. monde l'uranie et la physicienne*. Syntypes: Museum National d'Histoire Naturelle, Paris, MNHN-A.7792, 323 mm TL male, and MNHN-B.2962, 290 mm TL male, Waigiu (Waigeo), Indonesia. MNHN-A.7792 designated as lectotype by Dingerkus and DeFino, 1983, *Bull. American Mus. Nat. Hist.*, 176(1): 38.

Synonyms: ***Scyllium malaisianum*** Lesson, 1830: 94. pl. 6. Lectotype: Museum National d'Histoire Naturelle, Paris, MNHN-7767, 685 mm TL, baïe d'Offack, Waigiou, Irian Jaya, Indonesia, type status verified by Dingerkus and DeFino (1983: 38); designated as lectotype by Eschmeyer (1998: CD-ROM). ***Chiloscyllium malaianum*** Müller and Henle, 1838d: 20. Holotype: Museum National d'Histoire Naturelle, Paris, 73 cm (calculated from quoted length of 27 in, assuming 27 mm per contemporary German inch) specimen, "Meerbusen von Offack. Insel Waigiou", possibly MNHN-7767 (see above). Also ***Hemiscyllium malayanum*** Bleeker, 1852: 6 (variant spelling).

Other Combinations: ***Chiloscyllium freycineti*** (Cuvier, 1824).

FAO Names: En - Indonesian speckled carpet shark; **Fr** - Requin-chabot grivelé; **Sp** - Bamboa jaspeada.

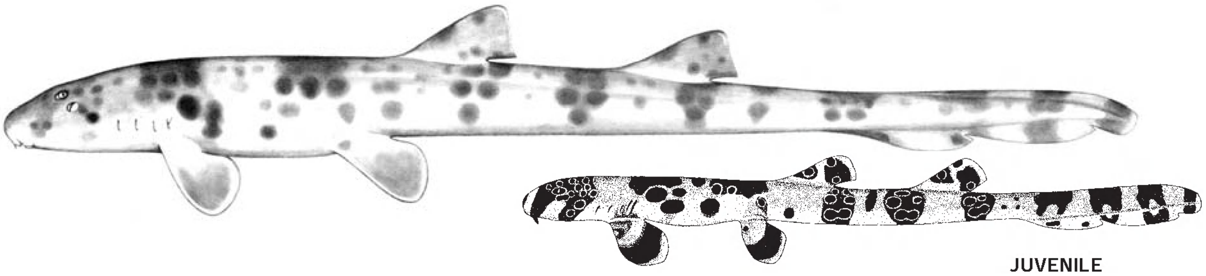
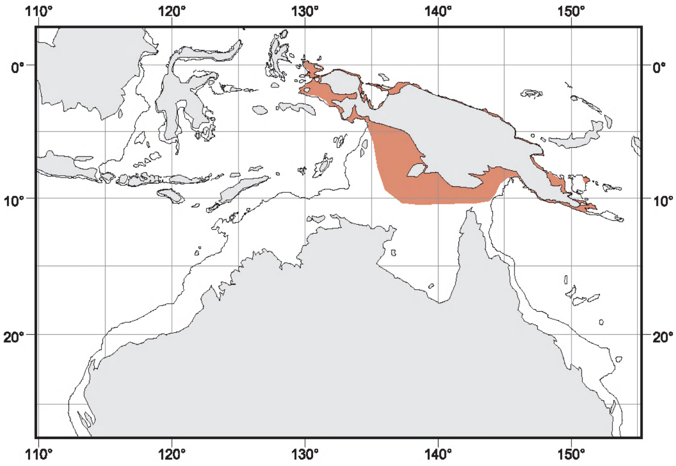


Fig. 151 ***Hemiscyllium freycineti***

Field Marks: Mouth well in front of eyes, spineless dorsal fins far posterior on tail, extremely elongated thick precaudal tail, long and low anal fin just anterior to caudal fin, large dark spots on snout, dark wide-spaced spots on body, a moderately large black spot on flanks above pectoral fins, no black hood or white spots.

Diagnostic Features: Colour: prebranchial head and snout without a black hood; underside of head uniformly light and without dark spots in adults, but with two broad dark bands in yound; several small to large dark spots mostly subequal to eye length present on preorbital snout. Black epaulette spot of shoulder moderately large, not in the form of a conspicuous white-ringed ocellus, nor with two or more additional round or oblong dark spots surrounding the posterior half of the epaulette spot. White spots absent from fins and body; fins and body covered with small to large and sparse dark spots that do not form a reticular network of light background colour between them; pectoral and pelvic fins with conspicuous dark webs and light margins in young, changing to scattered small and large dark spots in adults. Dark saddles on dorsal surface and sides of tail extending as dark crossbands onto ventral surface of the preanal tail (from pelvic-fin bases to anal-fin origin) in young, but saddles and crossbands are lost in adults which have uniform light ventral surfaces on their preanal tails.

Distribution: Western South Pacific: Indonesia (Irian Jaya, Waigeo), Papua New Guinea (Trobriand Islands from Kuia Island, Milne Bay, and east of Oro Bay).



Habitat: A little-known bottom shark, occurs on coral reefs, on sand, and in seagrass in shallow water.

Biology: Common in parts of New Guinea. Biology poorly known. It hides in reef crevices during the day and feeds at night.

Size: To at least 72 cm total length. Smallest freeliving individual recorded 18.7 cm; males maturing between 37 and 62 cm; adult female 72.2 cm.

Interest to Fisheries and Human Impact: Interest to fisheries none at present. It is not known if this shark is being affected by the aquarium trade. Its conservation status urgently needs to be assessed because part of its limited range is being impacted by expanding fisheries, including dynamite and poison fisheries that are destroying coral reefs, and possibly localized toxic pollution from riverine mining activities.

Local Names: Freckled carpet shark.

Literature: Garman (1913); Fowler (1941); Dingerkus and DeFino (1983); Compagno (1984); Michael (1993).

Hemiscyllium hallstromi Whitley, 1967 Fig. 152

Hemiscyllium hallstromi Whitley, 1967, *Australian Zool.*, 14(2): 178. Syntypes: Australian Museum, Sydney, AMS-I.15717-001, 730 mm adult male, and AMS-I.15584-001, 765 mm TL adult male, vicinity of Port Moresby, Papua-New Guinea. AMS-I.15717-001 designated as lectotype by Dingerkus and DeFino, 1983, *Bull. American Mus. Nat. Hist.*, 176(1): 40.

Synonyms: None.

Other Combinations: None.

FAO Names: En - Papuan epaulette shark; **Fr** - Requin-chabot épaulette; **Sp** - Bamboa hombrera.

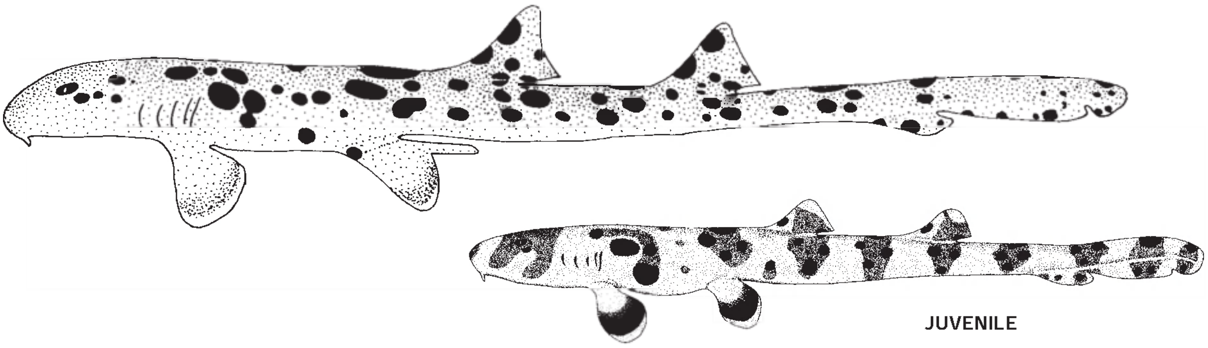


Fig. 152 *Hemiscyllium hallstromi*

Field Marks: Mouth well in front of eyes; spineless dorsal fins far posterior on tail, extremely elongated thick precaudal tail, long and low anal fin just anterior to caudal fin; no dark spots on snout, dark wide-spaced spots on body, a conspicuous large black ocellar spot on flanks above pectoral fins, surrounded by smaller black spots, no black hood or white spots.

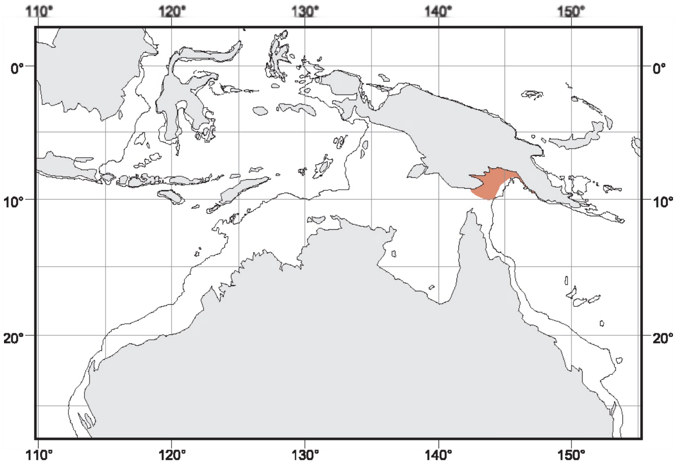
Diagnostic Features: Colour: prebranchial head and snout without a black hood; underside of the head uniformly light and without dark spots; preorbital snout without spots. Black epaulette spot of shoulder strongly marked, large, in the form of a conspicuous white-ringed ocellus and two or three large round black spots surrounding the posterior and dorsal part of the ocellus. White spots absent from fins and body; body and unpaired fins with small to large dark spots, some as large as epaulette spot, dark spots loose-set and not forming a reticular network of light background colour between them; pectoral and pelvic fins with conspicuous black webs and light margins in young, fading in adults to dusky, no light or dark spots on paired fins. Dark saddles on dorsal surface and sides of tail extending as dark crossbands onto ventral surface of preanal tail in young, but saddles and crossbands lost in adults which have uniform light ventral surfaces on their preanal tails.

Distribution: Western South Pacific: Papua-New Guinea (Port Moresby Area, Torres Strait, Murray Island).

Habitat: A little-known inshore bottom shark, possibly on coral reefs.

Biology: Essentially unknown. A 188 mm specimen (Australian Museum, Sydney, AMS IB.7938) was reported by Dingerkus and DeFino (1983: 40) as having been "born in the Taronga Zoo Park Aquarium; received 1967 (one of the syntypes was father)", but they did not specify if the species was ovoviviparous rather than oviparous as with other hemiscylliids.

Size: To about 77 cm total length. Smallest freeliving specimen 18.8 cm; males maturing between 47.6 and 63.9 cm; two adult males 73.0 and 76.5 cm.



Interest to Fisheries and Human Impact: Interest to fisheries none at present. It is not known if this shark is being affected by the aquarium trade. Its conservation status urgently needs to be assessed because of its rarity and restricted range. It is not known if it is being affected by pollution or destructive fisheries practices such as dynamiting or poisoning of coral reefs.

Literature: Whitley (1967); Dingerkus and DeFino (1983); Compagno (1984).

Hemiscyllium ocellatum (Bonnaterre, 1788) Fig. 153

Squalus ocellatus Bonnaterre, 1788, *Tabl. Encyclop. Method. Trois Reg. Nat., Ichthyol.*, Paris: 8. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN-1003, 353 mm TL (immature) male, "La mer du sud", vicinity of Cookstown, Queensland, Australia. Status of type confirmed by Dingerkus and DeFino, 1983, *Bull. American Mus. Nat. Hist.*, 176(1): 40.

Synonyms: ***Squalus oculatus*** Banks and Solander *in* Gray, 1827: 436. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN-1003, 353 mm TL (immature) male, vicinity of Cooktown, Queensland, Australia. Status of type confirmed by Dingerkus and DeFino (1983: 40).

Other Combinations: ***Scyllium ocellatum*** (Bonnaterre, 1788), ***Hemiscyllium oculatum*** (Gray, 1827).

FAO Names: En - Epaulette shark; **Fr** - Requin-chabot ocellé; **Sp** - Bamboa ocelada.

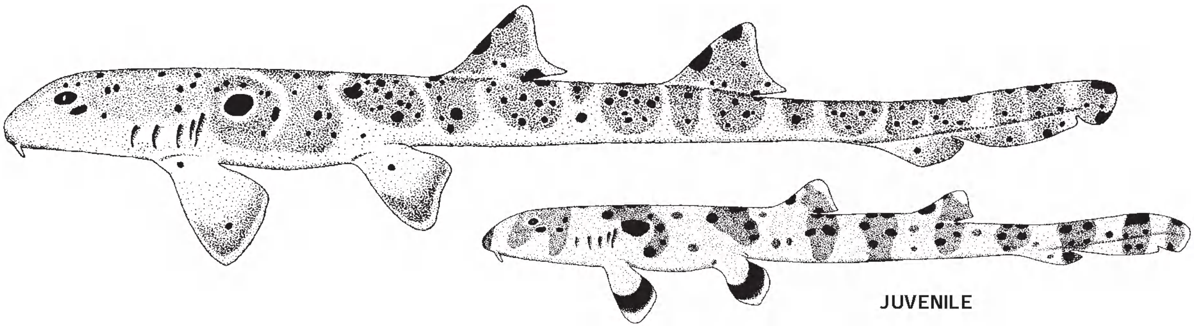
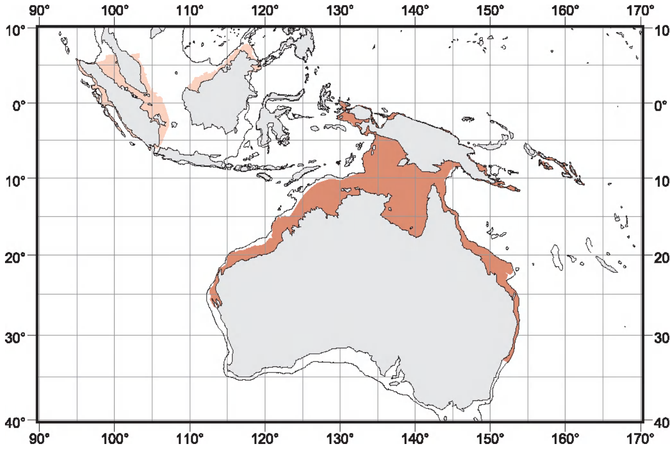


Fig. 153 *Hemiscyllium ocellatum*

Field Marks: Mouth well in front of eyes; spineless dorsal fins far posterior on tail, extremely elongated thick precaudal tail, long and low anal fin just anterior to caudal fin; no spots on snout, small dark wide-spaced spots on body, a conspicuous white-ringed black ocellus, without surrounding black spots, on flanks above pectoral fins, no black hood or white spots.

Diagnostic Features: Colour: prebranchial head and snout without a black hood; underside of the head uniformly light and without dark spots; preorbital snout without spots. Black epaulette spot of shoulder strongly marked, large, in the form of a conspicuous white-ringed ocellus, with scattered and inconspicuous small dark spots surrounding the posterior and dorsal part of the epaulette spot. White spots absent from fins and body; body and unpaired fins with small to medium-sized dark spots that are much smaller than the epaulette spot, dark spots loose-set and not forming a reticular network of light background colour between them; pectoral and pelvic fins with conspicuous black webs and light margins in young, fading in adults, sometimes a few small dark spots on paired fins of adults. Dark saddles on dorsal surface and sides of tail extending as dark crossbands onto ventral surface of preanal tail in young, but saddles and crossbands lost in adults which have uniform light ventral surfaces on their preanal tails.



Distribution: Western South Pacific: New Guinea (Papua New Guinea and Irian Jaya, Indonesia), Australia (Northern Territory, Western Australia, Queensland, New South Wales), Solomon Islands, possibly also Malaysia and Sumatra.

Habitat: An abundant, small, harmless tropical shark found on coral reefs in shallow water, often in tidepools and sometimes in water barely covering it. It prefers staghorn coral stands on reef faces, coral flats, and tide pools.

Biology: Particularly common on the Great Barrier Reef, where it can be seen crawling and clambering about and swimming on the bottom. It is more active after dark, particularly at dusk, but also coordinates its activities with tidal cycles, preferring to feed when the tide is out. It is unafraid of people and will come up to the feet of a 'reef-fossicker' (a person picking over a coral reef) and pick up small food items disturbed by the person. When disturbed it may make frantic attempts to find shelter under coral debris and in crevices, but is apparently satisfied, like the ostrich myth, if its head and pectoral region is covered and its tail is exposed. When captured and firmly held by hand the epaulette shark squirms violently without being able to escape, but may nip its captor.

Oviparous, eggs taking about 120 days to hatch. The male grabs the female by her pectoral fin while mating.

Eats primarily polychaete worms and small decapod crabs (Xanthidae, Portunidae and Ocypodidae), but also pistol shrimps (Alpheidae), mantis shrimps (Stomatopoda), amphipods, and teleost fishes (including dragonettes, Callyonymidae); also shelled molluscs. Young eat more worms, small fishes and amphipods than adults, which eat more crabs and shrimps, while adults eat larger crabs than young. While hunting for food it swims near the bottom, and may stop, and wave its snout back and forth over sandy bottom to locate prey (possibly using both electroreception and olfaction). In shallow water on sandy patches between coral heads the epaulette shark may arch its body, force its snout into the sand, and vigorously thrash its tail out of water while seeking and rooting out prey, then stops and masticates its catch.

This species is frequently infested with *praniza* larvae of gnathiid isopods. The parasites have a preference for the cloaca and clasper regions, but are also found in the buccal and branchial cavities. Heupel and Bennett (1999) believe the parasites do not adversely affect the health of the host.

Size: Maximum total length about 107 cm. Hatchlings are about 15 cm long; smallest freeliving specimen recorded at 16.7 cm; males maturing between 59 and 62 cm, with immature or adolescents up to 62 cm and adults as small as 59 cm; an adult female was 64.3 cm.

Interest to Fisheries and Human Impact: Interest to fisheries limited at present. Its importance to the aquarium trade needs to be assessed. It is a popular aquarium shark and is displayed in numerous public aquaria in Australia, Canada, and the United States. The conservation status of this shark is uncertain, but at least part of its habitat is protected in Australia. It is one of the sharks observed by divers and reef-fossickers on the Great Barrier Reef. It may nip people when provoked.

Local Names: Epaulette shark, Itar shark.

Remarks: Although this species has been reported from a fairly wide range in the Indo-Australian Archipelago, the review of Dingerkus and DeFino (1983) listed specimens only from Australia (mostly from Queensland but also northwestern Australia and New South Wales) and Solomon Islands. Last and Stevens (1994) mapped its distribution as including tropical Australia and both coasts of New Guinea. Nominal records from Malaysia and Sumatra (Stead, 1963) need confirmation.

Literature: Garman (1913); Whitley (1940); Fowler (1941); Stead (1963); Marshall (1964); Whitley and Pollard (1980); Grant (1982); Dingerkus and DeFino (1983); Compagno (1984); Michael (1993); Last and Stevens (1994); Heupel and Bennett (1998, 1999).

Hemiscyllium strahani Whitley, 1967

Fig. 154

Hemiscyllium strahani Whitley, 1967, *Australian Zool.*, 14(2): 176, fig. 1. Holotype: Australian Museum, Sydney, AMS-IB.7938, 735 mm adult female, vicinity of Port Moresby, New Guinea. Status of type confirmed by Dingerkus and DeFino, 1983, *Bull. American Mus. Nat. Hist.*, 176(1): 46.

Synonyms: None.

Other Combinations: None.

FAO Names: **En** - Hooded carpet shark; **Fr** - Requin-chabot moine; **Sp** - Bamboa capuchona.

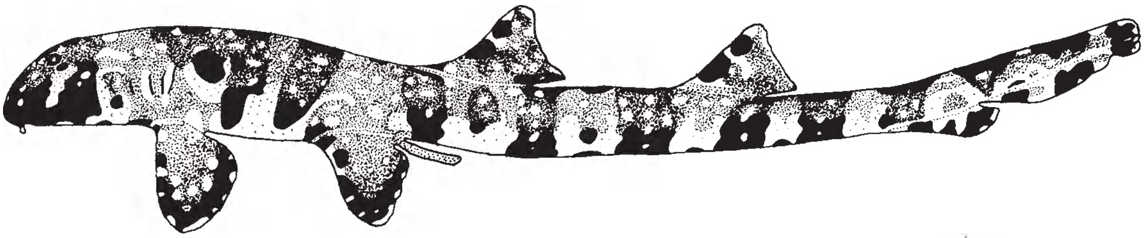
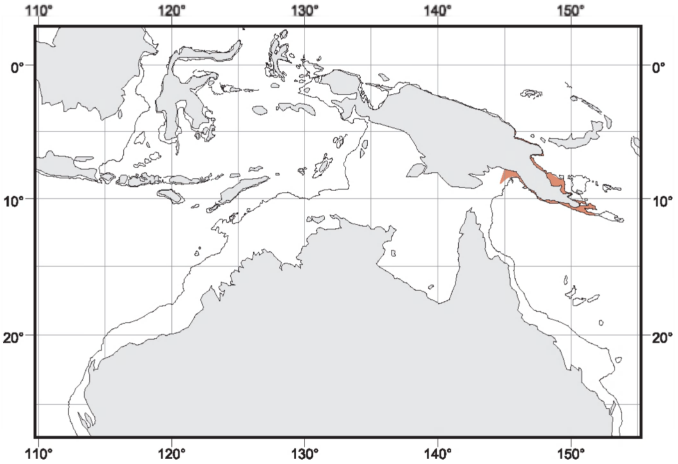


Fig. 154 *Hemiscyllium strahani*

Field Marks: Mouth well in front of eyes; spineless dorsal fins far posterior on tail, extremely elongated thick precaudal tail, long and low anal fin just anterior to caudal fin; white spots on body, and unique black hood on head.

Diagnostic Features: Colour: juvenile coloration unknown; prebranchial head and snout of adults with a unique black 'executioner's hood'; black spots and bands present on the underside of the head; no discrete small dark spots on snout. Black epaulette spot of shoulder partially merged with black shoulder saddle, no white ring or posterior curved spots surrounding it. Body and fins with numerous, conspicuously small to large white spots on dark saddles and blotches; no reticular network of fine dark spots on body and fins; pectoral and pelvic fins with conspicuous black webs and white-spotted margins and webs. Dark saddles on dorsal surface and sides of preanal tail extending onto ventral surface.



Distribution: Western South Pacific: Papua-New Guinea (Port Moresby area and Massas (Masas) Island).

Habitat: A little-known inshore bottom shark of singular and unique appearance, found on coral reefs on reef faces and flats and favouring areas with abundant hard corals. It may occur down to 18 m deep but Michael (1993) mostly observed it at depths of 3 to 13 m.

Biology: Apparently moderately common but with biology little-known. It is nocturnal, and hides in crevices and under table corals during the day. The holotype survived seven years in the Taronga Park Zoo aquarium among a breeding colony of ***Hemiscyllium ocellatum***, but it apparently did not hybridize with them.

Size: To about 80 cm total length. Formerly known only from two adult museum specimens (Dingerkus and DeFino, 1983), an adult male 59.4 cm long and an adult female 73.5 cm. Michael (1993) observed this species on night dives and reported specimens 75 to 80 cm long.

Interest to Fisheries and Human Impact: Interest to fisheries none at present. It is not known if this very attractive little shark is being affected by the aquarium trade. Its conservation status urgently needs to be assessed because of its rarity and because its limited range could be subject to problems including destructive reef fisheries and localized toxic pollution.

Remarks: Dingerkus and DeFino (1983) reported a juvenile ***Hemiscyllium*** from Irian Jaya, Indonesia, that is of uncertain identity but could be the young of this species (see discussion above).

Literature: Whitley (1967); Dingerkus and DeFino (1983); Compagno (1984); Michael (1993).

Hemiscyllium trispeculare **Richardson, 1843** **Fig. 155**

Hemiscyllium trispeculare Richardson, 1843, *Icones Piscium, Pl. Rare Fish*: 5, pl. 1, fig. 2. Holotype: Apparently not saved, Turtle Island, northwest Australia. Neotype: British Museum (Natural History), BMNH-1953.5.10.1, 576 mm adult male, northwestern Australia, the basis of a redescription of this species by Richardson, 1846, *Zool. Erebus Terror*, 2, Fishes: 43-44, pl. 28, and designated as neotype by Dingerkus and DeFino, 1983, *Bull. American Mus. Nat. Hist.*, 176(1): 51.

Synonyms: None.

Other Combinations: ***Chiloscyllium trispeculare*** (Richardson, 1843).

FAO Names: **En** - Speckled carpet shark; **Fr** - Requin-chabot marquéterie; **Sp** - Bamboa moteada.

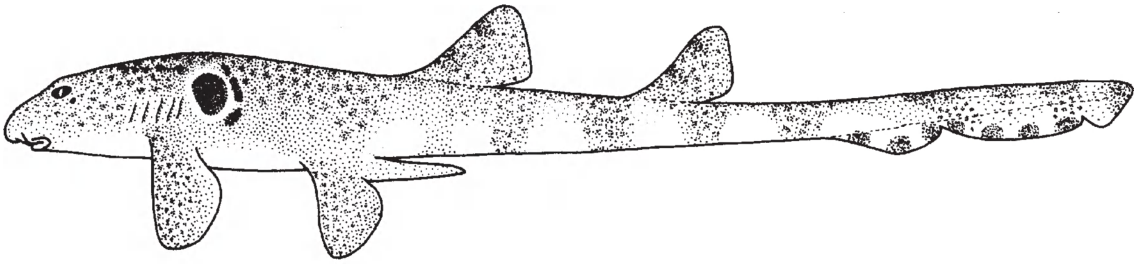


Fig. 155 ***Hemiscyllium trispeculare***

Field Marks: Mouth well in front of eyes; spineless dorsal fins far posterior on tail, extremely elongated thick precaudal tail, long and low anal fin just anterior to caudal fin; small dark spots on snout, numerous dark close-set spots forming a reticular pattern on body, a conspicuous white-ringed large black ocellus on flanks above pectoral fins, partly surrounded by smaller black spots, no black hood or white spots.

Diagnostic Features: Colour: juvenile coloration unknown; prebranchial head and snout of adults without a black hood; underside of the head uniformly light and without dark spots; numerous small dark spots mostly less than half eye length present on preorbital snout. Black epaulette spot of shoulder strongly marked, large, in the form of a conspicuous white-ringed ocellus and two curved black marks surrounding the posterior half of the spot. White spots absent from fins and body; fins and body covered with numerous small and large, densely spaced dark spots that form a reticular network of light background colour between them; pectoral fins with dusky webs and numerous small dark spots. Dark saddles on dorsal surface and sides of preanal tail extending as dark crossbands onto ventral surface.

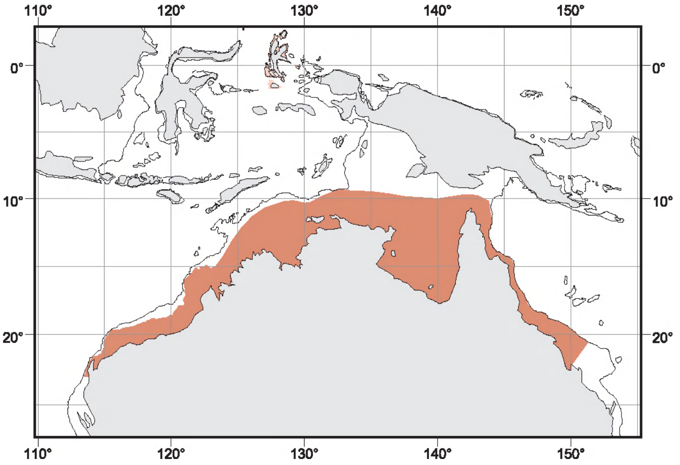
Distribution: Western South Pacific: ?Indonesia (Moluccas), Australia (Northern Territory, Western Australia, Queensland).

Habitat: A tropical continental shelf shark that is found on coral reefs in shallow water, including tide pools.

Biology: A common small shark, with biology poorly known. Often observed under table corals.

Size: Maximum total length 79 cm. Size at hatching unknown; adult males 57 to 64 cm total length; adult female 56 cm. Possibly a smaller species than ***H. ocellatum***.

Interest to Fisheries and Human Impact: Interest to fisheries none at present. The importance of this shark to the aquarium trade needs to be assessed. The conservation status of this shark is uncertain, but at least part of its habitat is protected in Australia.



Local Names: Speckled carpet shark, Speckled catshark or Cat shark.

Remarks: Indonesian (Moluccas) records of this species need confirmation.

Literature: Garman (1913); Fowler (1941); Stead (1963); Whitley and Pollard (1980); Grant (1982); Dingerkus and DeFino (1983); Compagno (1984); Michael (1993); Last and Stevens (1994).

2.3.5 Family STEGOSTOMATIDAE

Family: Subfamily Stegostomatinae Gill, 1862b, *Ann. Lyceum Nat. Hist. New York*, 7(32): 407, 408 (Family Scylliorhinoidae Gill, 1862). Also subfamily Stegostomatinae Fowler, 1934, *Proc. Acad. Nat. Sci. Philadelphia*, 85: 239 (Family Orectolobidae).

Type Genus: ***Stegostoma*** Müller and Henle, 1837.

Number of Recognized Genera: 1.

Synonyms: Family Stegostomatidae Applegate, 1974: 748. Type genus: ***Stegostoma*** Müller and Henle, 1837. Independently proposed as a family. Family Stegastomatidae Last and Stevens, 1994: 138. Apparent error for Stegostomatidae.

FAO Names: En - Zebra sharks; **Fr** - Requins zébres; **Sp** - Tiburones acebrados.

Diagnostic Features: Head broad, conical and somewhat flattened, without lateral flaps of skin. Snout very broadly rounded or truncated. Eyes laterally situated on head and without strong subocular ridges below them. Eyes without movable upper eyelids or subocular pockets and ridges. Spiracles large and subequal to eyes, without prominent raised external rims; spiracles behind but not below eyes. Gill slits small, fifth gill slit overlapping fourth; internal gill slits without filter screens. Nostrils with short pointed barbels but without circumnarial folds and grooves around incurrent apertures. Nasoral grooves long and strongly developed. Mouth moderately large, nearly transverse and subterminal on head. Lower lip trilobate and with lateral orolabial grooves connecting edge of lip with medial ends of lower labial furrows, no longitudinal symphysial groove on chin. Lower labial furrows ending medially far lateral to symphysis, not connected medially by a mental groove or groove and flap. Teeth not strongly differentiated in upper and lower jaws, with symphysial teeth not enlarged nor fang-like. Tooth row count 28 to 33/22 to 32. Teeth with a strong medial cusp, a pair of short lateral cusplets, and weak labial root lobes. Teeth orthodont with a central pulp cavity and no plug of osteodentine. Body cylindrical, with strong ridges on sides. Precaudal tail shorter than body. Caudal peduncle without lateral keels or precaudal pits. Pectoral fins large, broad and rounded. Pectoral fins semiplesodic and with fin radials partly expanded into fin web. Pectoral propterygium small and separate from mesopterygium and metapterygium; pectoral-fin radial segments three to nine, and with longest distal segments up to 1.3 times the length of longest proximal segments. Pelvic fins smaller than first dorsal fin but larger than second dorsal fin and as large or larger than anal fin, much smaller than pectorals and with anterior margins 0.4 to 0.6 times the pectoral-fin anterior margins. Claspers poorly known but probably without mesospurs, claws or dactyls. Dorsal fins with second dorsal much smaller than first. First dorsal-fin origin expanded well ahead of pelvic-fin origins and with insertion about over pelvic-fin bases. Anal fin larger than second dorsal fin, with broad base, angular apex, origin about opposite second dorsal-fin midbase or insertion, and insertion separated by a space or narrow notch much less than base length from lower caudal-fin origin. Caudal fin greatly elongated horizontally and not crescentic, weakly heterocercal with its upper lobe at a low angle above the body axis; dorsal caudal-fin margin about half as long as the entire shark. Caudal fin with a strong terminal lobe and subterminal notch but without a ventral lobe, preventral and postventral margins not differentiated and forming a continuous curve. Vertebral centra with well-developed radii. Total vertebral count 207 to 243, monospondylous precaudal count 43 to 49, diplospondylous precaudal count 38 to 50, diplospondylous caudal count 120 to 154, and precaudal count 81 to 101. Cranium broad and expanded laterally. Medial rostral cartilage moderately long and not reduced to a low nubbin. Nasal capsules elevated and not greatly depressed or fenestrated, internarial septum moderately high and slightly compressed. Orbits with small foramina for preorbital canals, medial walls not fenestrated around the optic nerve foramina. Supraorbital crests present on cranium and laterally expanded and pedicellate. Suborbital shelves moderately broad and not greatly reduced. Cranial roof solid, without a continuous fenestra from the anterior fontanelle to the parietal fossa. Basal plate of cranium with a pair of stapedial foramina widely separated from medial carotid foramina. Adductor mandibulae muscles of jaws with two divisions. Preorbitalis muscles extending onto posterodorsal surface of cranium. No anterodorsal palpebral depressor, rostromandibular, rostronuchal or ethmonuchal muscles. Valvular intestine of ring type with 18 turns. Development oviparous. Size large with adults between 147 and 233 cm and exceptionally over 300 cm total length while young are hatched at about 20 to 36 cm. A unique colour pattern of black saddles with light lines in young, changing to dark spots on a light background in juveniles and adults.

Remarks: The arrangement of this family follows Compagno (1973, 1984) and Applegate (1974), in recognizing a monotypic family Stegostomatidae for the highly distinctive zebra shark, ***Stegostoma fasciatum*** (Herman, 1783). Dingerkus (1986) included ***Stegostoma*** in an aggregate family Rhincodontidae for 'higher' orectoloboids (also including ***Rhincodon***, ***Pseudoginglymostoma***, ***Ginglymostoma*** and ***Nebrius***) but the earlier arrangement is followed here pending further work on the interrelationship of orectoloboids. Dingerkus (1986) suggested that ***Stegostoma*** was the immediate sister group of the whale shark, ***Rhincodon***, while Compagno (1988) suggested that ***Stegostoma*** was either the immediate sister group of ***Pseudoginglymostoma*** or of a group comprising ***Rhincodon*** plus ***Ginglymostoma*** and ***Nebrius***.

The present account follows most previous researchers in recognizing a single species of zebra shark. At least one early author, Gmelin (1788), apparently recognized separate species on the strikingly distinct juvenile (***Squalus tigrinus***) and subadult-adult (***S. longicaudatus***) colour patterns respectively. However, the zebra shark needs to be subjected to detailed morphological and biochemical comparisons over its vast range, to determine if it is a single species.

The earliest name for the zebra shark is ***Squalus varius*** Seba, 1758, which has been used by various writers (Garman, 1913; Klausewitz, 1960; and Bass, D'Aubrey and Kistnasamy, 1975a) as ***Stegostoma varium***. However, an examination of Seba's (1758) descriptions of fishes showed that his nomenclature was haphazardly uninomial, binomial, and polynomial, although the name of the zebra shark could be construed as binomial: "Squalus varius; naribus ori proximis; foraminibus pare oculos; spiraculis utrinque quaternis; cauda longifilis." (Seba, 1758).

In addition to the above name and diagnosis, Seba includes a long, accurate Latin description of the zebra shark, and a legend caption in French for a good illustration of a juvenile zebra shark with barred colour pattern (Seba, 1758, pl. 34, no. 1). I did not use Seba's name previously (Compagno, 1984) or here for this shark because his nomenclature was not consistently binomial, and the first valid usage of the name "varius" is ***Stegostoma varium*** Garman, 1913. The International Commission on Zoological Nomenclature would have to make a special ruling to make the name available. Extensive usage of ***Stegostoma fasciatum***, ***S. tigrinum***, and other names for the zebra shark in the literature make such an action unnecessary in the writer's estimation.

Stegostoma Müller and Henle, 1837

Genus: ***Stegostoma*** Müller and Henle, 1837a, *Ber. K. preuss. Akad. wiss. Berlin*, 2: 112.

Type Species: ***Squalus fasciatus*** Bloch and Schneider, 1801, by original designation, equals ***Squalus fasciatus*** Hermann, 1783.

Number of Recognized Species: 1.

Synonyms: Genus ***Stegostonea*** Regan, 1929: 293. Probable error for ***Stegostoma*** Müller and Henle, 1837. Genus ***Stegastoma*** Herre, 1934: 10. Probable error for ***Stegostoma*** Müller and Henle, 1837. Genus ***Stegastoma*** Last and Stevens, 1994: 138. Apparent error for ***Stegostoma*** Müller and Henle, 1837.

Diagnostic Features: See family Stegostomatidae above.

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Stegostoma fasciatum (Hermann, 1783) Fig. 156

Squalus fasciatus Hermann, 1783, *Tab. Affin.*: 302. Based on ***Squalus varius*** Seba, 1758. A senior homonym of ***Squalus fasciatus*** Bonnaterre, 1788 = ***Poroderma africanum*** (Gmelin, 1788). No types according to Eschmeyer (1998, *Cat. Fish.*: CD-ROM). Also, ***Squalus fasciatus*** Bloch, 1785, *Naturg. Ausl. Fische*, 1: 19, pl. 113. Holotype: Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin, ZMB-4449, 355 mm total length male, Indian Ocean from Tranquebar, according to Paepke and Schmidt (1988, *Mitt. Zool. Mus. Berlin*, 64(1): 163).

Synonyms: ***Squalus varius*** Seba, 1758: 105, pl. 34, fig. 1. No type locality or specimens. Name not available because Seba's usage of nomenclature was not consistently binomial (see remarks above). ***Squalus tigrinus*** Pennant, 1769: 24; (*nomen nudum*?). ***Squalus tygrinus*** Bonnaterre, 1788: 8, pl. 8, fig. 23. Type material uncertain. Type locality: "La mer des Indes". ***Squalus tigrinus*** Gmelin, *in* Linnaeus and Gmelin, 1788: 1493. Type material uncertain. Type locality: "Oceano indico". ***Squalus varius*** Seba, 1758 included in synonymy. This species was probably based on juveniles with a striped colour pattern. ***Squalus longicaudatus*** Gmelin, *in* Linnaeus and Gmelin, 1788: 1496. Type material uncertain, no locality given. ***Squalus varius*** Seba, 1758 included in synonymy. This was not strongly distinguished from ***S. tigrinus***, but may have been based on post-juveniles with a spotted colour pattern. ***Scyllia quinquecornuatum*** van Hasselt, 1823: 15. Reference to ***Squalus varius*** Seba, 1758, and presumably a replacement name for it. No types listed in Eschmeyer (1998: CD-ROM). ***Scyllium heptagonum*** Rüppell, 1837: 61, pl. 17, fig. 1. Lectotype: Senckenberg Museum, Frankfurt, SMF-3152, 105 cm stuffed specimen, possibly female, Djedda, Red Sea, according to Klausewitz (1960: 290). ***Stegostoma carinatum*** Blyth, 1847: 725, pl. 25, fig. 1. Type locality: India. Whereabouts of holotype unknown according to Eschmeyer (1998: CD-ROM). ***Squalus pantherinus*** Kuhl and van Hasselt, *in* Bleeker, 1852: 23. Name only, in synonymy of ***Stegostoma fasciatum*** Müller and Henle, 1838. Not ***Scyllium pantherinum*** Smith, 1837 = ***Poroderma pantherinum***. ***Squalus cirrosus*** Gronow, *in* Gray, 1854: 46. No locality. Reference to ***Squalus varius*** Seba, 1758, and presumably a replacement name for it. No types according to Eschmeyer (1998: CD-ROM). ***Stegostoma varium*** Garman, 1913: 59. Syntypes: At least two specimens, 330 mm (13 in) and about 1.53 m (5 ft) mentioned without further detail. According to Eschmeyer (1998: CD-ROM) syntypes include Museum of Comparative Zoology, Harvard, MCZ 55-S (possibly lost), MCZ-33437, and MCZ uncat. (shrunken skin and skull). Revival of ***Squalus varius*** Seba, 1758 and first valid use of the species name. ***Stegostoma tigrinum naucum*** Whitley, 1939: 229, fig. 2. Holotype: Australian Museum, Sydney, AMS-I.4174, Hawkesbury River, New South Wales, according to Paxton et al. (1989: 92). ***Scyllium quinquecarinatum*** Fowler, 1941: 102. Error or emendation for ***Scyllia quinquecornuatum*** van Hasselt, 1823.

Other Combinations: ***Stegostoma tigrinus*** or ***S. tigrinum*** (Pennant, 1769 or Gmelin, 1788), ***Stegostoma tygrinum*** (Bonnaterre, 1788).

FAO Names: En - Zebra shark; **Fr** - Requin zèbre; **Sp** - Tiburón acebrado.

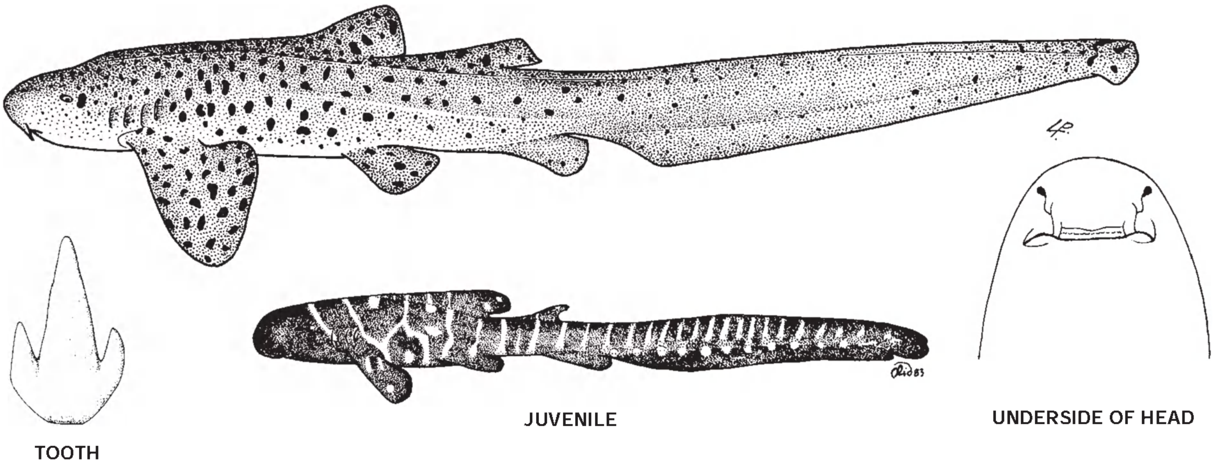
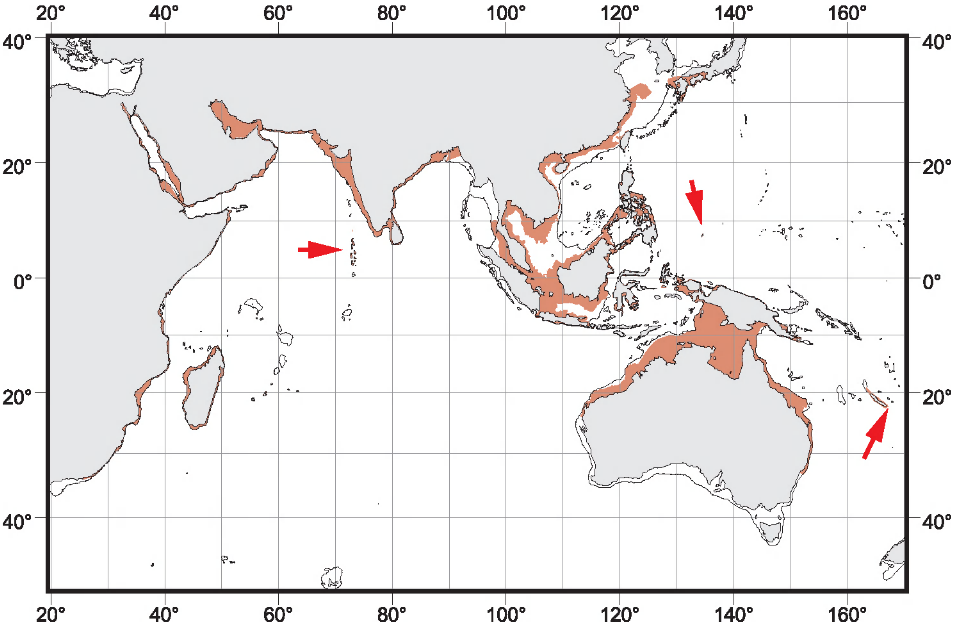


Fig. 156 *Stegostoma fasciatum*

Field Marks: Unique large sharks that combine a broad, low caudal fin about as long as the rest of the shark with nasoral grooves, barbels, a small transverse mouth in front of the lateral eyes, two spineless dorsal fins and an anal fin, the first dorsal fin much larger than the second and with its origin far forwards on back, prominent ridges on the sides of the body but no strong lateral keels on the caudal peduncle. **Colour:** colour pattern banded or spotted. Young sharks are dark brown above, yellowish below, with vertical yellow stripes and spots breaking the dorsal coloration into dark saddles; in specimens between 50 and 90 cm length the saddles break up into small brown spots on a yellow background, these becoming less linear and more uniformly distributed with further increase in size. There is considerable variation in the colour pattern between individuals of like size. An albino specimen was once collected.

Diagnostic Features: See family Stegostomatidae above.

Distribution: Indo-West Pacific: From the east coast of South Africa (Eastern Cape and KwaZulu-Natal Provinces), Mozambique, and Madagascar north to Tanzania and east to the Red Sea, Gulf of Aden, the Maldives, the Persian Gulf, Pakistan, India, Sri Lanka, Bangladesh, Malaysia (including Sarawak, Borneo), Singapore, Indonesia (Java, Macassar Strait, Sulawesi, Dobo and Aru Islands), Thailand, Viet Nam, Kampuchea, Philippines, China, Taiwan (Province of China), Japan, New Guinea, northern Australia (Western Australia, Northern Territory, Queensland, New South Wales), New Caledonia, and Palau.



Habitat: This is an inshore tropical shark of the continental and insular shelves of the Indo-West Pacific, that is very common on coral reefs but also occurs offshore on soft grounds. It ranges from the intertidal down to 62 m. It has been reported from fresh water in Philippines, but this needs to be confirmed. Adults and large spotted juveniles prefer lagoons, channels and faces of coral reefs, reef detritus and sandy places as rest areas, but the striped young are rarely seen and may prefer water below 50 m.

Biology: The biology of the zebra shark is sketchily known despite being relatively common and readily observed alive by divers on coral reefs and as catches in Indo-West Pacific fish markets. The behaviour and social organization of this shark is little known, but it has been photographed resting on sandy areas within reefs, sometimes propped up on its pectoral fins and facing a current with open mouth. According to Michael (1993), it is usually solitary, but is rarely seen in aggregations. It apparently is rather sluggish, at least during the daytime, and is more active at night as are nurse sharks (Ginglymostomatidae) or when motivated by the presence of food. Because of its rather slender, flexible body and caudal fin it is able to squirm into narrow cracks, crevices and channels while searching for food. In captivity, it spends most of its time resting on the bottom (at least during the day), but becomes active when food is introduced into its tank.

An immature male zebra shark about 1.3 m long was observed by the writer on two separate occasions in a large tank at the Waikiki Aquarium (February 2000). It sat on the bottom of its tank in the evening on one day but became highly active during feeding time in the early afternoon on a subsequent day. It swam about as fast as the 1.1 to 1.2 m long blacktip reef sharks (***Carcharhinus melanopterus***) that it was quartered with (speed estimated at 1.0 to 1.5 m per second), and during a half-hour's observation stayed near the top of the tank and swam continuously. It swam strongly, with prominent anguilliform undulations of its body and tail, and showed much manoeuvring and considerable agility while swimming. The shark broke the surface with its caudal fin on a few occasions, churning the water, but it was not obvious if it was using its tail in any special way. The caudal fin was held at a low but noticeable angle to the body axis. The elongated caudal fin seems less likely to be used as a weapon to herd and stun small fishes than the caudal fins of threshers (Alopiidae), but could be used during social activities, including courtship, as well as for facilitating entry into tight spaces.

Oviparous, laying eggs in large (17 cm long, 8 cm wide and about 5 cm thick), dark brown or purplish black cases with fine lateral tufts of hair-like fibres, which serve to anchor the cases to the substrate. Probably lays more than one or two eggs at once, as four fully formed, encased eggs were found in one oviduct of an adult female.

Feeds primarily on molluscs (gastropods and bivalves) but also crustaceans (crabs and shrimp), small bony fishes, and possibly sea snakes.

Size: Maximum possibly 354 cm, but most adults apparently below 2.5 m. Young hatching at a size between 20 and 36 cm; males maturing between 147 and 183 cm; females maturing between 169 and 171 cm and reaching at least 233 cm.

Interest to Fisheries and Human Impact: Regularly taken in inshore fisheries in Pakistan, India, Thailand, Malaysia, Taiwan (Province of China), and elsewhere where it occurs. It is caught in bottom trawls, in floating and fixed bottom gill nets, and with longlines and other line gear. It rarely takes baited hooks. The meat is utilized fresh and dried-salted for human consumption; livers processed for vitamins; fins dried and processed for the oriental sharkfin trade; and offal utilized for fishmeal.

This is a hardy shark, readily kept in captivity and is an attractive and lively aquarium exhibit. It is currently kept in several public aquaria in Australia, Japan, Portugal, Singapore, Spain, and the United States.

The zebra shark is unaggressive when approached underwater and has not bitten people although it is sometimes harassed by divers trying to ride it. It is popular for viewing by ecotouristic divers in the Red Sea, off the Maldives, off Phuket Island, Thailand, on the Great Barrier Reef in Queensland, Australia, and elsewhere in the Indo-West Pacific. According to Michael (1993), divers hand-feed these sharks off Phuket and the sharks allow divers to physically contact them and tolerate being stroked on the abdomen. It is uncertain if the sharks enjoy extended contact or are undergoing tonic immobility.

The conservation status of the zebra shark needs assessment, as it may have declined in areas such as the Gulf of Thailand where it was formerly more common. Also, it may have been adversely affected by the widespread use of explosives and poisons to fish out reefs in the eastern Indian Ocean and western Pacific as with other reef sharks. It is not known how this shark figures in and is influenced by the international aquarium trade. Although the adults and subadults can only thrive in large public aquaria, as with nurse and tawny sharks, the very attractive newly-hatched young are sufficiently small to live in the tanks of private collectors.

Local Names: Zebra shark (South Africa, Sri Lanka); Tiger shark, Sea tiger, Nurse shark, Shark with tiger-like spots, Leopard shark (Australia, South Africa); Tubaràо zebra (Mozambique); Variegated shark (Maldives); Baglul (Arabia); Monkey-mouth, Monkey-mouthed shark, Pollee makum, Komrasi, Oorookoolti sorrah, Potrava, Corungun sorrah (Tamil; India); Yu checkak, Yu tokek (Malay Peninsula); Ikan tjutjot matjan (Malay Samarang); Yu tokay (Malay Pinang); Chilarm seour (Tiger shark), Seaur talay (Sea tiger, Thailand); Torafuzame (Japan); Kongarasi (Telugu); Shinvala (Marathi); Butanding (Philippines, Bikol).

Literature: Seba (1758); Müller and Henle (1838d); Dumeril (1865); Günther (1870); Regan (1908a); Garman (1913); Whitley (1934, 1939, 1940); Barnard (1937); Fowler (1941, 1967a); Misra (1947); Herre (1953, 1958); Lindberg and Legeza (1959); Klausewitz (1960); Teng (1962); Chen (1963); Stead (1963); Gohar and Mazhar (1964); Marshall (1965); Bessednov (1969); Shiino (1972, 1976); Nakaya (1973); Bass, D'Aubrey and Kistnasamy (1975c); Faulkner (1975); Masuda, Araga and Yoshino, (1975); Fourmanoir and Laboute (1976); Grant (1982); Uchida (1982); Compagno (1984); Nakaya and Shirai (1984); Dingerkus (1986); Anderson and Ahmed (1993); Dibelius (1993); Michael (1993); Seret (1994); Last and Stevens (1994).

2.3.6 Family GINGLYMOSTOMATIDAE

Family: Ginglymostomatoidae Gill, 1862b, *Ann. Lyceum Nat. Hist. New York*, 7(32): 393, 395, 397, 406. Emended to family Ginglymostomatidae by Gill, 1872, *Smithsonian Misc. Coll.* (247): 24.

Type Genus: ***Ginglymostoma*** Müller and Henle, 1837.

Number of Recognized Genera: 3.

Synonyms: Family Ginglystomidae Jordan, 1923: 98 (emended or erroneous spelling for Ginglymostomatidae). Subfamily Nebriinae Fowler, 1934: 238 (Family Orectolobidae). Type genus: ***Nebrius*** Rüppell, 1837. Family Ginglymostomatidae Whitley, 1940: 68. Independently proposed as a separate family. Type genus: ***Ginglymostoma*** Müller and Henle, 1837.

FAO Names: En - Nurse sharks; **Fr** - Requins nourrices; **Sp** - Gatas nodriza.

Field Marks: Small to large sharks with nasoral grooves but no circumnarial grooves and folds, short to long barbels, small transverse mouths in front of eyes; small spiracles behind but not below eyes, no lateral skin flaps on head; two spineless dorsal fins and an anal fin, the second dorsal-fin origin well ahead of the anal-fin origin, and a short precaudal tail much shorter than the head and body.

Diagnostic Features: Head broad and flattened, without lateral flaps of skin. Snout broadly rounded or truncated. Eyes dorsolaterally or laterally situated on head, with or without strong subocular ridges below them. Eyes without movable upper eyelids or subocular pockets. Spiracles much smaller than eyes, without raised external rims; spiracles behind eyes but not below them. Gill slits small, fifth gill slit virtually overlapping fourth; internal gill slits without filter screens. Nostrils with short to moderately long pointed barbels but without circumnarial folds and grooves. Nasoral grooves long and strongly developed. Mouth moderately large, transverse, and subterminal on head. Lower lip trilobate or not, with or without lateral orolabial grooves connecting edge of lip with medial ends of lower labial furrows, no longitudinal symphysial groove on chin. Lower labial furrows extending medially but ending well lateral to symphysis and not connected medially by a mental groove or groove and flap. Teeth not strongly differentiated in upper and lower jaws, with symphysial teeth not enlarged and fang-like. Tooth row count 24 to 38/22 to 32. Teeth with a strong medial cusp, one to seven pairs of short lateral cusplets, and weak labial root lobes. Teeth orthodont with a central pulp cavity and no plug of osteodentine (***Pseudoginglymostoma***), or osteodont with a core of osteodentine in the crown (***Ginglymostoma*** and ***Nebrius***). Body cylindrical or moderately depressed, without ridges on sides. Precaudal tail shorter than body. Caudal peduncle without lateral keels or precaudal pits. Pectoral fins moderately large, broad and rounded to narrow and falcate. Pectoral fins aplesodic (***Pseudoginglymostoma***), semiplesodic (***Ginglymostoma***) or fully plesodic (***Nebrius***), with fin radials variably expanded into fin web or not. Pectoral propterygium moderately large and separate from mesopterygium and metapterygium; pectoral-fin radial segments 4 to 9, and with longest distal segments 0.4 to 0.7 times the length of longest proximal segments. Pelvic fins somewhat larger to somewhat smaller than dorsal fins and anal fin, much smaller than pectoral fins and with anterior margins 0.4 to 0.7 times pectoral-fin anterior margins. Claspers without mesospurs, claws or dactyls. Dorsal fins either equal-sized (***Pseudoginglymostoma***) or with second dorsal fin considerably smaller than first (***Ginglymostoma***, ***Nebrius***). First dorsal-fin origin varying from slightly anterior to pelvic-fin origins to over their bases, insertion just behind the pelvic-fin rear tips. Anal fin about as large as second dorsal fin, with broad base and angular apex, origin about opposite second dorsal-fin origin or midbase, and insertion separated by a space much less than its base length from lower caudal-fin origin. Caudal fin horizontally elongated and not crescentic, heterocercal, with its upper lobe at a moderate angle above the body axis; dorsal caudal-fin margin less than two-fifths as long as the entire shark. Caudal fin with a strong terminal lobe and subterminal notch but without a ventral lobe or with a very short one, preventral and postventral margins not differentiated and forming a continuous curve (***Pseudoginglymostoma***) or weakly differentiated in adults (***Nebrius***, ***Ginglymostoma***). Vertebral centra with well-developed radii. Total vertebral count 135 to 195, monospondylous precaudal count 35 to 57, diplospondylous precaudal count 41 to 53, diplospondylous caudal count 49 to 96, and precaudal count 85 to 103. Cranium narrow to moderately broad but not greatly expanded laterally. Medial rostral cartilage moderately long and not reduced to a low nubbin. Nasal capsules elevated and not greatly depressed or fenestrated, internarial septum low and compressed or moderately depressed. Orbits with small foramina (***Pseudoginglymostoma***) or enlarged fenestra (***Ginglymostoma***) for preorbital canals, medial walls not fenestrated around the optic nerve foramina. Supraorbital crests present on cranium and laterally expanded and pedicellate. Suborbital shelves moderately broad and not greatly reduced. Cranial roof either solid (***Pseudoginglymostoma***) or with a continuous fenestra from the anterior fontanelle to the parietal fossa. Basal plate of cranium with a pair of stapediocarotid foramina (***Pseudoginglymostoma***) or separate carotid and stapedial foramina (***Ginglymostoma***). Adductor mandibulae muscles of jaws with three divisions (***Ginglymostoma***). Preorbitalis muscles extending onto posterodorsal surface of cranium. No anterodorsal palpebral depressor, rostromandibular, rostronuchal or ethmonuchal muscles. Valvular intestine of ring type with 15 to 24 turns. Development ovoviviparous as far as is known (***Ginglymostoma*** and ***Nebrius***). Size small to large with adults between 53 and at least 304 cm, while young are born between 27 and 79 cm (***Ginglymostoma*** and ***Nebrius***). Colour pattern plain or with a few dark spots in young, no saddles, reticulations or white spots.

Distribution: These are common, small to large, nocturnal, inshore bottom sharks with a circumglobal distribution in subtropical and tropical continental and insular waters. ***Ginglymostoma*** currently occurs in the eastern Pacific and tropical Atlantic, ***Nebrius*** has a wide range in continental waters of the Indo-West Pacific, while ***Pseudoginglymostoma*** has a restricted distribution in the western Indian Ocean off East Africa. They do not occur off oceanic islands far from land and have not penetrated the Central Pacific to the Hawaiian Island chain.

Habitat: Nurse sharks occur in inshore waters in depths from the intertidal down to at least 70 m. They occur on coral and rocky reefs, in sandy areas, in reef lagoons, mangrove keys, and at the surf zone, usually close inshore and sometimes in water deep enough only to cover them.

Biology: Members of the genera ***Nebrius*** and ***Ginglymostoma*** are social animals that occur in small groups while resting on the bottom; they often lie atop one another in a pile.

Development is ovoviviparous in ***Ginglymostoma***, with young that are nourished primarily by yolk while in the uterus; litters of 20 to 30 young have been reported. ***Nebrius*** is ovoviviparous and practices uterine cannibalism, with a form of oophagy in which the developing young apparent eat large, cased, unfertilized eggs; litters are smaller, up to four. The reproductive mode of ***Pseudoginglymostoma*** is uncertain; one female laid eggs with stout egg-cases in captivity (unfertilized), suggesting that it is oviparous.

These sharks cruise and clamber on the bottom with their mouths and barbels close to the substrate while searching for food; when they contact a food item with their barbels, they quickly reverse and use their short, small mouths and large mouth cavities as a bellows to suck in their prey. The presence of small, active reef fishes in the stomachs of large, seemingly clumsy nurse and tawny nurse sharks suggest that they may stalk and suddenly suck in such items, or merely suck them in when the prey fishes are torpid and lying on the bottom at night. Food items include a variety of bottom and reef organisms, bony fishes, crabs, shrimp, lobsters, and other crustaceans, squid, octopi, and other molluscs, corals, sea urchins and sea squirts.

Interest to Fisheries and Human Impact: The larger species of nurse sharks are or were formerly common in shallow marine waters and are often caught in local inshore fisheries. They are utilized for human consumption, for liver oil, and for their thick and exceptionally tough hides, which make extremely good leather. ***Ginglymostoma*** and ***Nebrius*** are very tough and hardy sharks that can survive over a decade in captivity and are often kept in large public aquaria and oceanaria, while young ***Ginglymostoma*** figure importantly in the aquarium trade. ***Pseudoginglymostoma*** is seldom kept in captivity but is also very hardy and is more suitable for smaller aquaria. ***Nebrius*** and especially ***Ginglymostoma*** should be treated with respect, as they will occasionally bite and clamp on to a human tormentor when provoked; their vice-like jaws may need to be pried lose from a victim. ***Ginglymostoma cirratum*** has bitten people without provocation, but more often will bite and otherwise defend itself when harassed by divers. The small prey, small mouths and small teeth of these sharks suggest that occasional incidents are agonistic or defensive and not predatory. ***Ginglymostoma*** and ***Nebrius*** are popular subjects of ecotouristic dive tours.

Local Names: Nurse sharks, Tubarões de leite (Mozambique).

Remarks: This family is recognized following the works of Compagno (1973, 1982, 1984, 1988) and Applegate (1974), which revived the Ginglymostomatidae and other orectoloboid family-group taxa of Gill (1862b). The genus ***Nebrius*** was sometimes considered a synonym or subgenus of ***Ginglymostoma*** (Agassiz, 1838; Dumeril, 1853, 1865; Günther, 1870; Fowler, 1941), or ***Ginglymostoma*** was synonymized with ***Nebrius*** (Gray, 1851), ***Nebrius*** is recognized as a separate genus from ***Ginglymostoma*** following Garman (1913), Whitley (1940), Bigelow and Schroeder (1948), Garrick and Schultz (1963), Compagno (1973, 1984, 1988), Applegate (1974), Bass, D'Aubrey and Kistnasamy (1975c), and Dingerkus (1986).

Nebrius and ***Ginglymostoma*** are usually distinguished by structural tooth characters. According to Bigelow and Schroeder (1948), ***Ginglymostoma*** has teeth with the "central cusp" largest and with several series functional, while ***Nebrius*** has teeth with "all cusps equal" (cusps as large as cusplets) and with only one or two series functional. However, ***Nebrius*** material examined by the writer varied considerably in cusp size, but in no instance were the cusps as small as the cusplets (cusps were smallest in young sharks, largest in adults). The number of functional tooth series was 2 or 3 in ***Nebrius*** specimens but overlapped ***Ginglymostoma cirratum*** with 3 or 4. Hence the arrangement and definition of these genera are revised (Compagno, 1984, and unpublished work), and the two are readily distinguished otherwise by tooth arrangement, external morphology, and anatomical characters (see diagnostic features of the genera).

Compagno (1984) provisionally placed ***Ginglymostoma brevicaudatum*** in the same genus as ***G. cirratum***, but noted that the former is strongly divergent morphologically from ***G. cirratum***, which is closer to ***Nebrius ferrugineus***, and differs from the other two species in having orthodont tooth structure, much smaller cusplets, larger cusps and narrower crowns on its teeth, smaller barbels, more posterior first dorsal-fin origin, equal-sized dorsal fins, a shorter caudal fin, as well as other external and cranial differences. Compagno (1984) suggested that ***G. brevicaudatum*** was generically distinct from ***Ginglymostoma*** proper, and, following a suggestion by D. Ward (pers. comm.), might be referable to the fossil tooth genus ***Eostegostoma*** Herman and Crochard, 1977.

Eostegostoma was proposed by Herman and Crochard (1977: 133) for ***Ginglymostoma angustum*** Nolf and Taverne 1977, based on fossil teeth from the Eocene of Belgium. These authors considered ***Eostegostoma*** an early stegostomatid (hence the name), but Cappetta (1987), who recognized ***Eostegostoma*** as a genus, suggested that it was closer to ***Brachaelurus*** and fell in the family Brachaeluridae instead of Stegostomatidae. Compagno (1988) suggested that ***Eostegostoma*** was more ***Stegostoma***-like than ***G. brevicaudatum***, and that the latter requires its own genus. Dingerkus (1986) erected a new genus, ***Pseudoginglymostoma***, for ***G. brevicaudatum***, which was recognized by Compagno (1988, 1999) and which is adopted here. Whatever the relationships of ***Eostegostoma*** it apparently is not congeneric with ***Pseudoginglymostoma***.

Dingerkus (1986) presented a hand-fitted cladogram of the orectoloboids, and included the genera herein placed in the Ginglymostomatidae in the family Rhincodontidae along with ***Rhincodon*** and ***Stegostoma***. In Dingerkus' analysis his genus ***Pseudoginglymostoma*** was considered the sister taxon of the other members of his Rhincodontidae, which formed two pairs of sisters, ***Nebrius*** with ***Ginglymostoma*** and ***Rhincodon*** with ***Stegostoma***. Compagno (1988) independently produced a similar hand-fitted cladogram with two variants, placing "***G. brevicaudatum***" (= ***Pseudoginglymostoma***) as the sister of the 'advanced' orectoloboids (***Stegostoma*** the sister of the group ***Rhincodon*** plus the sister pair ***Ginglymostoma*** and ***Nebrius***), or, less probably with ***Pseudoginglymostoma*** as the sister of ***Stegostoma*** alone, with these taxa the sister of ***Rhincodon*** plus ***Ginglymostoma*** and ***Nebrius***.

Further work on the morphology of ***Pseudoginglymostoma***, including its orolabial structures, neurocranium and pectoral-fin skeleton, confirms its distinctiveness, and suggests that Dingerkus (1986) and Compagno (1988) were correct in placing it as the sister taxon of the advanced orectoloboids. Pending a detailed study of the morphology of the genus, ***Pseudoginglymostoma*** is retained in the Ginglymostomatidae, which may make the family paraphyletic. It may be necessary in the future to place ***Pseudoginglymostoma*** in its own family as an alternative to lumping all of the advanced and highly divergent orectoloboids in the Rhincodontidae as per Dingerkus (1986), but as a stopgap ***Pseudoginglymostoma*** is placed in a subfamily of its own within Ginglymostomatidae, defined as follows:

> Pseudoginglymostomatinae: Eyes very small and 0.8 to 1.0% of total length. Nasal barbels very short, stubby, not very tapered, less than 1% of total length, and not reaching mouth. Lower lip not trilobate and without orolabial grooves. Tooth rows 24 to 27/22 to 27. Teeth not compressed, tooth crown feet very narrow, cusps large, cusplets very small and one or two on each side; teeth with moderately broad basal ledges. Teeth orthodont and with a central pulp cavity. Pectoral fins broadly rounded and not falcate in adults; pectoral fins semiplesodic and with radials reaching only 55% into fin web, radial segments four. First dorsal-fin origin over or slightly behind pelvic-fin midbases. Second dorsal fin about as large as first dorsal fin. Anal fin posterior margin ends in front of lower caudal-fin origin. Caudal fin short with dorsal caudal-fin margin less than 25% of total length (adults). Total vertebral count 135 to 143, monospondylous precaudal count 35 to 37, diplospondylous caudal count 49 to 54 and 36 to 39% of total count. Jaws broadly arcuate. Adults small, less than 1 m long.
>
> Ginglymostomatinae: Eyes small but usually over 1% of total length. Nasal barbels moderately elongated, tapered, slender and over 1% of total length, reaching past mouth. Lower lip trilobate and divided by shallow orolabial grooves connecting mouth with lower labial furrows. Tooth rows 29 to 42/26 to 34. Teeth moderately to greatly compressed, tooth crown feet broad, cusps moderately tall to very short, cusplets moderately large and three or more on each side, basal ledges moderately broad to very broad. Teeth osteodont, with pulp cavity filled by osteodentine. Pectoral fins semifalcate or falcate in adults, fins plesodic and with radials reaching about 80% into fin web, radial segments seven to eleven in longest radials. First dorsal-fin origin about over or slightly behind pelvic-fin origins. Second dorsal fin distinctly smaller than first dorsal fin. Anal free rear tip and posterior margin extending behind level of lower

caudal-fin origin. Caudal fin elongate with dorsal caudal-fin margin over 25% of total length in adults. Total vertebral count 168 to 195, monospondylous precaudal count 48 to 57, diplospondylous caudal count 73 to 96 and 43 to 50% of total count. Adults large, 230 cm or longer.

Literature: Müller and Henle (1838d); Dumeril (1865); Günther (1870); Regan (1908a); Garman (1913); Fowler (1941, 1967a); Whitley (1940); Bigelow and Schroeder (1948); Stead (1963); Compagno (1973, 1984, 1988); Applegate (1974); Dingerkus (1986); Michael (1993); Last and Stevens (1994).

Key to Genera:

1a. Nasal barbels greatly reduced, not reaching mouth; lower lip not trilobate, no shallow orolabial grooves connecting edge of lip with lower labial furrows; second dorsal and anal fins about as large as first dorsal fin; caudal fin short, less than 20% of total length (Pseudoginglymostomatinae) (Fig. 157a and b). . ***Pseudoginglymostoma***

1b. Nasal barbels elongated, reaching mouth; lower lip trilobate, with shallow orolabial grooves connecting edge of lip with lower labial furrows; second dorsal and anal fins much smaller than first dorsal fin; caudal fin longer, over 25% of total length (Ginglymostomatinae) (Fig. 158a and b). . . . → ***2***

2a. Eyes and gill openings dorsolateral on head; teeth not compressed on sides of jaw, not imbricated; pectoral, dorsal and anal fins apically rounded, pectoral fins broad and not falcate or semifalcate (Fig. 158b) . . . ***Ginglymostoma***

2b. Eyes and gill openings lateral on head; teeth more or less compressed on sides of jaws, forming imbricated series; pectoral, dorsal and anal fins apically angular, pectoral fins narrow and falcate (Fig. 159). . . . . ***Nebrius***

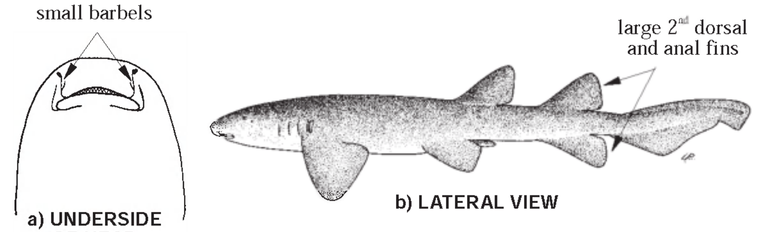


Fig. 157 ***Pseudoginglymostoma brevicaudatum***

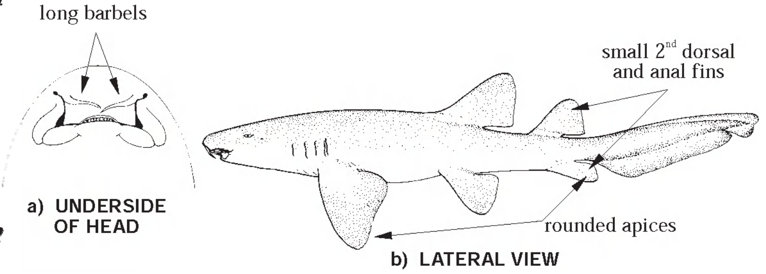


Fig. 158 ***Ginglymostoma cirratum***

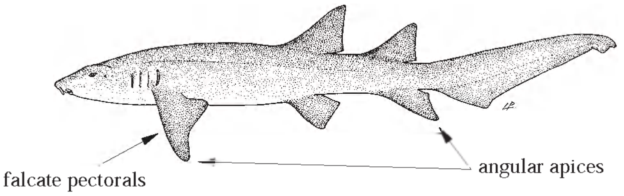


Fig. 159 ***Nebrius ferrugineus***

Ginglymostoma Müller and Henle, 1837

Genus: ***Ginglymostoma*** Müller and Henle, 1837a, *Ber. K. preuss. Akad. wiss. Berlin*, 2: 113; Müller and Henle, 1837b, *Arch. Naturg.*, 3: 396; Müller and Henle, 1838a, *Mag. Nat. Hist., new ser.*, 2: 35; Müller and Henle, 1838b, *L'Institut*, 6: 64 (no species mentioned); Müller and Henle, 1838d, *Syst. Beschr. Plagiost.*, pt. 1: 22 (two species, ***G. concolor*** and ***G. cirratum***, but no type allocation); Müller and Henle, 1838, *in* Bonaparte, 1838, *Nuov. Ann. Sci. Nat., Bologna*, ser. 1, 2: 212 (one species mentioned, "***Ginglymostoma cirrosum***, Mull. et Henle").

Type Species: ***Squalus cirratus*** Gmelin, 1788, by subsequent designation of Jordan and Gilbert, 1883, *Bull. U.S. Natl. Mus.*, 16: 18, equals ***S. cirratus*** Bonnaterre, 1788. Gill (1862b, *Ann. Lyceum Nat. Hist. New York*, 7[32]: 406) designated "***Ginglymostoma concolor***" (Müller and Henle, 1838 = ***Nebrius concolor*** Rüppell, 1837), but this would make ***Ginglymostoma*** and ***Nebrius*** synonyms. Bonaparte's restriction of ***Ginglymostoma*** to "***G. cirrosum***" (a synonym of to ***S. cirratus***) and Jordan and Gilbert's (1883) designation are followed here. See also Bigelow and Schroeder (1948, *Mem. Sears Fnd. Mar. Res.*, (1), 1: 180), who cited Hay's (1902, *U.S. Geolog. Surv. Bull.*, 179: 310) subsequent type designation of ***S. cirratus***, and Eschmeyer (1998, *Cat. Fish.*: CD-ROM).

Number or Recognized Species: 1.

Synonyms: Genus ***Ginglimostoma*** Agassiz, 1838: 85. Error or emendation of ***Ginglymostoma***. Genus ***Gynglimostoma*** Dumeril, 1859: 261. Probable error for ***Ginglymostoma***. Genus ***Gingylostoma*** Springer, 1938: 13. Apparent error for ***Ginglymostoma***.

Diagnostic Features: Head in dorsal or ventral view broadly arcuate in young, narrower and U-shaped in adults. Snout bluntly wedge-shaped in lateral view, short and with mouth width about 2.3 to 2.6 times preoral length. Eyes small but usually over 1% of total length, positioned dorsolateral on head and with strong subocular ridges below them. Eyes with ventral edges just above level of dorsal ends of gill slits. Gill openings dorsolaterally situated on head and not or hardly visible from below but just reaching horizontal head rim in dorsal view. Nostrils nearly terminal on snout. Nasal barbels moderately elongated, tapered, slender and over 1% of total length, reaching past mouth. Lower lip trilobate and divided by shallow orolabial grooves connecting mouth with lower labial furrows. Distance between lower labial furrows about 1.5 times their length. Tooth rows 30 to 42/28 to 34, functional tooth series at least 7 to 9/8 to 12. Teeth moderately compressed, not imbricated but in alternate overlap pattern, functional series not separated from replacement series by toothless space. Tooth crown feet broad, cusps moderately tall, cusplets moderately large and 2 to 6 on each side, basal ledges moderately broad. Teeth osteodont, with pulp cavity filled by osteodentine. Body semifusiform. Lateral trunk denticles broad and rhomboid in adults, with three strong parallel ridges and a very short, blunt cusp. Pectoral fins broad and rounded-angular in young and semifalcate in large specimens, apices rounded. Pectoral-fin origins slightly behind to slightly in front of third gill slits. Pectoral fins plesodic and with radials reaching about 80% into fin web, radial segments 7 or 8 in longest radials. Pelvic fins rounded in young, possibly subangular in adults. Dorsal fins apically rounded. First dorsal-fin origin about over, slightly in front, or slightly behind pelvic-fin origins. Second dorsal fin distinctly smaller than first dorsal fin. Anal fin distinctly smaller than second dorsal fin, apically rounded. Anal-fin origin about opposite, slightly behind, or slightly in front of midbase of second dorsal-fin, with apex about under anal-fin base and posterior margin extending behind level of lower caudal-fin origin. Caudal fin long with dorsal caudal-fin margin over 25% of total length (adults). Caudal fin narrow and shallow with dorsal caudal-fin margin 3.2 to 3.6 times caudal-fin depth; no ventral caudal-fin lobe in young but a weak one in adults; preventral caudal-fin margin much shorter than postventral margin and 43 to 67% of it; terminal lobe short and 15 to 19% of dorsal caudal-fin margin. Total vertebral count 168 to 175, monospondylous precaudal count 48 to 50, diplospondylous caudal count 73 to 83 and 43 to 48% of total count. Jaws broadly arcuate. Intestinal valve count 16 to 17. Development ovoviviparous with young nourished on yolk sac only, litter size 21 to 30. Adults 230 cm long or larger, size at birth 27 to 30 cm. **Colour:** yellowish to grey-brown above and light whitish brown below, young with small dark, light-ringed ocellar spots and obscure dorsal saddle markings, adults and subadults without spots or saddles.

Remarks: Scope of this genus is modified from Compagno (1973, 1984), and Applegate (1974), and follows Dingerkus (1986) in recognizing a single living species, ***Ginglymostoma cirratum***. ***Ginglymostoma brevicaudatum*** is placed in the genus ***Pseudoginglymostoma*** (see below). There are numerous fossil species of ***Ginglymostoma*** (Cappetta, 1987).

Ginglymostoma cirratum (Bonnaterre, 1788)

Fig. 160

Squalus cirratus Bonnaterre, 1788, *Tabl. Encyclop. Method. Trois Reg. Nat., Ichthyol.*, Paris: 7. Lectotype: Museum National d'Histoire Naturelle, Paris, MNHN-A.7654, 458 mm immature female, "Les mers de la Amerique." From unpublished addendum to Bertin (1939b, *Bull. Mus. Nat. Hist. Nat.*, 2e ser., 12(6): 51-98) by M.L. Bauchot (pers. comm.), also Eschmeyer (1998, *Cat. Fish.*: CD-ROM). Separately described as ***Squalus cirratus*** Gmelin, *in* Linnaeus and Gmelin, 1788, *Syst. Nat.*, ed. 13, Pisces 1(3): 1492. Types?

Synonyms: ***Squalus punctulatus*** Lacépède, 1800: 119, pl. 4, fig. 3. Type locality: "Guiane". No types known according to Eschmeyer (1998: CD-ROM). ***Squalus cirrhatus*** Bloch and Schneider, 1801: 128. Based on ***S. cirratus*** Gmelin, *in* Linnaeus and Gmelin, 1788, possibly an emended or erroneous spelling. Also ***Ginglymostoma cirrhatum*** Jordan, 1905: 533. ***Squalus punctatus*** Bloch and Schneider, 1801: 134. Based on the "Gata" of Parra, 1787: 86, pl. 34, fig. 2, from Cuba. No types known according to Eschmeyer (1998: CD-ROM). ***Scyllium cirrhosum*** Griffith and Smith, *in* Cuvier, Griffith and Smith, 1834: 10, pl. 30. Variant spelling? ***Ginglymostoma cirrosum*** "Müller and Henle", *in* Bonaparte, 1838: 213. Variant spelling. ***Squalus argus*** Bancroft, 1832: 82. Holotype possibly in British Museum (Natural History) according to Eschmeyer (1998: CD-ROM), who indicates that this species was not characterized in the original account, but was described in an accompanying account by Bennett (1832: 86-91). Type locality: West Indies. ***Ginglymostoma fulvum*** Poey, 1858: 342; also Poey, 1860, pl. 19, figs. 15-16. Holotype: 839 mm female, Cuba. Paepke and Schmidt (1988: 162) list Institut für Spezielle Zoologie und Zoologisches Museum, Berlin, ZMB-5508, 965 mm TL specimen, as a possible syntype. ***Ginglymostoma caboverdianus*** Capello, 1867: 167. Cape Verde. Three syntypes according to Eschmeyer (1998: CD-ROM), but status of these types otherwise uncertain. ***Ginglymostoma cirrotum*** Gudger, 1914: 176. Erroneous spelling?

Other Combinations: ***Nebrius cirratum*** (Bonnaterre, 1788), ***Scyllium cirratum*** (Bonnaterre, 1788).

FAO Names: En - Nurse shark; **Fr** - Requin nourrice; **Sp** - Gata nodriza.

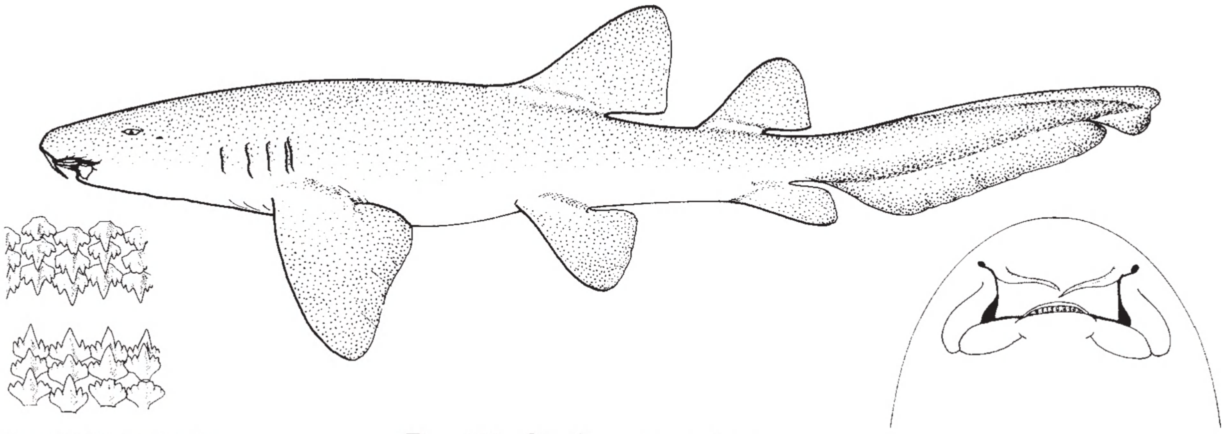
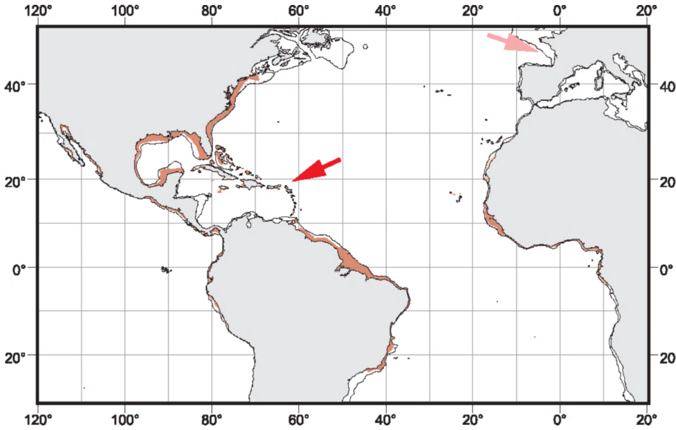


Fig. 160 *Ginglymostoma cirratum*

Field Marks: Moderately long barbels, nasoral grooves present but no circumnarial grooves; eyes dorsolateral, mouth well in front of eyes, spiracles minute; precaudal tail shorter than head and body; two spineless, broadly rounded, dorsal fins and an anal fin, first dorsal fin much larger than second dorsal and anal fins, caudal fin moderately long, over one-fourth of total length; colour yellow-brown to grey-brown, young with small dark, light-ringed ocellar spots and obscure dorsal saddle markings, adults and subadults without spots or saddles.

Diagnostic Features: See genus ***Ginglymostoma*** above.

Distribution: Western Atlantic: Rhode Island to southern Brazil, including United States (exceptionally Rhode Island and North Carolina, South Georgia and Florida and Gulf coast from Florida to Texas), Mexico (Gulf of Mexico and Caribbean coasts), Bermuda, Bahamas, Turks and Caicos Islands, Cuba, Puerto Rico, Haiti, the Lesser Antilles, Belize, Jamaica, Barbados, Trinidad, French Guiana, Guyana, Panama, and Brazil (south to Rio de Janeiro). Eastern Atlantic: Cape Verde Islands, Senegal, Cameroon to Gabon, and rarely north to Gulf of Gascony, France. Eastern Pacific: Mexico (Baja California Sur, Gulf of California) south to Costa Rica, Panama, Ecuador, and Peru. The known distribution of the nurse shark suggests at least three geographically isolated populations (eastern Pacific, western Atlantic and eastern Atlantic), but their differentiation, if any, has yet to be studied.



Habitat: This is an inshore bottom shark of the continental and insular shelves in tropical and subtropical waters, often occurring at depths of 1 m or less in the intertidal, but down to at least 12 m and off Brazil between 40 and 130 m. The nurse shark is often found on rocky and coral reefs, in channels between mangrove keys and on sand flats.

Biology: This is a large nocturnal and facultatively social shark that is proverbially sluggish during the daytime but strong-swimming and active at night; it rests on sandy bottom or in caves and crevices in rocks and coral reefs in shallow water during the day, often in schools or aggregates of three to three dozen individuals that are close to, or even piled on one another while resting. Swimming speed was measured at 31 to 78 cm/sec for a 250 cm captive individual (Hussain, 1991). In addition to swimming near the bottom or well off it, the nurse shark can clamber on the bottom using its flexible, muscular pectoral fins as limbs. Preliminary studies suggest that the nurse shark shows a strong preference for certain day-resting sites, and repeatedly homes back to the same caves and crevices after a night's activity. Nurse sharks fitted with conventional and sonic tags show little if any local movement, but adults have a larger range than young (Carrier, 1990). This suggests that groups of these animals are site-localized and vulnerable to local extirpation from overexploitation. This shark has been historically common or abundant in some areas where it occurs, particularly in the tropical western North Atlantic and off Tropical West Africa.

Courtship and copulatory behaviour has been observed in captivity (Klimley, 1980) and studied in detail in the wild (Carrier, Pratt and Martin, 1994), and is apparently rather complex. In captivity a pair or sometimes a triplet of adults engage in synchronized parallel swimming, with the male abreast or slightly behind and below the female, but with sides nearly touching. A pair may rest on the bottom on their bellies in parallel after bouts of parallel swimming. While parallel-swimming, the male may grab one of the female's pectoral fins with his mouth, which in turn may induce the female to pivot 90° and roll on her back on the bottom. The male then nudges the female into a position parallel to him, swims on top of the female in parallel, inserts a single clasper in her vent, and then rolls on his back to lie motionless besides the inverted female with clasper still inserted. Carrier, Pratt and Martin divided nurse shark mating into five stages based on field observations of free-ranging individuals in a mating area in the Dry Tortugas, Florida: *Precoupling*, in which a male or group of males approached a female that was resting or swimming, in the latter case with parallel or tandem swimming, and with males approaching alongside and slightly behind the female with heads close to her pectoral fins. *Coupling*, in which the male grabs the female's pectoral fin, sometimes with two males grabbing both pectoral fins and with other males circling in close proximity. *Positioning*, in which the male, or two males, roll the female onto her back, and with the male rolling and aligning his tail and pelvic fins prior to copulation. *Insertion and copulation*, in which the male copulates with the female, inserting his right clasper if holding her right pectoral, and his left clasper if holding her left pectoral, and thrusts against the female who remains quiescent. *Postcopulation*, in which the male removes his claspers, releases the female's pectoral, and either the two depart or lie on the bottom in parallel with ventral surfaces down. Over half the copulatory bouts involved more than one male, with a few insertions and copulations involving two or more males.

Reproduction is ovoviviparous, with intrauterine development of young being sustained primarily by the large supply of yolk in their yolk-sacs. Young are common in late spring and summer in waters off Florida, when females give birth. Numbers of intrauterine eggs or young are 20 to 30 in a litter. The gestation period is about five to six months and it reproduces every other year. Nursery areas are in shallow turtle-grass beds and on shallow coral reefs. Nurse sharks are slow-growing, with free-ranging tagged juveniles (average about 126 cm long) growing at about 13 cm per year. Males may be 10 to 15 years old at maturity and females 15 to 20 years old (Carrier, 1990; Carrier and Luer, 1990).

The nurse shark feeds heavily on bottom invertebrates such as spiny lobsters, shrimps, crabs, sea urchins, squid, octopi, marine snails and bivalves, and also fish including herring (Clupeidae), sea catfish (Ariidae), mullet (Mugilidae), parrotfish (Scaridae), surgeonfish (Acanthuridae), puffers (Tetraodontidae), and stingrays (Dasyatidae). Algae is occasionally found in its stomach and may be sucked in along with prey animals. Its small mouth and large, bellows-like pharynx allow it to suck in food items at high speed. This powerful suction feeding mechanism and its nocturnal activity pattern may allow the nurse shark to take small, active prey like bony fishes that are resting at night but would be too active and manoeuvrable for this big, lumbering shark to capture in the daytime. When dealing with big, heavy-shelled conchs the nurse shark flips them over and extracts the snail from its shell, presumably by grabbing its body with its teeth and by suction. It will dig under coral detritus and in sand with its head to root out prey.

Young nurse sharks have been observed resting with their snouts pointed upward and their bodies supported off the bottom on their pectoral fins; this has been interpreted as possibly providing a false shelter for crabs and small fishes that the shark then ambushes and eats. In captivity the nurse shark, when stimulated by food in the form of cut fish, will cruise in circles close to the bottom searching for the food, with its barbels touching or nearly touching the bottom; when it contacts a chunk of food, it may overshoot it but then quickly backs up and rapidly sucks it in. It may even work over vertical surfaces with its barbels.

Size: Maximum said to be 430 cm long but most adults are under 3 m long and the largest reliably reported were 280 to 304 cm. Newborn young are about 27 to 30 cm. Males mature at about 210 cm and adult males reach at least 257 cm; females are immature at 225 to 235 cm and mature mostly at about 230 to 240 cm (though one adult female 152 cm long has been reported) and reach over 259 cm.

Interest to Fisheries and Human Impact: This shark is commonly captured in local artisanal fisheries in some areas where it occurs, particularly the tropical western Atlantic. It was, however, rare in a localized broad-spectrum fishery out of Guaymas, Mexico (examined by the writer in 1974). It has been prized for its extremely tough, thick, armour-like hide, which makes an exceptionally good leather, but is also used fresh and salted for human consumption, as well as for liver oil and fish meal. The stratoconidia (earstones) of this shark and other species are said to be used as a diuretic by local fishermen in southern Brazil. It is easily captured with line gear, gill nets, fixed bottom nets and bottom trawls, and spears. It can be readily captured on sportsfishing tackle, but is generally regarded as being too sluggish to be much of a game fish (unlike the tawny nurse shark in Australia). Divers have sometimes speared nurse sharks, which is inane 'sport' because of its senselessness. The sharks are often sitting ducks for spearfishing divers on the bottom, and the modest speed of these sharks even when active make them no great challenge to hit. However, the toughness of these sharks may make them difficult to subdue underwater, and a diver that spears one may receive a well-deserved bite. The nurse shark was regarded as a pest by fishermen in the Lesser Antilles because it rifled fish traps for food.

The nurse shark is generally regarded as harmless to people, because of its sluggishness during the day and relatively small teeth, and is a popular subject for ecotouristic divers, with dive sites to view this shark mostly in the Bahamas but also off Belize, Turks and Caicos, and Florida. In the Caribbean and off Florida people frequently come in contact with it underwater, and it mostly will not respond defensively when approached and usually swims away when disturbed. There have been a small number of nonfatal, unprovoked incidents of nurse sharks biting swimmers and divers. Nonfeeding aggression, possibly related to courtship, defensive threat, or a defensive response to physical contact is possible as the motivation for such encounters. The small prey taken by these sharks and lack of mammalian meat in their diet suggests that predation on people is most improbable. In one unusual and somewhat amusing (but not to the diver) unprovoked incident a large nurse shark grabbed a diver's chest with its teeth, then appeared to hold onto his body with its pectoral fins; the encounter suggests displaced courtship, but unfortunately the sex of the shark was not recorded. More commonly people attempt to ride, spear, grab or otherwise harass this shark, or accidentally step on one while wading, and get bitten as a result. Juveniles are thought to be more prone to turn and bite than adults, which often swim away. Although its teeth are small, the jaws and associated muscles of the nurse shark are powerful and vice-like; in some instances nurse sharks have bitten people and held on, and had to be pried loose with a tool. Hence one should treat these sharks with due respect and enjoy their presence underwater without harassing them.

Nurse sharks are very hardy and capable of surviving a wide range of temperatures and dissolved oxygen levels in captivity. They grow to adult size when obtained as young and kept in aquaria of sufficient size, and will even give birth in captivity. Specimens have been kept for 24 to 25 years. The young make interesting pets and can be trained to feed at the surface. These sharks have often been used for experimental behavioural and physiological research in captivity, for which they are excellent subjects because of their hardiness and ability to learn. These sharks are ideal for public display in aquaria and are important for the aquarium trade. They are currently kept in numerous aquaria in Brazil, Europe, Mexico, the United States, and probably elsewhere.

The conservation status of the nurse shark needs to be assessed throughout its range, but particularly off West Africa, parts of the tropical western Atlantic and in the eastern Pacific where intensive inshore fisheries are being pursued and the distribution and abundance of these sharks is sketchily known. They are regarded as particularly vulnerable to overexploitation because of their slow growth, low reproductive rate, inshore habitat, apparent site-specificity, their presence in areas with intense inshore fisheries, and very little catch data available. The USA was the only country reporting nurse shark catches (214 t in 1995) to FAO over the vast range of this shark, and this was only reported during the last decade. Apart from their vulnerability to inshore fisheries, these sharks have been increasingly captured for private and public aquaria, and may have declined in some areas as a result of exploitation. Carrier (1996) and Carrier and Pratt (1998) suggested that public entry should be banned during the late spring and summer at one nurse shark breeding site in the Dry Tortugas National Park, Florida Keys, to avoid disturbing the mating of the sharks in shallow water. These sharks are a major asset to ecotourism in the Caribbean, and probably generate far more revenue there as live sharks viewed by divers than as fisheries products.

Local Names: Nurse shark, Sand shark, Gata (Mexico, West Indies), Gata atlantica, Cacao lixa (Brazil).

Literature: Gray (1851); Dumeril (1853, 1865); Günther (1870); Garman (1913); Fowler (1936, 1967a); Beebe and Tee-Van (1941a, b); Bigelow and Schroeder (1948); Cadenat (1950, 1957); Orces (1952); Springer (1960, 1963, 1973); Randall (1961, 1963, 1967, 1968, 1996); Garrick and Schultz (1963); Limbaugh (1963); Clark (1963); Clark and von Schmidt (1965); Kato, Springer and Wagner (1967); Sadowsky (1967); Böhlke and Chaplin (1968); Klimley (1974, 1980); Applegate et al. (1979); Cadenat and Blache (1981); Castro (1983); Compagno (1984, 1988); Neto, Bezerra, and Gadig (1989); Springer (1990); Carrier (1990); Carrier and Luer (1990); Michael (1993); Carrier, Pratt and Martin (1994); Bonfil (1997); Moore (1997); Carrier and Pratt (1998); Hoese and Moore (1998); McEachran and Fechhelm (1998); Castro, Woodley and Brudek (1999).

Nebrius Rüppell, 1837

Genus: ***Nebrius*** Rüppell, 1837, *Neue Wirbel. Fauna Abyssinien gehör., Fische Rothen Meeres*, (1835-1838): 62.

Type Species: ***Nebrius concolor*** Rüppell, 1837, by monotypy.

Number of Recognized Species: 1.

Synonyms: Genus ***Nebrodes*** Garman, 1913: 56. Replacement name for ***Nebrius*** Rüppell, 1837, thought by Garman to be previously occupied by ***Nebria*** Latrielle, 1802 (Insecta) and ***Nebris*** Cuvier and Valenciennes, 1830 (Osteichthyes), and hence taking the same type species, ***Nebrius concolor*** Rüppell, 1837. Unjustified replacement, as ***Nebria*** and ***Nebris*** are not senior homonyms of ***Nebrius***.

Diagnostic Features: Head in dorsal and ventral view narrow and more or less U-shaped at all stages. Snout wedge-shaped in lateral view, moderately elongated, with preoral length about 63% of mouth width. Eyes small but usually over 1% of total length, situated laterally on head and with no subocular ridges below them but with strong supraocular ridges above them; eyes with ventral edges below level of dorsal ends of gill slits. Gill openings laterally situated on horizontal head rim and prominently visible from above and below. Nostrils distinctly ventral on snout. Nasal barbels moderately elongated, tapered, slender, over 1% of total length, and reaching past mouth. Lower lip trilobate and divided by shallow orolabial grooves connecting mouth with lower labial furrows. Distance between lower labial furrows about 2.1 times their length. Tooth rows 29 to 33/26 to 28, functional series 2 to 4/2 to 4. Teeth greatly compressed, with imbricate overlap pattern, and functional series separated from replacement series by narrow toothless space. Tooth crown feet broad, cusps small, three or more moderately large cusplets on each side, and greatly widened basal ledges. Teeth osteodont and with pulp cavity filled by osteodentine. Lateral trunk denticles more or less rounded-rhomboid in adults, with four or five incomplete weak radial ridges and a very short, blunt cusp. Pectoral fins narrow and falcate at all stages, apically angular. Pectoral-fin origins about opposite or slightly anterior to fourth gill slits. Pectoral fins plesodic and with radials reaching about 80% into fin web, radial segments 10 or 11 in longest radials. Pelvic fins angular. Dorsal fins apically angular. First dorsal-fin origin about over or slightly ahead of pelvic-fin origins. Second dorsal fin distinctly smaller than first dorsal fin. Anal fin as large or slightly larger than second dorsal fin, apically angular. Anal-fin origin varying from slightly in front of origin of second dorsal fin to about opposite its midbase, apex behind rear tip of second dorsal fin, posterior margin extends behind level of lower caudal-fin origin. Caudal fin elongate with dorsal caudal-fin margin over 25% of total length (adults); caudal fin narrow and shallow with depth 28 to 31% of dorsal caudal-fin margin; a short and weak ventral caudal-fin lobe usually present at all stages; preventral margin much shorter than postventral margin and 36 to 45% of it; terminal lobe very short and 10 to 15% of dorsal caudal-fin margin. Total vertebral count 189 to 195, monospondylous precaudal count 55 to 57, diplospondylous count 92 to 96 and 47 to 50% of total count. Jaws narrowly arcuate. Intestinal valve count 23 to 24. Development ovoviviparous but with yolk sac reabsorbed and uterine cannibalism in the form of oophagy present, litter size possibly1 to 4. Adults 230 cm long or longer, size at birth at least 60 cm and possibly 78 cm. Background colour tan, reddish or yellowish to dark grey-brown above and light whitish brown below, no spots or other markings as far as is known; lower eyelid strikingly light in colour in young.

Remarks: Scope of this genus follows Applegate (1974), Bass, D'Aubrey and Kistnasamy (1975c), Compagno (1984), and Dingerkus (1986), in recognizing a single living species. There are also several fossil species of ***Nebrius*** (Cappetta, 1987).

Compagno (1984) included ***Nebrius concolor*** and its synonyms in the synonymy of ***N. ferrugineus***. This was accepted by some subsequent researchers including Last and Stevens (1994) though Dingerkus (1986) recognized ***N. concolor*** as the only valid species in this genus. Translation of Lesson's (1830) short and unillustrated description of his ***Scyllium ferrugineum*** suggests that this synonymy is correct, and that Lesson was the first scientific discoverer of the Indo-Pacific tawny nurse shark. There are only two other orectoloboids known from Waigiu, one of which Lesson described as ***Scyllium malaianum*** (= ***Hemiscyllium freycineti***), and the other is ***Eucrossorhinus dasypogon***. Lesson described ***S. ferrugineum*** from a single specimen of "roussette" (French term for scyliorhinid catsharks and catshark-like orectoloboids) that was rusty-fawn without markings above, rosy white below, and had a white eye (the conjunctiva and upper and lower eyelids of the tawny nurse shark are conspicuously white, though the iris is black), had a conical short head, anterior mouth and nostrils, long barbels, large rounded labial folds at mouth, triangular teeth (exact shape not stated), body tapering from the head, a large, triangular first dorsal fin slightly behind midlength of body, smaller triangular second dorsal, large elevated broad caudal fin, lobate pectoral fin, quadrilateral pelvic fins (with claspers), a lobate sharp-apiced anal fin, and was relatively large (137 cm [54 in] if tail length is exclusive of body length). These characters taken in combination fit the tawny nurse shark and eliminate other Indo-Australian orectoloboids including Hemiscylliidae, Parascylliidae, Stegostomatidae, Orectolobidae and Rhincodontidae. Although Lesson's description is not as specific and detailed as Rüppell's (1837) account and illustration of ***Nebrius concolor*** from the Red Sea, it is adequate to validate the earliest name for the tawny nurse shark as ***Scyllium ferrugineum***.

Nebrius ferrugineus and ***N. concolor*** were often retained as separate species and sometimes placed in different genera as ***Ginglymostoma ferrugineum*** and ***Nebrius concolor***. Compagno (1984) synonymized the two species and suggested that the dentitional differences used to separate them (Garman, 1913; Fowler, 1941) may be due to growth changes in a single species (ontogenic heterodonty). The supposed differences were more compressed, more low-cusped teeth in ***N. concolor*** and less compressed, more high-cusped teeth in ***N. ferrugineus***. At least in the material of ***Nebrius*** examined by the writer from the Gulf of Thailand, Philippines, and elsewhere, larger specimens over 2 m long have teeth of the ***N. ferrugineus*** type, while specimens about a metre long or less have teeth of the ***N. concolor*** type. Teeth of a specimen 1.8 m long pictured by Bass, D'Aubrey and Kistnasamy (1975c) are roughly intermediate. Growth changes apparently include increase in size of cusps relative to cusplets, shortening and broadening of the labial flange (basal ledge), and thickening and broadening of the teeth relative to their height.

Nebrius ferrugineus (Lesson, 1830)

Fig. 161

Scyllium ferrugineum Lesson, 1830, *Voy. aut. monde corv. La Coquille*, 2(1): 95. Holotype: Specimen with body 101.5 cm (3 ft 4 in) and tail 35.5 cm (14 in) mentioned, possibly not saved. Type locality, Port Praslin, New Ireland, and Baie d'Offack, Waigiou (Waigeu), New Guinea.

Synonyms: ***Nebrius concolor*** Rüppell, 1837: 62, pl. 17, fig. 2. Lectotype: Naturmuseums Senckenberg, Frankfurt, SMF-3583, 85 cm TL stuffed specimen, Massaua, Red Sea. ***Ginglymostoma rueppelli*** Bleeker, 1852: 91. Apparently an unnecessary replacement name for ***Nebrius concolor*** Rüppell, 1837, as latter is listed as a synonym. Holotype: Specimen mentioned by Bleeker is a male 1.5 m (730 lines) TL, probably from Singapore. Holotype listed as Rikjsmuseum van Natuurlijke Histoire, Leiden, RMNH 7400, by Eschmeyer (1998: CD-ROM). ***Ginglymostoma muelleri*** Günther, 1870: 408. Apparently based on ***Ginglymostoma concolor*** Müller and Henle, 1838d: 22, pl. 6, thought by Günther to be distinct from ***Nebrius concolor*** Rüppell, 1837. Syntypes: Two stuffed specimens mentioned by Müller and Henle, in the Institut für Spezielle Zoologie und Zoologisches Museum, der Humboldt Universität, Berlin, but possibly not extant, India. No types mentioned by Eschmeyer (1998: CD-ROM). ***Scymnus porosus*** Hemprich and Ehrenberg, *in* Klunzinger, 1871: 670 (name only, in synonymy of ***Ginglymostoma muelleri***). Also Hemprich and Ehrenberg, 1899: 8, pl. 6, fig. 3, Red Sea; possibly no type material, see Paepke and Schmidt (1988: 162). ***Nebrodes macrurus*** Garman, 1913: 58, pl. 8, figs 7-10. Holotype: Museum of Comparative Zoology, Harvard, MCZ-820-S, 80 cm (31.5 in) TL immature male, Port Louis Harbor, Mauritius, according to Hartel and Dingerkus (1997: xxxvii-xxxviii). ***Nebrodes concolor ogilbyi*** Whitley, 1934: 183, fig. 1. Holotype: Queensland Museum I.1216, 955 mm female, Darnley Island, Queensland, Australia. Type status confirmed by Eschmeyer (1998: CD-ROM). ***Nebrius doldi*** Smith, 1953a: 512, fig. 30A; Smith, 1953b: 8, pls. Types: Drawing by M.M. Smith based on photographs of a 2.9 m (9.5 ft) female? specimen from south of Beira, Mozambique, apparently no type material.

Other Combinations: ***Ginglymostoma ferrugineum*** (Lesson, 1830), ***Ginglymostoma concolor*** (Rüppell, 1837).

FAO Names: En - Tawny nurse shark; **Fr** - Requin nourrice fauve; **Sp** - Gata nodriza atezada.

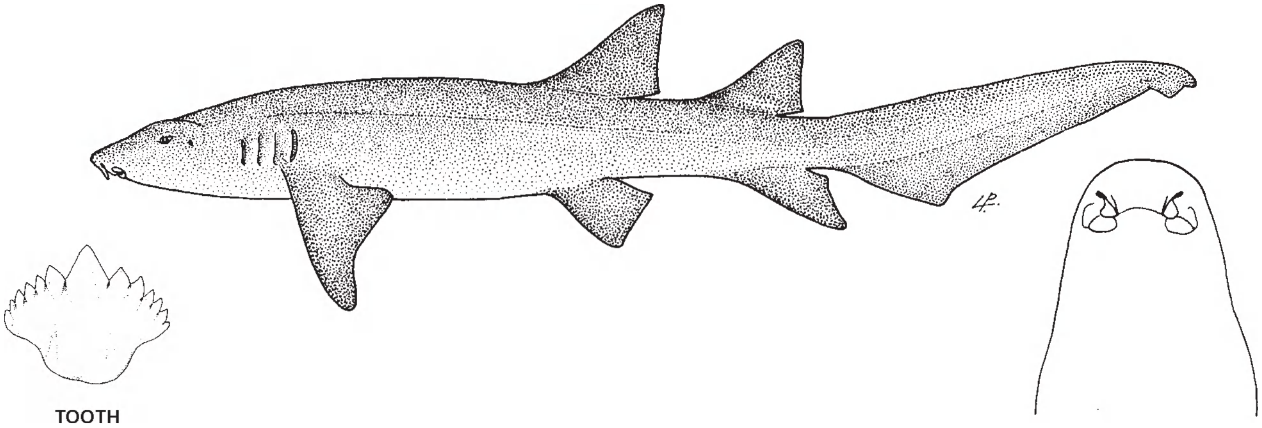
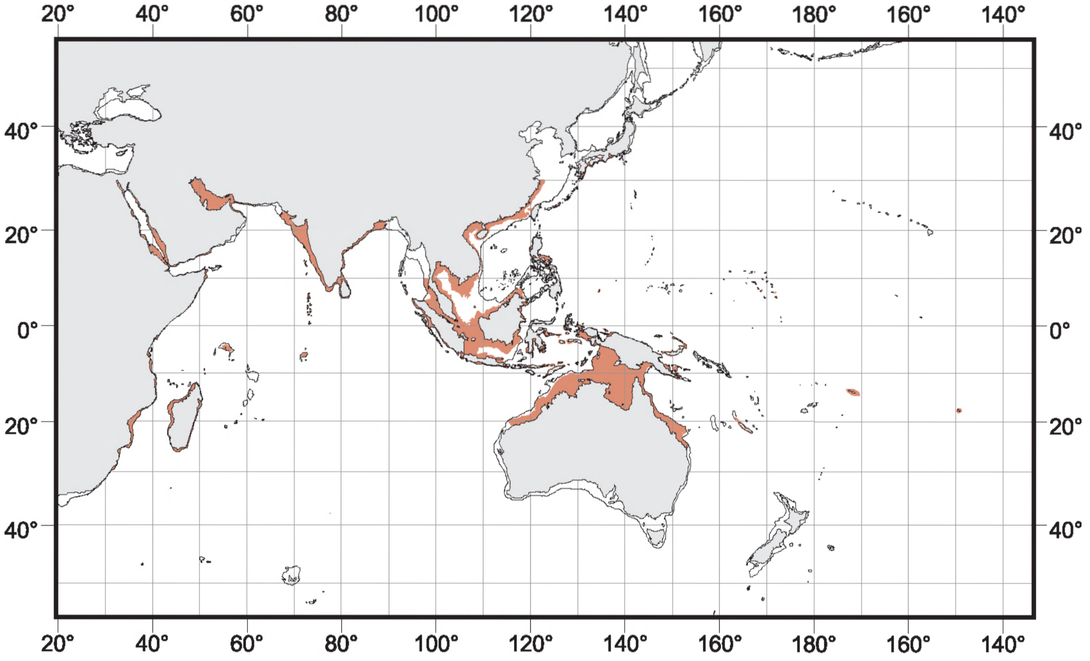


Fig. 161 ***Nebrius ferrugineus***

Field Marks: Moderately long barbels, nasoral grooves present but no circumnarial grooves, mouth well in front of eyes, eyes and gill openings lateral, spiracles minute, precaudal tail shorter than head and body, two spineless, angular dorsal fins and an anal fin, first dorsal fin much larger than second dorsal and anal fins, first dorsal-fin base over pelvic-fin bases, pectoral fins falcate, caudal fin moderately long, over one-fourth of total length. **Colour:** colour brown, from tan to rufous or yellowish to dark grey-brown according to habitat, and slowly changeable by the individual.

Diagnostic Features: See genus ***Nebrius*** above.

Distribution: Wide-ranging in the Indo-West and Central Pacific: South Africa (KwaZulu-Natal), Mozambique, Mauritius, Seychelles, Chagos Archipelago and Madagascar to Red Sea, Maldives, Persian Gulf, India, Malaysia, Indonesia, Singapore, Thailand, Viet Nam, China, Taiwan (Province of China), Japan (Ryukyu Islands, southern Honshu), Philippines (Luzon), Papua New Guinea, Australia (Western Australia, Northern Territory, and Queensland), New Caledonia, New Ireland, Samoa, Palau, Marshall Islands, and Tahiti.



Habitat: A large, tropical inshore shark of the continental and insular shelves of the Indo-Pacific, often in the intertidal in water scarcely able to cover it and from the surf line down to a few metres depth, commonly at 5 to 30 m and ranging down to at least 70 m on coral reefs. It occurs on or near the bottom in lagoons, in channels, or along the outer edges of coral and rocky reefs, in areas with seagrass and sand on reefs, sandy areas near reefs and off sandy beaches. It prefers sheltered areas in crevices and caves on reefs but often occurs in more exposed areas in depressions or crevices. Young prefer crevices in shallow lagoons but adults are more wide-ranging.

Biology: The tawny nurse shark is primarily nocturnal, resting in the daytime in shelters but prowling slowly about around reefs at night, although some individuals may be active in the day. In Madagascar it is described as day and night-active, and in captivity they get quite active and vigorous when food is presented to them during the day. They are social, gregarious sharks when at rest and form resting aggregations of two to a half-dozen or more in shelters, and are often seen piled inertly across or on top of one another. When resting, they are extremely sluggish. This shark has a limited home range, and individuals often return to the same area every day after foraging.

Reproduction ovoviviparous (aplacental viviparous) with cannibal vivipary or uterine cannibalism in the form of oophagy. This shark has been described as an oviparous or post-oviparous shark that retains the egg-cases until they hatch and the young are born, but recent evidence indicates that this is incorrect. Pregnant females collected from Okinawa have had one or two foetuses per uterus, 297 to 595 mm (the latter near term), with the yolk sac reabsorbed and a greatly expanded stomach filled with yolky material in foetuses 338 and 595 mm long, and also had cased eggs in the uterus. Apparently this species practices oophagy on relatively large, cased nutritive eggs (unlike many lamnoids which have very small nutritive eggs), and is the first orectoloboid known to have uterine cannibalism. It is not known whether foetuses of this species eat other foetuses (adelphophagy) as with the sand tiger (***Carcharias taurus***). The presence of two foetuses 338 and 297 mm in the same uterus, with the smaller one slender and the larger bloated with yolk, suggests that competition between siblings for the relatively big eggs is likely and could even eliminate the less successful sibling. Adelphophagy is less likely although early stages need to be examined to eliminate it. Number of young per litter uncertain; at least four young per uterus has been suggested from cased eggs, but the size and enormous girth of the near-term Okinawan foetus and the two smaller foetuses in a litter suggests that litters are smaller, possibly one or two per uterus or even one per female, and that numbers of cased eggs in the uteri cannot be used to extrapolate litter sizes in this species. In captivity adult females lay cased eggs on the bottom, but these do not develop, and could be nutritive and unfertilized. Such free eggs may have been the basis of the suggestion that this species is oviparous. The tawny nurse shark breeds in July and August off Madagascar.

Food of this shark includes corals, crabs, lobsters and other crustaceans, octopi, squid and probably other cephalopods, sea urchins, and reef fish including surgeonfish (Acanthuridae), queenfish (Carangidae) and rabbitfish (Siganidae), and occasionally sea snakes. While foraging the tawny shark moves along the bottom and explores depressions, holes and crevices in reefs. When it detects prey it places its small mouth very close to the victim, and uses its large pharynx as a powerful suction pump to rapidly suck in reef organisms that may be out of reach of its teeth. A few large individuals dissected by the writer had quantities of small, active reef fishes in their stomachs, presumably sucked in by the sharks as the prey fishes lay inert in shelters or on the bottom at night. Individuals caught by fishermen may reverse this sucking action, and blast streams of water out of their mouths and into the faces of their captors; they are said to make a grunting sound between blasts. It is not known if spitting water is deliberate and defensive or if the sharks are actually aiming the water at the anglers. They also tend to spin when hooked on a line, making them difficult to handle and subdue.

The body form of the tawny nurse shark (littoral morphotype) is more fusiform and streamlined than other nurse sharks, with narrow-based, falcate, plesodic pectorals, pointed dorsal and anal fins with the anal-fin apex raked posterior to the free rear tip, a short ventral caudal-fin lobe, lateral eyes and gills, a narrow head, flat wedge-shaped snout, and compressed, semi-blade-like, imbricate teeth in discrete series. The tawny nurse shark superficially resembles certain other large, partly or mostly sympatric, active reef sharks including the sand tiger shark (***Carcharias taurus***), sicklefin lemon shark (***Negaprion acutidens***), and reef whitetip shark (***Triaenodon obesus***). Whether it is behaviourally divergent from other nurse sharks awaits a detailed comparative study of nurse shark behaviour. Its status as a game fish in Australia, unlike the nurse shark in the western Atlantic, suggests that it may be a more active swimmer when not resting on the bottom.

Size: Maximum about 314 to 320 cm, though most individuals are smaller; size at birth has been reported as about 40 cm (Fourmanoir and Laboute, 1976) but subsequent data from a pregnant female captured off Okinawa suggest that it may reach 60 cm or more at birth (Teshima et al. 1995), while a 79 cm female from Navotas market in Manila, Philippines, examined by the writer, has a somewhat bloated stomach full of yolk, suggesting that it was newborn or a term foetus; males are mature at about 250 cm and reach at least 301 cm; adult females are 230 to at least 290 cm.

Interest to Fisheries and Human Impact: Common or formerly common in areas where it occurs, and caught inshore by fishermen in Pakistan, India, Thailand, and Philippines, and probably widely captured elsewhere. It is utilized fresh and dried-salted for human food, its liver is rendered for oil and vitamins, its fins are used in the oriental sharkfin trade, and offal is processed into fishmeal. Its thick, armour-like hide is potentially valuable for leather. Off Queensland, Australia, it has been fished as a big-game shark, and large individuals are prized as powerful fighters by sports anglers. Apart from anglers who target this fish, it is apparently primarily caught only as an untargeted bycatch of fisheries in inshore waters in nets, on line gear, and in fish traps.

This has been described as a much more docile species than its close relative, ***Ginglymostoma cirratum***, and apparently tolerates close proximity of divers and usually allows humans to touch and play with it without biting. However, there are a few records of these sharks biting their tormentors, and clamping tightly onto them. Because of its size, strength, powerful jaws and small but sharp cutting teeth, the tawny shark should be treated with the respect due it. It is a favourite species for observation by ecotouristic divers within its enormous range, and dive sites where it is viewed are known from Thailand (Andaman Sea) and the Solomon Islands.

This is a tough, hardy shark that readily survives in captivity and makes an excellent and handsome display animal. It is kept in aquaria in Europe, Japan (Okinawa), Singapore, and the United States. In Singapore in 1996 the writer saw several large ***Nebrius*** about 2 m long being hand-fed by a SCUBA diver in a big oceanarium tank. The sharks piled on top of their benefactor and hid him from sight while eagerly scrambling to obtain food.

The conservation status of this shark is uncertain and urgently needs investigation despite its wide range. In some areas, including the Gulf of Thailand where it was commonly caught in the 1960s, it may have been depleted due to increasing fisheries activity and habitat degradation. Also, reef habitats have been extensively damaged or destroyed by dynamiting and poisoning in parts of its range, including Indonesia and Philippines, which probably have had an adverse effect on this species both directly and through decimation or elimination of its prey. Its docility and inshore habitat makes it particularly susceptible to a wide variety of fishing gear, to harassment and injuries by divers, and to reef destruction and pollution.

Local Names: Tawny shark, Spitting shark, Rusty shark, Rusty catshark, Sleepy shark, Madame X (Australia); Giant sleepy shark (South Africa); Roussette ferrugineuse (French); Yahiya (Madagascar); Endormi (Seychelles); Kalouyon (Guébéens); Koumoune (Waigiu); Be kal mora (Sinhalese); Ô-tenjikuzame (Japan).

Remarks: Several individuals from Okinawa and Honshu, Japan and at least one from Taiwan (Province of China) have been found with their second dorsals missing or rudimentary. It is not known why this occurs in these localities, but there are some interesting possibilities that might be investigated including teratogenic effects of chemical pollutants.

Literature: Lesson (1830); Rüppell (1837); Müller and Henle (1839); Gray (1851); Dumeril (1865); Günther (1870); Jordan and Seale (1906); Garman (1913); Whitley (1934, 1940); Fowler (1941); Misra (1947); Bigelow and Schroeder (1948); Fourmanoir (1961); Gohar and Mazhar (1964); Marshall (1965); Applegate (1974); Bass, D'Aubrey and Kistnasamy (1975c); Fourmanoir and Laboute (1976); Johnson (1978); Randall (1980); Yoshino et al. (1981); Uchida (1982); Compagno (1984, 1988); Nakaya and Shirai (1984); Bass (1986); Dingerkus (1986); Taniuchi and Yanagisawa (1987); Compagno, Ebert and Smale (1989); Anderson and Ahmed (1993); Michael (1993); Seret (1994); Last and Stevens (1994); Teshima et al. (1995, 1999).

Pseudoginglymostoma Dingerkus, 1986

Genus: ***Pseudoginglymostoma*** Dingerkus, 1986, *Proc. 2nd. Int. Conf. Indo-Pacific Fishes, Tokyo*: 240.

Type Species: ***Ginglymostoma brevicaudatum*** Günther, *in* Playfair and Günther, 1866, by original designation.

Number of Recognized Species: 1.

Synonyms: None.

Diagnostic Features: Head in dorsal or ventral view very broad and parabolic in adults. Snout bluntly rounded in lateral view, short and with preoral length about 34.5 to 41.6% of mouth width. Eyes very small and 0.8 to 1.0% of total length, situated dorsolateral on head and with strong subocular ridges below them; ventral edges of eyes just above level of dorsal ends of gill slits. Gill openings dorsolaterally situated on head and not visible from below, just reaching horizontal head rim from above. Nostrils nearly terminal on snout. Nasal barbels very short, stubby, not very tapered, less than 1% of total length, and not reaching mouth. Lower lip not trilobate and without orolabial grooves. Distance between lower labial furrows about 1.2 to 1.4 times their length. Tooth rows 24 to 27/22 to 27 (adults), functional series at least 3 to 4/4 to 5. Teeth not compressed and not imbricated, functional series not separated from replacement series by toothless space. Tooth crown feet very narrow, cusps large, cusplets very small and one or two on each side; teeth with moderately broad basal ledges. Teeth orthodont and with a central pulp cavity. Body cylindrical. Lateral trunk denticles teardrop-shaped and elongated in adults, with a low medial ridge, lateral ridges weak or absent, and with a fairly narrow pointed cusp. Pectoral fins broad and not falcate in adults, apically rounded. Pectoral-fin origins slightly in front of third gill slits. Pectoral fins semiplesodic and with radials reaching only 55% into fin web, radial segments four. Pelvic fins rounded in adults. Dorsal fins apically rounded. First dorsal-fin origin over or slightly behind pelvic-fin midbases. Second dorsal fin about as large as first dorsal fin. Anal fin about as large as first dorsal fin, with rounded apex. Anal-fin apex about under anal free rear tip, origin about opposite second dorsal-fin origin, posterior margin ends in front of lower caudal-fin origin. Caudal fin short with dorsal caudal-fin margin less than 25% of total length (adults); caudal fin broad and deep with depth 40 to 45% of dorsal caudal-fin margin; no ventral caudal-fin lobe in adults; preventral caudal-fin margin about as long as postventral margin and 80 to 100% of it; terminal caudal-fin lobe moderate and 22.2 to 26.3% of dorsal caudal-fin margin. Total vertebral count 135 to 143, monospondylous precaudal count 35 to 37, diplospondylous caudal count 49 to 54 and 36 to 39% of total count. Jaws broadly arcuate. Intestinal valve count 15. Mode of reproduction and litter size unknown. Adults 59 to 75 cm long, size at birth or hatching unknown but probably less than 30 cm. **Colour:** background colour dark brown above and slightly lighter below but noticeably dark on both surfaces; no spots or other markings in adults but colour of young unknown; lower and upper eyelids dark in adults.

Remarks: Scope of this genus follows Dingerkus (1986), with a single living species, ***Pseudoginglymostoma brevicaudatum***.

Pseudoginglymostoma brevicaudatum (Günther, 1866) **Fig. 162**

Ginglymostoma brevicaudatum Günther, *in* Playfair and Günther, 1866, *Fish. Zanzibar*, London: 141, pl. 21. Holotype: British Museum (Natural History), BMNH-1867.3.9.423, stuffed dried adolescent male about 590 mm TL, length in original account 640 mm, Zanzibar.

Synonyms: None.

Other Combinations: None.

FAO Names: En - Short-tail nurse shark; **Fr** - Requin-nourrice à queue courte; **Sp** - Gata nodriza rabicorta.

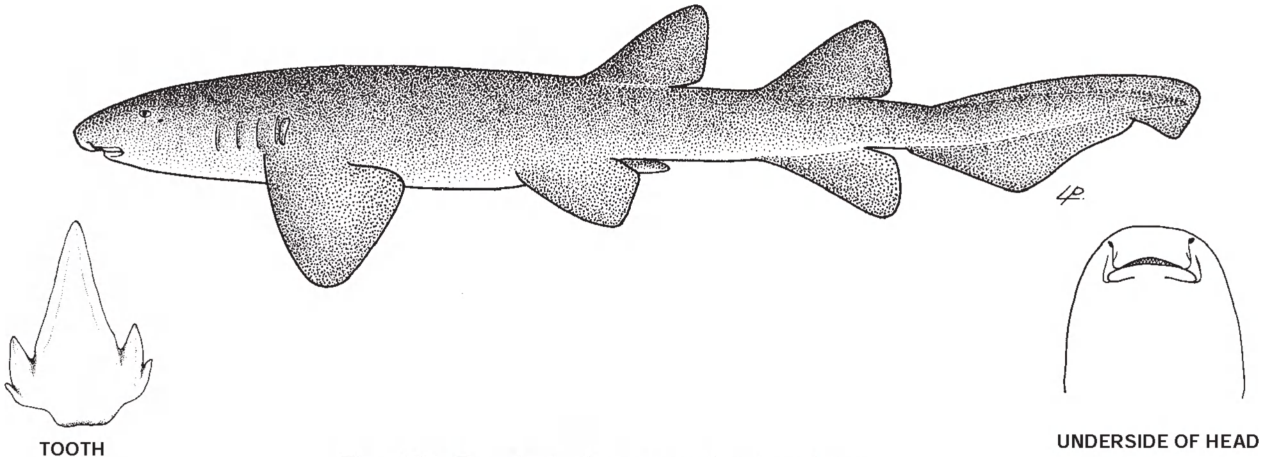
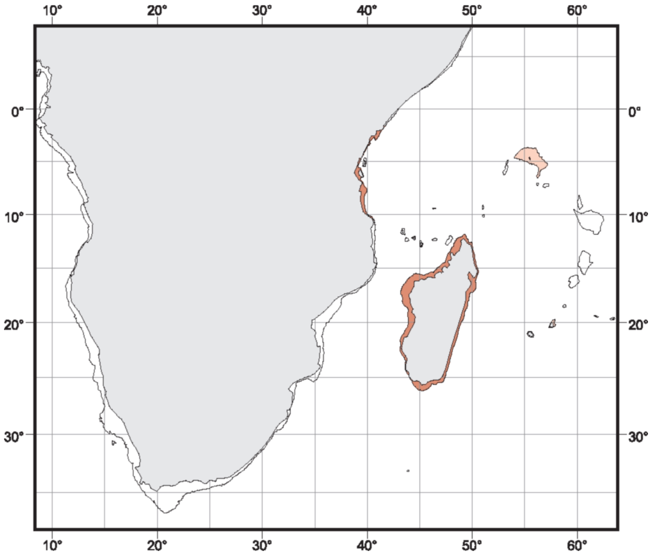


Fig. 162 ***Pseudoginglymostoma brevicaudatum***

Field Marks: Very short barbels, nasoral grooves present but no circumnarial grooves; eyes and gill openings dorsolateral, mouth well in front of eyes, spiracles minute, precaudal tail shorter than head and body, two spineless, broadly rounded, equal-sized dorsal fins and an equally large anal fin, caudal fin short, less than one-fourth of total length, colour dark brown, without spots or other markings.

Diagnostic Features: See genus ***Pseudoginglymostoma*** above.



Distribution: Confined to the western Indian Ocean off Tanzania, Kenya, Madagascar and possibly Mauritius and the Seychelles.

Habitat: This little-known inshore bottom shark occurs on the continental and insular shelves of East Africa and Madagascar, but details are lacking on its habitat except that it occurs on coral reefs. Depth data are not available.

Biology: The biology of the short-tail nurse shark, including breeding and feeding habits, is poorly known. An adult or near-adult female had large nidamental glands, suggesting that the species may be egg-laying but this needs confirmation (see below). It also is not known if this species is social and congregates in groups as with the larger nurse sharks. It is reported to survive for several hours out of water. Abundant off East Africa a few decades ago (Bass, D'Aubrey and Kistnasamy, 1975c), but its current status is uncertain.

A female short-tailed nurse shark has lived over 33 years and a male three years in captivity at the Artis Zoo, Amsterdam. These are under study by A. Dral, E. Bruins and P. Bor (pers. comm.), who are preparing a detailed account for publication. Both individuals are alive at the time of writing and the female has laid infertile eggs in strong egg cases two at a time for the past ten years. This suggests that the short-tailed nurse shark is oviparous but needs confirmation. These sharks mate in captivity but so far no eggs have been hatched as the pair eat their eggs. These sharks are slow-moving, nocturnally active, sit on the open bottom or hide in holes or crevices during the day, and will only move during the day when fed. They eat annelid worms, raw and cooked mussels, cut raw fish and shrimps; presumably the species eats small fishes, molluscs and crustaceans in the wild. The two sharks are non-aggressive in community tanks and the female has been kept with much larger nurse sharks (***Ginglymostoma cirratum***) without incident.

Size: Maximum at least 75 cm; two adult males examined were 59 to 75 cm while a live captive adult male (Artis Zoo, Amsterdam) is 65 cm long; a female examined was immature at 52 cm while another was adolescent at 56 cm and a third was adult or nearly so (with large oviducts and nidamental glands but without oviducal eggs or foetuses) at 53 cm. A captive adult female at the Artis Zoo is 70 cm long.

Interest to Fisheries and Human Impact: Interest to fisheries probably limited, apparently fished locally in artisanal fisheries and landed as a bycatch of other fisheries. The skin of this shark is exceptionally tough, as in other nurse sharks, and is possibly of use for leather. It is readily amenable to captivity and grows to a more reasonable maximum size for smaller aquaria than ***Nebrius ferrugineus*** or ***Ginglymostoma cirratum***, but it's status in the aquarium trade is uncertain. It apparently is seldom kept in public aquaria. The conservation status of this interesting and distinctive little shark is unknown but is of concern as it has a limited distribution in inshore tropical waters of East Africa and occurs in some areas that currently support heavy inshore fisheries. It could be adversely affected by overfishing and destruction of coral reefs.

Local Names: Nurse shark, Shorttail nurse shark, Papa isengezi or Sleepy shark (Zanzibar), Endormi (Seychelles).

Remarks: The writer examined the holotype in the British Museum (Natural History) and five other specimens in the collections of the J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa.

Literature: Günther *in* Playfair and Günther (1866); Günther (1870); Garman (1913); Fowler (1941, 1967a); Smith and Smith (1963); Bass, D'Aubrey and Kistnasamy (1975c); Compagno (1984, 1988); Dingerkus (1986); Bass (1986); Anton Dral, Eugene Bruins and Peter Bor (pers. comm.).

2.3.7 Family RHINCODONTIDAE

Family: Rhinodontes Müller and Henle, 1839, *Syst. Beschr. Plagiost.*, pt. 2: 77. Placed on the Official List of Family-Group Names in Zoology (Name no. 559) by the International Commission on Zoological Nomenclature, 1984, Opinion 1278, *Bull. Zool. Nomen.*, 41(4): 215 as the emended Family Rhincodontidae.

Type Genus: ***Rhincodon*** Smith, 1829.

Number of Recognized Genera: 1.

Synonyms: Subfamily Rhinodontini Bonaparte, 1846, v. 3 (no pagination); Tribe Rhineodontiana (Family Squalidae) Gray, 1851: 66. Family Rhineodontis "Müll. and Henle" Gray (1851: 66). Family Rhinodontoidei Bleeker, 1859: XII. Family Rhinodontoidae Owen, *in* Gill, 1862b: 397. Family Rhinodontidae Günther, 1870: 396. Family Rhineodontidae Jordan and Fowler, 1903: 626. Subfamily Rhinodontinae (Family Lamnidae) Goodrich *in* Lankester, 1909: 150. Family Rhincodontidae Garman, 1913: 12, 41. Type genus: ***Rhincodon*** Smith, 1829. Subfamily Rhineodontini (Family Orectolobidae) Berg, 1940: 380. Subfamily Rhincodontinae (Family Rhincodontidae) Fowler, 1947: 10. Family Rhiniodontidae Compagno, 1973: 28. Type genus: ***Rhiniodon*** Smith, 1828, emendation of Family Rhinodontes Müller and Henle, 1839, used by Compagno (1984: 209).

FAO Names: En - Whale sharks; **Fr** - Requins baleine; **Sp** - Tiburones ballena.

Diagnostic Features: Head very broad and greatly flattened, without lateral flaps of skin. Snout truncated. Eyes laterally situated on head and without subocular ridges below them. Eyes without movable upper eyelids or subocular pockets and ridges. Spiracles moderate-sized but much smaller than eyes, without raised external rims; spiracles behind but not below eyes. Gill slits very large, fifth gill slit well-separated from fourth and not overlapping it; internal gill slits with unique filter screens, consisting of transverse lamellae that cross each gill slit, with ramose processes on their inner surfaces that interconnect to form the filters. Nostrils with rudimentary barbels and no circumnarial folds and grooves. Nasoral grooves very short and shallow. Mouth very large, transverse and terminal on head. Lower lip not trilobate and without lateral orolabial grooves connecting edge of lip with medial ends of lower labial furrows, without a longitudinal symphysial groove on chin. Lower labial furrows ending far lateral to symphysis, not connected medially by a mental groove or groove and flap. Teeth not strongly differentiated in upper and lower jaws, with symphysial teeth not enlarged and fang-like. Tooth row count extremely high, in over 300 rows in either jaw of adults and subadults. Teeth with a strong medial cusp, no cusplets and no labial root lobes. Teeth osteodont with crown partially filled with a plug of osteodentine. Body cylindrical or moderately depressed, with prominent ridges on sides. Precaudal tail shorter than body. Caudal peduncle with strong lateral keels and an upper precaudal pit. Pectoral fins very large, relatively narrow and falcate. Pectoral fins plesodic and with fin radials strongly expanded into fin web. Pectoral propterygium small and fused to mesopterygium; pectoral-fin radial segments 3 to 10, and with longest distal segments about 0.8 times the length of longest proximal segments. Pelvic fins much smaller than first dorsal fin but subequal to second dorsal and anal fins, much smaller than pectoral fins and with anterior margins about 0.3 times the pectoral-fin anterior margins. Claspers without mesospurs, claws or dactyls. First dorsal fin much larger than second. First dorsal-fin origin well anterior to pelvic-fin origins and over abdomen behind pectoral-fin free rear tips, first dorsal-fin insertion over the pelvic-fin bases. Anal fin about as large as second dorsal, with broad base, angular apex, origin about opposite first third of second dorsal fin base, and insertion separated by a space somewhat greater than base length from lower caudal-fin origin. Caudal fin elongated and semicrescentic, strongly heterocercal with its upper lobe at a high angle above the body axis (lower in young than adults and subadults); dorsal caudal-fin margin less than a third as long as the entire shark. Caudal fin with a vestigial terminal lobe and subterminal notch but with a strong ventral lobe (longer in adults than young), preventral and postventral margins strongly differentiated and deeply notched. Vertebral centra with well-developed radii and prominent annuli connecting them. Total vertebral count 174, monospondylous precaudal count 42, diplospondylous precaudal count 40, diplospondylous caudal count 92, and precaudal count 82. Cranium very broad and greatly expanded laterally. Medial rostral cartilage rudimentary, reduced to a low nubbin. Nasal capsules greatly depressed, slightly fenestrated anteriorly, internarial septum low, broad and depressed. Orbits with enlarged fenestrae for preorbital canals, medial walls not fenestrated around the optic nerve foramina although foramen itself is very large. Supraorbital crests present on cranium and laterally expanded and pedicellate. Suborbital shelves very broad and not greatly reduced. Cranial roof with a continuous fenestra from the anterior fontanelle to the parietal fossa. Basal plate of cranium with pairs of separate carotid and stapedial foramina. Adductor mandibulae muscles of jaws with three divisions. Preorbitalis muscles extending onto posterodorsal surface of cranium. No anterodorsal palpebral depressor, rostromandibular, rostronuchal or ethmonuchal muscles. Valvular intestine of ring type with 69 to 74 turns. Development ovoviviparous. Size gigantic with adults 700 cm or longer, while young are born at about 55 to 64 cm. Colour pattern unique, consisting of small to large white or yellowish spots and vertical and horizontal stripes in the form of a checkerboard on a dark background.

Local Names: Whale sharks, Ching sha k'o, Jimbeizame-ka (Japan); Kitovye akuly (Russia).

Remarks: As recognized here the family Rhincodontidae includes only a single genus and species, the whale shark, ***Rhincodon typus***. The genus and species were first described as ***Rhiniodon typus*** by Smith (1828) in a Cape Town newspaper from a specimen stranded in Table Bay, South Africa. A separate family Rhinodontes was later proposed for it by Müller and Henle (1839) who used a variant spelling ***Rhinodon*** for the genus. There has been considerable variation in spelling of the generic name (***Rhinodon***, ***Rhineodon***, ***Rhincodon***, ***Rhiniodon***, ***Rhinecodon***, ***Rhinocodon***, ***Rineodon*** and ***Rhinchodon***) and by extension the family name of the whale shark (Rhinodontidae, Rhincodontidae, Rhineodontidae and Rhiniodontidae), and much usage of certain of the variants. Andrew Smith, the describer of the whale shark, and Johannes Müller and Friedrich Henle, the describers of a family for it, used several variants on the genus, which caused confusion for subsequent authors. Although the original ***Rhiniodon*** has priority, the variants ***Rhincodon*** and particularly ***Rhineodon*** and ***Rhinodon*** have had far more usage over the last two centuries.

Following Bigelow and Schroeder (1948) the variant ***Rhincodon*** has received considerable use, and proposals to stabilize it (Robins and Lea, 1975; Swift, 1977; Wheeler, 1982) were presented to the International Commission on Zoological Nomenclature. Brooke and Bass (1976) supported the earliest published spelling, ***Rhiniodon***, although noting that ***Rhiniodon*** Smith, 1828 was a possible misspelling that Andrew Smith had hand-corrected to ***Rineodon*** on a bound copy of his paper (Smith, 1828). ***Rineodon*** was also used by Müller and Henle (1838a), possibly on the advise of Andrew Smith, but later changed to ***Rhinodon*** (Müller and Henle, 1839). Hubbs, Compagno and Follett (1976) proposed that the earliest spelling, ***Rhiniodon*** should be preserved for the whale shark because of priority, more correct orthography than ***Rhincodon***, and because the use of ***Rhincodon*** has not been universal since Bigelow and Schroeder's work (and little-used prior to it compared to ***Rhinodon*** and particularly ***Rhineodon***). Compagno (1984) preferred to use the earliest spelling (***Rhiniodon*** and emended family name Rhiniodontidae) but while that work was in press the International Commission on Zoological Nomenclature (1984, Opinion 1278) stabilized ***Rhincodon*** and Rhincodontidae.

Dingerkus (1986) included the genera ***Pseudoginglymostoma***, ***Ginglymostoma***, ***Nebrius*** and ***Stegostoma*** in this family, but the original arrangement of ***Rhincodon*** alone in Rhincodontidae is followed here on the basis of the extremely derived morphology of the whale shark, uncertain relationships with other 'higher' orectoloboids, and pending further studies on orectoloboid phyletics.

Rhincodon Smith, 1829

Genus: ***Rhincodon*** Smith, 1829, *Zool. J.*, 4: 443. Placed on the Official List of Generic Names in Zoology (Name no. 2219, International Commission on Zoological Nomenclature, 1984, *Bull. Zool. Nomen.*, 41(4): 215). ***Rhincodon*** was used twice in the 1829 publication.

Type Species: ***Rhiniodon typus*** Smith, 1828, as interpreted by the International Commission on Zoological Nomenclature, 1984, Opinion 1278, *Bull. Zool. Nomen.*, 41(4): 215.

Number of Recognized Species: 1.

Synonyms: Genus ***Rhiniodon*** Smith, 1828: 2. Type species: ***Rhiniodon typus*** Smith, 1828, by monotypy and by use of the species name ***typus***. Placed on the Official Index of Rejected and Invalid Generic Names in Zoology (Name no. 2141) by the International Commission on Zoological Nomenclature (1984, Opinion 1278: 215). ***Rhiniodon*** was twice cited in the original description, but possibly was a typographical error or correction by the printer (Brooke and Bass, 1976: 5). Genus ***Rhinchodon*** Smith, 1829: 534 (index). Variant spelling. Genus ***Rineodon*** Müller and Henle, 1838a: 37. Also Swainson, 1838: 142. Variant spelling. Genus ***Rhineodon*** Müller and Henle, 1838c: 84. Variant spelling. Genus ***Rhinodon*** Müller and

Henle, 1839: 77. Variant spelling. Genus ***Rhiniodon*** Swainson, 1839: 317. Variant spelling. Genus ***Rhinecodon*** Agassiz, 1845: 55. Variant spelling. Genus ***Rhinodon*** Smith, 1849: pl. 26 and accompanying text, pages not numbered; Smith used ***Rhinodon*** in this extended account and illustration of the whale shark rather than his earlier ***Rhiniodon*** or ***Rhincodon***. Variant or emended spelling. Genus ***Micristodus*** Gill, 1865: 177. Type species: ***Micristodus punctatus*** Gill, 1865, by monotypy. Genus ***Rhinocodon*** International Commission on Zoological Nomenclature, 1984: 216). Attributed to Herald, 1961, but examination of the writer's copy indicated uniform usage of ***Rhincodon*** in the text (p. 22) and index (p. 302), suggesting that the variant spelling if correctly cited was a possible typographical error in a different edition of Herald's book.

Diagnostic Features: See family Rhincodontidae above.

Rhincodon typus (Smith, 1828)

Fig. 163

Rhiniodon typus Smith, 1828, *S. African Comm. Adv.*, 3(145): 2. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN 9855, 4 600 mm stuffed, mounted male specimen, Table Bay, South Africa. The specific name ***typus*** Smith, 1828 was placed on the Official List of Species Names in Zoology (Name no. 2901) by the International Commission on Zoological Nomenclature, 1984, Opinion 1278, *Bull. Zool. Nomen.*, 41(4): 215.

Synonyms: ***Rhincodon typus*** Smith, 1829: 443. ***Rhinodon typicus*** Müller and Henle, 1839: 77, pl. 35. Variant or emended spelling of ***Rhincodon typus***. This spelling was also used by Smith, 1849: pl. 26 and accompanying text, pages not numbered, in his extended description of the whale shark. ***Micristodus punctatus*** Gill, 1865: 177. Holotype: US National Museum of Natural History, USNM-27234, renumbered as USNM-232756, a pair of dried dental band halves, Gulf of California. Status of holotype from Howe and Springer (1993: 12) and by the writer's examination of the specimen. ***Rhinodon pentalineatus*** Kishinouye, 1901: 694, figs 1-2. Holotype: Specimen originally in private collection of T. Oseko, from Cape Inubo, Japan, whereabouts unknown according to Eschmeyer (1998: CD-ROM).

Other Combinations: ***Rhineodon typus*** (Smith, 1828), ***Rhineodon typicus*** (Müller and Henle, 1839).

FAO Names: **En** - Whale shark; **Fr** - Requin baleine; **Sp** - Tiburón ballena.

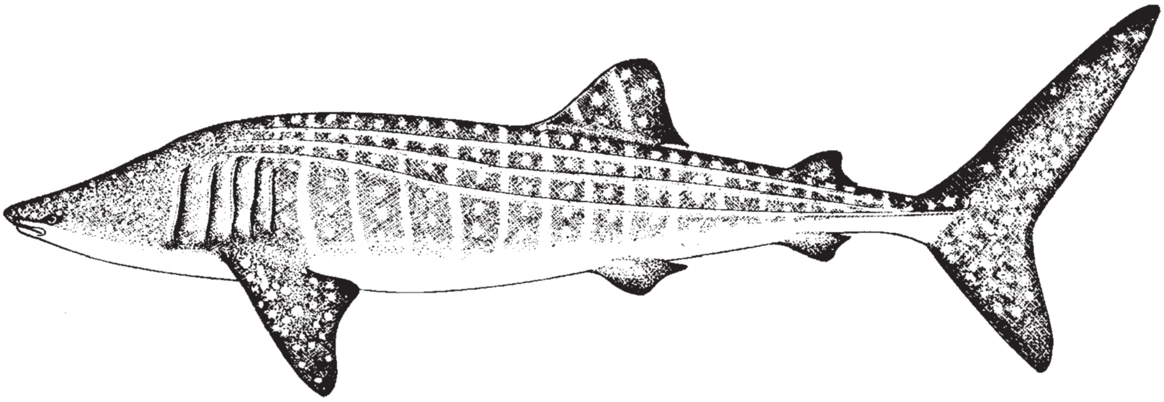


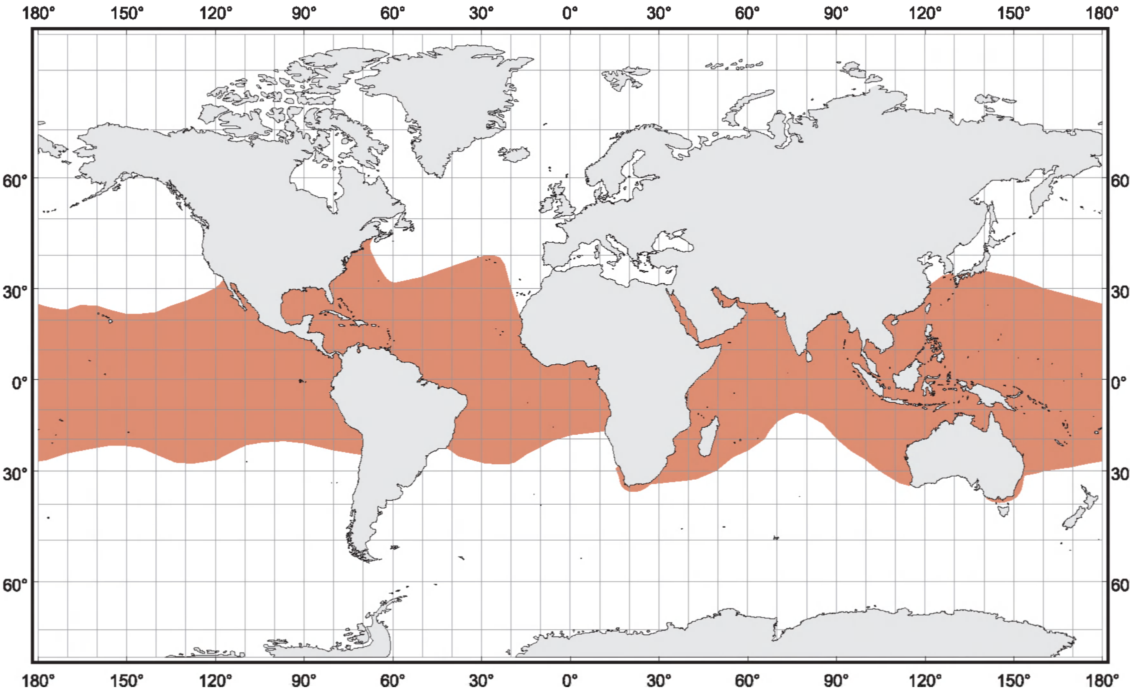
Fig. 163 ***Rhincodon typus***

LATERAL VIEW OF HEAD

Field Marks: An unmistakable huge shark, one of three large filter-feeding species (apart from devel rays), with a broad, flat head and truncated snout, immense transverse and virtually terminal mouth in front of eyes, minute, extremely numerous teeth, and unique filter screens on its internal gill slits; prominent ridges on sides of body with the lowermost one expanding into a prominent keel on each side of the caudal peduncle, a large first dorsal and small second dorsal and anal fin, lunate or semilunate caudal fin without a prominent subterminal notch. **Colour:** a unique checkerboard pattern of white or yellow spots, horizontal and vertical stripes on a grey, bluish, reddish or greenish brown dorsal surface, abruptly white or yellowish on the underside of the body.

Diagnostic Features: See family Rhincodontidae above.

Distribution: Circumglobal in all tropical and warm temperate seas, oceanic and coastal. Western Atlantic: Canada (south of Nova Scotia), United States (Gulf of Maine and New York south to North Carolina and Florida, and Gulf of Mexico coast from Florida to Texas), Mexico (Gulf of Mexico coast to Quintana Roo), Belize, Honduras, Panama, Colombia, Venezuela, and central Brazil, also Bermuda, Bahamas, Caribbean including Cuba and Haiti. Eastern Atlantic: Azores, Senegal, Mauritania, Cape Verde Islands, Côte d'Ivoire, Gulf of Guinea, Gabon, Angola, South Africa (Western Cape Province). Indo-West and Central Pacific: East coast of South Africa (Western Cape, Eastern Cape, KwaZulu-Natal), Mozambique, Madagascar, Seychelles, Kenya, Tanzania, Somalia, the Red Sea and Straits of Bab-al-Mandab (Eritrea, Sudan, Saudi Arabia), Yemen, Oman, Persian Gulf, the Maldives, Pakistan, India (both coasts), Sri Lanka, possibly Bangladesh, Malaysia (including Sabah, Borneo), Singapore, Thailand (including Gulf of Thailand), Viet Nam, China, Taiwan (Province of China), Japan (Southeastern Honshu, Okinawa, and Bonin Islands), Philippines, Indonesia (Kalimantan, Borneo; Java), New Guinea (Papua-New Guinea and Irian Jaya, Indonesia), Australia (Western Australia, Queensland, Northern Territory, with isolated records from New South Wales and Victoria), New Caledonia, Hawaiian Islands, Tuomotu Archipelago, Phoenix Islands. Eastern Pacific: United States (southern California), Mexico (Baja California and Gulf of California south to Acapulco, Oaxaca, and Chiapas), El Salvador, Nicaragua, Costa Rica, Panama, Ecuador, Peru, and northern Chile (including open ocean from west of Cabo San Lucas to the Galapagos Islands, and between Panama and the Hawaiian Islands).



Habitat: An epipelagic and neritic, oceanic and coastal, tropical and warm-temperate pelagic shark, often seen far offshore but regularly coming close inshore off beaches and coral reefs and sometimes entering lagoons of coral atolls. In the western Pacific it apparently prefers areas where the surface temperature is 21 to 25°C with cold water of 17°C or less upwelling into it, and salinity of 34.0 to 34.5 ppt. Recent satellite tagging (Eckert and Stewart, 1996) in the Gulf of California suggested that the sharks prefer water over 26°C and up to 34°C, although they were recorded in water masses at temperatures down to 10°C; the sharks tended to move out of parts of the Gulf of California where surface water cooled below 26°C with upwelling. These conditions may be optimal for production of plankton and small to moderate-sized nektonic organisms, all of which are prey of the whale shark. The whale shark is generally seen or otherwise encountered close to or at the surface in warm waters, although recent satellite tagging in the Caribbean Sea off Belize shows that the whale shark may dive to depths of 700 m and may transit in cold deep water down to 7.8°C (R. Graham, pers.comm.). Off Ningaloo Reef in Western Australia a sonic-tagged shark frequently dived during two 18 hr tracks and ranged from the surface to near the bottom at depths of 40 to 70 m (Stevens et al., 1997), with salinity at 34.9 to 35.2 ppt and temperatures of 26.8 to 27.5°C at the surface to 26.4 to 25.4°C at the bottom.

Strandings of whale sharks are common in some areas, including both coasts of South Africa, and it is suspected that off the west coast of South Africa whale sharks ride the warm Agulhas current during the summer into areas where upwelling occurs and plumes of cold bottom water hit the surface. It was thought that sharks may be stunned or even killed by sudden chilling and then wash up on the shore with no signs of disease or physical damage (Beckley et al., 1997). Tracking of whale sharks in water down to 10°C in the Gulf of California and their presence near patches of upwelling water down to 6°C (Eckert and Stewart, 1996) makes this simple explanation suspect however, and an explanation for the phenomenon of stranding off the Western Cape requires further research. Rough seas and sudden storms along the narrow continental shelves of KwaZulu-Natal, South Africa (which is subtropical and optimal for whale sharks) may contribute to strandings on the beaches there.

Biology: The whale shark is a facultatively social shark, and has been recorded as single individuals or in schools or aggregations of up to hundreds of sharks. In the Indian Ocean it is common around the Seychelles, Mauritius, Zanzibar, Kenya, Madagascar, Mozambique and northernmost KwaZulu-Natal. In the western Pacific it is common in the Kuroshio current in the fishing grounds for skipjack (Scombridae). It is reportedly abundant in the Gulf of California and from Cabo San Lucas to Acapulco in the eastern Pacific, and in the Gulf of Mexico and the Caribbean in the western Atlantic. Aerial spotting of whale sharks has been successfully attempted off Kenya, South Africa, and Western Australia, as well as whale shark surveys by boat in these same localities (Gifford, 1994; Wamukoya, Mirangi and Ottichilo, 1995; Beckley et al., 1997; Stevens et al. 1997; Colman, 1997), while whale shark observation records are collected routinely from dive operators in Western Australia (as with the various basking shark sighting programs in the United Kingdom). The US Shark Research Institute (http://www.sharks.org) runs an Internet-based program encouraging people who sight whale sharks to send in reports by eMail to their central database, which so far has received several hundred responses.

Whale sharks are highly migratory, with their movements probably timed with localized blooms of planktonic organisms and changes in temperatures of water masses. Several whale sharks have been tagged with radio satellite tags using the ARGOS system in the Gulf of California (Eckert and Stewart, 1996) over times of up to a year, with maximum speed recorded about 2.3 km/hr. Satellite tracking has revealed extensive movements, and tagged whale sharks have moved out of the Gulf of California along rugged bottom topography of the Clipperton Fracture Zone to the Revilligigedo and Clipperton Islands, with one shark travelling 1 723 km in about three months and another 3 708 km in five months. Satellite tagging suggested that whale sharks in the Gulf of California showed some segregation by size, with smaller sharks frequenting the northern Gulf and possibly absent from the southern part. Observation of whale sharks off Ningaloo Reef, Western Australia suggests that mostly adolescent males between 6 and 7.5 m length are seen there, with one (possibly mature) male measured live with a rope at 9.1 m; between 80 and 91% of the sharks seen in 1996 and 1997 were male (Stevens et al., 1997; Gunn et al. 1999). Some 53 individuals were 'body-printed' with scarring and colour patterns recorded, and 29 resighted from one to 14 times (Stevens et al. 1997) over at least two years. In South Africa SCUBA divers working under the auspices of the US Shark Research Institute tag whale sharks underwater using modified spearguns with detachable spearheads attached to giant spaghetti tags, and have resighted the tagged sharks later by approaching them closely and reading the tag numbers (Gifford, 1994); at least one of these sharks had been resighted off the Seychelles (ca 3 700 km). Satellite tagging has also been attempted on whale sharks off KwaZulu-Natal, South Africa, and off Ningaloo Marine Park, with tracks of limited range so far.

Whale sharks are often associated with schools of pelagic fish, especially scombrids. They apparently show curiosity in the presence of people and will approach divers and boats, possibly to examine them. The behaviour and sociobiology of the whale shark is sketchily known at present, but as with the basking and white sharks their detailed behaviour should be amenable to elucidation by divers and observers in boats using cinematography as well as telemetry. The most extensive close-in behavioural research to date has been at the famous whale shark viewing site at Ningaloo Reef (Ningaloo Marine Park), Australia (Stevens et al., 1997; Gunn et al., 1999), where sonic tracking and archival tagging showed that whale sharks made numerous dives during a 24 hour period, ranging from the surface to near the bottom and varying in speed from 0.1 to 1.8 m/sec. The sharks' dives appeared to be independent of hydrographic features and seemed to be associated with food search. Whale sharks showed an ability to accurately sense the bottom and swim very close to it without colliding. Some behaviour patterns observed in association with and in part in reaction to ecotouristic snorkel-divers at Ningaloo include *diving*, where sharks descended out of view of the divers; *porpoising*, a movement away from the surface, but not out of sight; *changes in speed*, where sharks go *slow* (snorkelers easily keep up with the sharks at 0 to 1 knots), *medium* (where divers strain to keep up at a speed of 1 to 2 knots), and *fast* (where sharks pull away from the divers at over 2 knots); degree of *mouth distension* (mouth closed to fully open on a six-point scale, possibly related to feeding); *banking*, in which the shark rolls and presents its dorsal surface towards the recorder; and *eye-rolling*, which was observed by divers next to the whale shark's head.

The mode of reproduction of the whale shark is apparently ovoviviparous, but it was long disputed and assumed to be oviparous by some authors. In 1953 a large eggcase, 30 cm long, 14 cm wide and 9 cm high containing a nearly full-term, 36 cm embryo whale shark was collected from the Gulf of Mexico, and the assumption was made that the species is oviparous (Baughman, 1955; Reid, 1957; Garrick, 1964; Bass, D'Aubrey and Kistnasamy, 1975c). However, the rarity of 'free-living' whale-shark eggs, the extreme thinness of its walls and lack of tendrils on the only known deposited eggcase, the considerable yolk and partially developed gill sieve in the embryo within it, and the presence of umbilical scars on larger freeliving specimens 55 cm long suggested an alternative explanation (Wolfson, 1983), that the Gulf of Mexico egg was aborted before term, and that the whale shark is normally ovoviviparous. This was recently confirmed by an adult female whale shark caught in Taiwan (Province of China) which had some 300 young (sex ratio of 237 young with about 1.0:1.1 male:female ratio) in her uteri (Joung et al., 1996). These young whale sharks were three size classes: embryos with yolk sacs in egg cases that were 42 to 52 cm long, embryos with yolk sacs in egg cases 52 to 58 cm long, and apparent term foetuses without egg cases and with reabsorbed yolk sacs between 58 and 64 cm long. The type of ovoviviparity practised by the whale shark is possibly a relatively simple sort very similar to that of the related nurse sharks (Ginglymostomatidae: ***Ginglymostoma***), with retention of the egg case *in utero* until the embryo hatches from it, and then is born. The three classes of young reported in the Taiwan (Province of China) female suggest that successive batches of eggs are retained in utero, with the oldest hatching and then being born. One additional adult female whale shark from Taiwan (Province of China) was recorded as having 16 egg cases in her uteri while another was reported as having 200 eggs in her ovary. Although many whale sharks have been caught in the Taiwan (Province of China) fishery, very few have been reported as obviously mature females over the last half of the twentieth century (Joung et al., 1996). The gestation period is not known, but Castro, Woodley and Brudek (1999) suggest that the whale shark may reproduce every other year as with the nurse shark (***Ginglymostoma cirratum***).

The smallest free-living whale sharks are 55 to 59 cm long, some of which have an umbilical scar. Such small whale sharks have been found off tropical West Africa in the East-Central Atlantic and near Central America in the eastern Pacific, near continental waters and in the open ocean far from land (Wolfson, 1983; Kukuyev, 1996), suggesting that young may be born in the ocean and that pupping grounds and possibly nursery areas exist there.

The whale shark is a versatile suction filter-feeder, and feeds on a wide variety of planktonic and nektonic organisms. Whale sharks are known to appear off coral reefs when these are producing blooms of planktonic organisms and the corals are spawning (Colman, 1997). Masses of small crustaceans (including copepods) are regularly reported as food, along with small and not so small fish such as sardines, anchovies, mackerel, and even small tunas and albacore as well as squid. Whale sharks may aggregate along with tuna in association with spawning of lanternfish (***Diaphus***, Myctophidae) in the

Coral Sea off Queensland; and off Christmas Island in the eastern Indian Ocean between Java and Western Australia in association with mass spawning of red crabs (***Geocarcoidea natalis***; Colman, 1997). Recent research (Heyman et. al, in press) indicates that large (ca. 25 individuals) and predictable groups of whale sharks gather around snapper (***Lutjanus cyanopterus*** and ***L. jocu***) spawning aggregations at Gladden Spit, in the barrier reef off Belize. Whale sharks feed at dusk and dawn on the released gametes of the snappers, during the full moon periods between April and June and show good site fidelity between one spawning period and the next.

The whale shark feeds at or close to the surface, and often assumes a vertical position with its mouth up above its body. Phytoplankton often occurs in the stomachs of whale sharks, but whether this is a major component of the diet of this shark is rather doubtful. Small whale sharks 3.2 to 5.2 m long have been observed feeding on copepods at the surface in the Gulf of California (Clark and Nelson, 1997); they aimed at patchy areas of dense concentrations of copepods (at least 13 species, mostly ***Acartia clausi***) and turned from side to side, lifted the dorsal surfaces of their heads partially out of the water with the upper jaw exposed, and opened and closed their mouths and gill openings at rates of 7 to 28 times per minute, apparently gulping in plankters. Turning movements increased with gulping rate, and, when sharks passed through copepod concentrations into clear water, they sharply turned and circled back to the concentrations to renew feeding. When not feeding the sharks dropped their heads below the surface with mouth slightly open, and stopped moving their mouths and gill openings and swam faster while apparently ram-ventilating their gills. Larger whale sharks 6 to 10 m were observed by Clark and Nelson to feed underwater with their heads not exposed, but with a similar gulping action of 16 to 20 times per minute. Clark and Nelson also noted that similar feeding behaviour is shown by whale sharks kept at the Okinawa Expo Aquarium, fed by ladle at the surface. Some air may be swallowed during feeding, but it is unknown if it is expelled or can function for assisting buoyancy as in the sand tiger sharks (***Carcharias taurus***).

The suction-filter mechanism of the whale shark is more versatile than the dynamic filter mechanism of the basking shark in the range of prey species that can be taken. The basking shark, with its huge scoop-like mouth, hydrodynamically 'clean' gill rakers, and huge gill slits, has little if any suction capacity and must depend for the most part on its relatively slow forward motion to carry animals into its mouth; this limits it to eating small planktonic crustaceans and other invertebrates trapped on mucus on its gill rakers. The whale shark is not dependent on forward motion to operate its filters, and can probably achieve relatively high intake velocities of water into its mouth, that enable it to readily ingest larger, active nektonic prey in addition to masses of planktonic crustaceans. A disadvantage of the suction plankton feeding of the whale shark over the dynamic method used by the basking shark is that the structures involved can filter a far smaller volume of water per unit time and hence are far less efficient in concentrating diffuse plankters. Hence the whale shark may be more dependent on higher concentrations of plankters than the basking shark to optimally utilize such food (such as reef blooms or copepod aggregations), but has the option of utilizing much larger nektonic organisms for prey that cannot be caught by the basking shark or are marginal for that species. Observations by Clark and Nelson (1996) suggest that the whale shark is capable of homing in on such concentrations and adjusts its activities to target them.

The predators of whale sharks are little-known apart from humans. A newborn specimen was found inside the stomach of a blue shark (***Prionace glauca***; Kukuyev, 1996), and other large pelagic and coastal carcharhinoid and lamnoid sharks may take young whale sharks also. Adult whale sharks, with their thick hides and great size, may have few natural predators, killer whalea, (***Orcinus***) and large white sharks being two possibilities; the giant extinct megatooth shark ***Carcharodon megalodon*** is another likely candidate. The chief predator of whale sharks is humanity.

Pauly (in press) used a von Bertalanffy growth curve partially based on data for the basking shark (***Cetorhinus maximus***) to give a tentative estimate of age and growth for this species. Using a conservative maximum length of 14 m he suggested that the whale shark may be especially long-lived, with a tentative longevity of about 100 years, "which strikes one as rather high, but may not be impossible" (Pauly, in press). His growth curve suggests that adult males at about 7 m would be about 20 years old. In contrast, Castro, Woodley and Brudek (1999) suggested that, based on captive growth of a term foetus in Taiwan (Province of China) from the adult female reported by Joung et al. (1996), as well as the few records of small whale sharks in the 1 to 3 m range, the whale shark may prove to be the fastest-growing shark. Long-term tagging and bodyprinting of free-ranging individuals with periodic remeasuring of registered individuals that return to viewing sites over several years (as per the methodology of Stevens et al., 1997), may clarify this seeming disparity, and the writer suspects that very fast initial growth (if also shown by free-living neonates) would slow down markedly as the sharks approach maturity.

A preliminary DNA analysis of cytochrome b genes from several whale shark skin samples from the Gulf of California, and a few from Philippines and South Africa, showed no variation (Eckhart and Stewart, 1996). Further studies are underway with other genes to determine if there are any genetic indications of differences within whale sharks from a given area or from distant areas.

Size: This is by far the world's largest fish-like vertebrate, with an uncertain maximum size. Old sight records as well as recent tagging studies and whale shark fishers' reports suggest a maximum length of 17 to 18 m or even 21.4 m. Specimens are uncommon above 12 m, and 30 specimens reported from South Africa by Beckley et al. (1997) were 4 to 11 m long. A length of 13.7 m is often given as the maximum size measured, 12.1 m the most recently accurately measured, while most reported in the literature are between 3 and 12 m long. The late Margaret M. Smith showed the writer a letter describing a beach-stranded specimen from Angola, with measurements suggesting it was about 15.9 m long.

Size at birth of the whale shark is between 55 and 64 cm, with freeliving individuals as small as 55 and term foetuses known at 58 to 64 cm. Males are immature at 299 cm or less and adolescent at 390 to 540 cm while adult males of 705 to 1 026 cm have been recorded. Females from 340 cm or less, to 760 cm, were immature, while a pregnant female was about 10.6 m long (Joung et al. 1996) and weighed 16 t; and another adult female may have been about 12 m long.

Pauly (in press) assumed a maximum length of 14 m and a weight of approximately 20 t for the whale shark using an isometric length-weight equation also used with the basking shark: $W(t) = 0.0075TL(m)^3$. Recent records suggest a higher maximum length, however. Eckert and Stewart (1996) tracked 12 whale sharks by satellite tags for which size estimates were given to a tenth of a metre; 10 of their tagged sharks were 3.0 to 7.1 m long, but two big females tagged in 1996 and tracked for four months were 15.0 and 18.0 m long. Taiwanese fishers reported several whale sharks between 15 and 36 t weights (Joung et al., 1996), suggesting lengths of about 12 to 17 m using Pauly's equation.

Interest to Fisheries and Human Impact: Apparently of limited value for conventional fisheries despite expanding markets and increasing values for whale shark products. Small harpoon fisheries traditionally existed in Pakistan and India for local utilization; it is also taken by harpoon in the Maldives, China, Taiwan (Province of China), and Philippines, and has been captured and utilized in Senegal; it is also caught as a bycatch in fish traps in Philippines but was generally released until it increased in value and was killed for export, and hopefully is now being released again following nation-wide protection. More importantly, an increase in demand for whale shark meat in Taiwan (Province of China) stimulated the development of a targeted fishery for whale sharks developed by ex-whalers operating in the Bohol Sea. Whaling harpoons or gaffs were used to subdue them and knives (bolos) to kill them (WWF-Philippine Program, 1996). It is also caught with longlines and in gill nets in Taiwan (Province of China).

Whale shark meat is eaten by people fresh, fresh-frozen, dried or dried-salted, the skin is eaten in Taiwan (Province of China), the fins enter the oriental fin trade at a high value because of their size, the dried gill rakers have been utilized in the Philippines, and the flesh has been used to treat boat hulls in Pakistan.

The whale shark is generally considered harmless despite its size, and moderate-sized to very large individuals have been repeatedly approached closely by divers and have been touched, ridden and otherwise contacted by them without the sharks reacting aggressively. They may suddenly dive or flee the vicinity of divers when disturbed but without showing much excitement. Their docility and ready access in shallow water in many localities has popularized them as the subject of ecotouristic diving charters. The best known site is off Ningaloo Reef (Ningaloo Marine Park) in Western Australia, but sites also exist off the KwaZulu-Natal coast of South Africa, off Mozambique, Kenya, Seychelles, Thailand, Philippines, the Hawaiian Islands, the Gulf of California (Mexico), the Pacific coast of Costa Rica and Colombia, Chile, the Gulf of Mexico coast of the United States (Texas, Florida), and Belize. These sites allow divers to examine whale sharks underwater, and in some instances (Ningaloo Marine Park) access to whale sharks is restricted by a strict code of conduct limiting interference with these sharks by divers and boats (Colman, 1997). The effect of ecotourism on the behaviour and local abundance of whale sharks off Western Australia is currently under detailed study (Stevens et al., 1997). The whale shark dive industry is highly regulated by the Western Australian government, with limited numbers of operators and vessels (16 in 1993 decreasing to 14 in 1996 according to Colman, 1997). Operators require commercial tourist licences with yearly or two-year renewal, and pay a fee per tourist per day. A benefit of ecotouristic activity with whale sharks, particularly in Western Australia but also in the Gulf of California, South Africa and elsewhere, is a rise in scientific activity focusing on the whale shark, often in cooperation with ecotouristic dive operators.

There have been a few cases of whale sharks butting sportsfishing boats (Smith, 1967), possibly after becoming excited by hooked fishes being played from the boats or by bait, but ordinarily they do not contact boats although they may investigate them very closely. Far more commonly human beings inadvertently ram whale sharks with ships and boats as the sharks bask or swim on the surface (documented in numerous papers by Eugene W. Gudger, cited in Wolfson and de Sciara, 1981).

During 1998, a whale shark swam into and became caught in a cooling water intake of a coastal nuclear power station at Koeberg, Western Cape, South Africa. The affected reactor had to be shut down and boats and divers were called in to extract the shark. The shark was still alive after about a day and divers 'walked' it until it increased its vigour and swam away! The shark may have been attracted to the warm plume of water released by the power plant, and whale sharks have been sighted in the immediate vicinity of the powerplant before.

The whale shark has been kept in captivity in Japan and Taiwan (Province of China) and is relatively hardy if properly fed and handled. At least 14 largish (3.9 to 6.3 m) individuals have been kept in Japan, primarily in a large oceanarium tank at the Okinawa Expo Aquarium (Clark and Nelson, 1997) for extended periods of over a year. These have learned to feed at the surface of the tank when presented with a long-handled ladle filled with food such as euphausiid shrimp, squid, and fish, and so fed do not require planktonic food in their tank. More recently term foetuses from a pregnant female whale shark were successfully kept in captivity in Taiwan (Province of China) and Japan.

The conservation status of the whale shark is of major concern to scientists and to the public, with expanding fisheries and increasing value of whale shark products such as flesh and fins in Philippines, India, Taiwan (Province of China) and elsewhere in the late 1990s. This runs counter to the increasing international popularity of live whale sharks as subjects of ecotouristic dives, as well as increasing public sympathy for these animals worldwide as harmless "gentle giants" or "gentle monsters of the deep" (Clark, 1992) that (as with cetaceans) should be conserved because of their intrinsic worth and emotional appeal.

Although whale sharks have been caught off Taiwan (Province of China) for many decades of the twentieth century, whale shark flesh became very popular fresh for human consumption in Taiwan (Province of China) over the past two decades, which caused a major increase in the value of whale shark products there, encouraged Taiwanese fishers to catch more whale sharks, apparently caused a decline in catches of whale sharks off Taiwan (Province of China), but also stimulated the fishing of whale sharks in Philippines until the fishery declined and it was banned in 1998. The Taiwanese market has also stimulated expanded and substantial export fisheries for whale sharks off India, which developed from traditional artisanal fisheries there and which are apparently declining at present due to overfishing. Whale shark meat was valued at about 400 New Taiwanese Dollars per kilo in 1996 (Joung et al., 1996; equivalent to US$13 in 2000 and nearly US$200 000.00 for the meat alone from a 36 t shark if two-fifths of its weight is muscle). Fin prices are uncertain but are probably very high at present as with fins of other large sharks.

It is uncertain what effects the now banned drift net fisheries had on whale sharks (and for that matter mantas and devil rays) as discarded bycatch during the peak period of their use during the late 1980s and early 1990s. No countries that report shark catch statistics to FAO currently report whale shark catches.

The whale shark has been listed on the IUCN Red List for the past few years, is protected by the United States east coast shark management plan, and in the Maldives. More recently (1998), it was protected by the Philippine government with bans on killing and selling them following steep declines in numbers in Philippine waters; similar protection was given to this species off Gladen Spit, Belize (2000). Ecotouristic viewing of whale sharks is being actively promoted by the World Wide Fund for Nature as an economic alternative to whale shark fisheries in Philippines (M.N.R. Alava and A.A.S.P. Yaptinchay, pers. comm.). After lobbying by the US Shark Research Institute and the Hubbs-Sea World Research Institute the Honduran government declared total protection for the whale shark off Honduras in 1999 (M. Levine, pers. comm.). The species is under consideration for total protection in South Africa also (1999 to 2000). International protection for the whale shark is probably necessary, perhaps in the form of a CITES listing with a worldwide ban on fishing them for international trade as well as regional agreements and national regulations for protecting them or limiting exploitation. Whale shark fins and meat fall into international trade and regulation, but the highly migratory whale shark ranges close inshore and is also subject to local fisheries supplying local markets as well as pelagic fisheries and international exporters.

There is considerable concern that whale sharks are extremely vulnerable to overexploitation due to their relatively low abundance, large size, ease of access at the surface, and possibly very slow growth and exceptional longevity (see above). They are a ready target of coastal and pelagic fishing operations, and are easily harvested by small boats in shallow coastal waters. It is a natural extension, as in Philippines, for former whale-hunters to transfer their activities to whale sharks. This parallels whale fisheries that also took basking sharks. With the current high values of whale shark flesh and fins, whale sharks could be targeted in international waters by long-range fishing vessels run like miniature whale factory ships (for example, a few converted ocean-going stern trawlers of modest displacement set up for processing carcasses and blast-freezing the meat and fins) and using small 'killer' boats, harpoon-guns, light helicopters or microlight aeroplanes as spotters, and even remote sensing from satellites to fish these sharks pelagically. Small specialist killer boats with harpoon-guns already exist in the declining basking shark fishery, and could be applied to the whale shark fishery for shore-based operations or serving small factory ships. Fortunately this has not happened to date, and hopefully will never happen, as the effect of even a few such vessels or a small fleet could be devastating in short order. It may be possible that decreases of whale sharks from shore-based small operations may preclude high-technology pelagic whale shark fishing on economic impracticality.

Pauly (in press) suggested that because of the whale shark's slow growth and other life-history parameters any plan for targeted exploitation of whale sharks as fisheries resources would lead to a quick collapse of numbers, and that even ecotouristic viewing of whale sharks on feeding and mating grounds should be carefully monitored to prevent even indirect mortality which these sharks probably could not accommodate. His prediction apparently was verified while his paper was in press (1997 to 2000), with the steep decline of the Taiwanese and Philippine whale shark fisheries and possible declines of whale sharks in the western Indian Ocean following the developing Indian fishery.

It is quite possible, however, that whale sharks are far more valuable in terms of long-term and long-range revenue generated from ecotourism than current fisheries, which have the potential to decimate them and remove the source of revenue. For Ningaloo Marine Park, Western Australia, revenue from whale shark ecotourism has been growing at 15% per year and is estimated at being worth A$12.8 million in the year 2000 despite being highly seasonal and of short duration, between March and May of each year (Colman, 1997). If the same sharks visit different viewing sites, as is suggested by long-range tagging and tracking, and are long-lived, they each may generate far more revenue as a live animal viewed repeatedly by diving ecotourists over several decades and at several sites rather than that received as a one-off fee from killing them (and with low value often received by fishers in Developing countries compared to fin and meat dealers in the developed world). This may be particularly important in places such as the Philippine Islands, where ex-whale shark fishers are becoming involved in whale shark ecotourism (M.N.R. Alava and A.A.S.P. Yaptinchay, pers. comm.) and even a whale shark museum. Extraordinarily high profits from flesh and fins drive the current fisheries, but their existence is probably ephemeral as whale sharks may be unable to sustain them for very long because of their biological limits.

Local Names: Basking shark, East Indian basking shark; Mhor, Chagrin; Tiburón ballena, Pintado; Dominó, Tiburón dama (Mexico); Tubarâo baleia, Whale shark (Azores); Chlarm plawarn (Thailand), Jimbeizame, Yasurizame (Japan); Tofu sa (Taiwan (Province of China)); Isdang tuku, Tuk, Tuku, Tuki Tuki (Philippines).

Literature: Smith (1828, 1829, 1849); Müller and Henle (1839); Regan (1908a); Garman (1913); Gudger (1915, 1931, 1935, 1940, 1941a,b,c); White (1930, 1937); Herre (1925, 1953); Fowler (1936, 1941, 1967a); Denison (1937); Bigelow and Schroeder (1948); McCann (1954); Baughman (1955); Reid (1957); Garrick (1964); Smith (1967); Iwasaki (1970); Compagno (1973, 1984, 1988, 1990a, b); Bass, D'Aubrey and Kistnasamy (1975c); Johnson (1978); Wolfson and de Sciara

(1981); Cadenat and Blache (1981); Uchida (1982, 1984); Castro (1983); Wolfson (1983, 1986); Nakaya and Shirai (1984); Dingerkus (1986); Sadowsky et al. (1986); Uchida, Toda and Kamei (1990); Au (1991); Clark (1992); Anderson and Ahmed (1993); Michael (1993); Last and Stevens (1994); Gifford (1994); Seret (1994); Randall (1995); Wamukoya, Mirangi and Ottichilo (1995); Joung et al. (1996); Eckert and Stewart (1996); WWF-Philippine Program (1996); Kukuyev (1996); Beckley et al. (1997); Bonfil (1997); Clark and Nelson (1997); Colman (1997); Santos, Porteiro and Barreiros (1997); Stevens et al. (1997); McEachran and Fechhelm (1998); Castro, Woodley and Brudek (1999); Gunn et al. (1999); Heyman et al. (in press); Pauly (in press); M.N.R. Alava and A.A.S.P. Yaptinchay (pers. comm.); M. Kroese (pers. comm.); M. Levine (pers. comm.); S. Uchida (pers. comm.).

There is currently an annotated whale shark bibliography at the Scripps Institution of Oceanography website by Fay Henry Wolfson and Giuseppe Notarbartolo-di-Sciara: http://scilib.ucsd.edu/sio/indexes/whalshrk.html.

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3. LIST OF SPECIES BY MAJOR FISHING AREAS

Species	page	GEOGRAPHICAL DISTRIBUTION																			
		Major Areas for Statistical Purposes																			
		Fresh water	18 ARC	21 WNA	27 ENA	31 WCA	34 ECA	37 MED	41 WSA	47 ESA	48 ANC	51 WIO	57 EIO	58 ANE	61 WNP	67 ENP	71 WCP	77 ECP	81 WSP	87 ESP	88 ANW
Alopias pelagicus	81									●		●	●		●		●	●	●	●	
Alopias superciliosus	83			●	●	●	●	●	●	●		●	●		●		●	●	●	●	
Alopias vulpinus	86			●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	
Brachaelurus waddi	145												●				●		●		
Carcharias taurus	58			●	●	●	●	●	●	●		●	●		●		●		●		
Carcharodon carcharias	100		●	●	●	●	●	●	●	●		●	●		●	●	●	●	●	●	
Cetorhinus maximus	91			●	●	●	●	●	●	●	●		●		●	●	●	●	●	●	
Chiloscyllium arabicum	167											●									
Chiloscyllium burmensis	168												●								
Chiloscyllium griseum	169											●	●		●		●				
Chiloscyllium hasselti	171												●		●		●				
Chiloscyllium indicum	172											●	●		●		●				
Chiloscyllium plagiosum	173											●	●		●		●				
Chiloscyllium punctatum	175											●	●		●		●				
Cirrhoscyllium expolitum	133														●		●				
Cirrhoscyllium formosanum	134														●						
Cirrhoscyllium japonicum	135														●						
Eucrossorhinus dasypogon	151												●				●				
Ginglymostoma cirratum	192		●	●	●	●	●	●										●		●	
Hemiscyllium freycineti	179																●				
Hemiscyllium hallstromi	180																●				
Hemiscyllium ocellatum	181												●				●		●		
Hemiscyllium strahani	182																●				
Hemiscyllium trispeculare	183												●				●				
Heterodontus francisci	36																	●		●	
Heterodontus galeatus	38												●				●		●		
Heterodontus japonicus	39														●						
Heterodontus mexicanus	41														●						
Heterodontus portusjacksoni	42												●				●		●		
Heterodontus quoyi	45																			●	
Heterodontus ramalheira	46											●									
Heterodontus **sp. A**	49											●									
Heterodontus zebra	48												●		●		●				
Heteroscyllium colcloughi	147																●				
Isurus oxyrinchus	109			●	●	●	●	●	●	●		●	●		●	●	●	●	●	●	
Isurus paucus	115			●	●	●	●	●	●	●		●	●		●		●	●	●		
Lamna ditropis	119		●												●	●		●			
Lamna nasus	121			●	●	●	●	●	●	●	●	●	●	●			●		●	●	●
Megachasma pelagios	75						●		●				●		●		●	●			
Mitsukurina owstoni	69				●	●	●			●		●	●		●			●	●		
Nebrius ferrugineus	196											●	●		●		●	●			
Odontaspis ferox	64			●	●	●	●	●	●			●	●		●		●	●	●	●	
Odontaspis noronhai	66					●	●		●			●			●		●	●			
Orectolobus japonicus	154														●		●				
Orectolobus maculatus	155												●		●		●		●		
Orectolobus ornatus	158												●		●		●		●		
Orectolobus **sp. A**	161												●				●				
Orectolobus wardi	159												●				●				
Parascyllium collare	137												●				●		●		
Parascyllium ferrugineum	138												●						●		
Parascyllium **sp. A**	141												●								
Parascyllium variolatum	140												●						●		
Pseudocarcharias kamoharai	72					●	●		●	●		●	●		●		●	●	●	●	
Pseudoginglymostoma brevicaudatum	200											●									
Rhincodon typus	203			●	●	●	●		●	●		●	●		●		●	●	●	●	
Stegostoma fasciatum	186									●		●	●		●		●		●		
Sutorectus tentaculatus	162												●								

4. APPENDIX

4.1 Keeping Sharks for Scientific Study

4.1.1 Generalities About Shark Collections

Many countries have natural history museums, and these often have fish research collections with sharks in them. These collections are essentially ‘libraries’ of preserved specimens, which have a wide variety of uses, specifically in systematic, morphological and phylogenetic studies but more generally for natural history, biology, ecology, feeding, reproduction, parasitology, distribution, conservation, and other disciplines. Although sharks form a moderately large and important group of fishes, they are poorly known systematically and biologically, and many described species are inadequately represented in museum collections. Also, new species are still being collected at a good rate, especially deepwater benthic species collected by trawl and longline gear on continental and insular slopes, seamounts, submarine ridges, and other topographic features in the open ocean, as well as the offshore and inshore tropics of the Indo-West Pacific. It is not impossible that readers of this catalogue may come upon unusual sharks including rare species that are interesting and important to science or even new species, and may want to save them for later identification, deposition, and study in a museum collection. Hence it is desirable to outline conventional methods of preparing sharks for scientific study along with some background on their use.

In the eighteen and nineteenth centuries sharks intended for research collections were often skinned and their skins dried and either stuffed or mounted flat (like herbarium specimens) and stored dry along with shark jaws, sawfish saws, stingray spines, and other dried skeletal parts. As the years went by, dry storage of whole specimens was supplemented and largely replaced by wet storage, which is more satisfactory for systematic collections because of less dehydration damage and ready accessibility of internal structures through dissection, clearing and staining, radiography, and other techniques. Specimens are prepared first by **fixation**, stopping putrefaction in fresh material using a powerful antiseptic solution that modifies fresh tissues to stable forms that are resistant to agents of decay; and **preservation**, long-term storage in an antiseptic solution. Ordinary table salt (Sodium chloride, NaCl) was used as brine (high concentrations of salt in water) to fix or ‘pickle’ whole wet specimens or skinned specimens, and also used as a drying and antiseptic agent to pack, dehydrate, and fix dry specimens. High concentrations (70% or more) of ethyl alcohol (CH_3CH_2OH) in water, including high-proof alcoholic drinks, served to fix and preserve whole specimens. Salt and strong alcoholic drinks are old substitutes for fixing and preserving specimens when nothing else is available.

Traditional fixation and preservation. By the beginning of the twentieth century fixation in water solutions of formaldehyde gas (CH_2O) or formalin, followed by preservation in aqueous solutions of ethyl, isopropyl ($CH_3CHOHCH_3$) or n-propyl (CH_3CH_2CHOH) alcohols became the standard mode of preparation and storage of whole wet fish specimens including sharks. The preferred preservative for such collections is 70 to 75% ethyl alcohol, but it has the disadvantages of excessively dehydrating some material such as skeletal parts, is highly flammable, and may be more expensive and more subject to tariffs and storage regulations than other alcohols because of its consumption by people. Isopropyl or n-propyl alcohols (particularly the former) in 50% aqueous solution may be more suitable for storage of larger specimens over 60 cm long or wide, but are less suitable for preserving smaller whole specimens below that size. This particularly applies to small delicate specimens because of poorer long-term preservation. Large alcohol-preserved collections may present a fire hazard in some countries with histories of seismic activity, volcanism, and large urban fires resulting from natural and human-induced disasters. Alcohol collections are costly to maintain due to the expense of alcohol, its high evaporation rate, the need to provide facilities with adequate ventilation and fire protection, and the need for constant vigilance and service to protect these collections from dehydration. Hence some collections preserve sharks and other fishes in weak formalin, sometimes buffered with hexamine or carbonates. However, formalin preservation is far less desirable than alcohol because of the excessive hardening of soft parts including fins, decalcification of hard tissues, and the toxic hazard and nastiness of working with formalin. Formalin fixation and preservation in ethyl alcohol is best for long-term maintenance of specimens large and small, with isopropyl a substitute for ethyl alcohol when ethyl alcohol is prohibitively priced or regulated.

Alternatives for fixation and preservation. A 1% solution of propylene phenoxcetol with 5% ethylene glycol in water has been used in some museums as a substitute preservative for formalin-fixed specimens. In some instances phenoxcetol preservation has been excellent, but in others specimens began to decay because the phenoxcetol lost its antiseptic qualities. Non-aqueous, antioxidant and antiseptic fixing and preserving fluids have been used experimentally for preserving the life colours of tropical reef fishes, but have not been used much with sharks. There is at least one institution that has tried long-term preservation of sharks by storing them in freezers, but these specimens became dehydrated and mummified after long storage.

Dried shark parts may be useful for identification if nothing else is available. Shark parts such as jaws, saws, and stings, as well as small whole sharks, can be dried in sunlight or indoors at room temperature or with artificial heat sources. Jaws and other shark parts should be thoroughly washed of blood and have most skin and muscle removed before drying. Formalin, alcohol, brine fixation, or salting of the cleaned parts before drying will retard bacterial growth and insect damage, but if specimens are to be dried without fixation they should be protected to keep out insects. Alternatively, ant colonies in the field and dermestid beetle colonies in museum facilities can be used to remove flesh from semi-dried but unfixed shark jaws or other parts. Likewise marine isopods can be used to remove muscle from fresh jaws or whole skeletons hung in perforated containers from piers in harbours or placed on the bottom in protected waters such as pools. Cleaned shark jaws should be pinned to a board (a large piece of Styrofoam or rubberised foam will suffice) or tied to a frame to keep them from becoming distorted as they dry.

Freeze-drying whole sharks may produce better results than stuffing them for display, but is not utilized in systematic collections to any extent and has several disadvantages over conventional wet-storage of sharks including stiffness and problems with studying internal structures. Making moulds of specimens can produce high-fidelity casts of whole animals or parts for museum displays and as museum specimens, but as with stuffed specimens these have less utility than wet material.

Small formalin-fixed sharks including foetuses are suitable for clearing and staining of skeletons with various techniques. The writer prepares skeletal material from fresh or thawed-frozen sharks of all sizes by maceration of soft tissue in boiling water and dissecting and washing off the tissue. The cleaned skeletal material is then fixed and preserved in 50% isopropyl alcohol to avoid the brittleness of formalin-fixed cartilage. There are several other techniques for preparing skeletal material including wax-impregnation of skeletal parts for dry storage (see Compagno, 1988).

Tissue samples for DNA and protein analysis are best obtained from fresh material that is frozen and stored at low temperatures or, depending on techniques, fixed in full-strength alcohol (ethyl or isopropyl). Alcohol-fixed and preserved whole specimens and dried fresh material such as shark jaws or sawfish saws can be used for some biochemical techniques, but not formalin-fixed material.

4.1.2 Practical Advice for Creating Shark Collections

Collection and handling of specimens. Most smaller sharks a meter or less long, including small species or small specimens of larger species, can be readily fixed and even preserved intact in the field as well as in a dedicated laboratory. If it is not possible to fix and preserve whole large specimens, their heads, fins and vertebral columns can be readily accommodated in barrels and other containers. To prepare a large non-batoid shark for compact storage measure first its total length and other basic measurements (see section 1.2.2 Measurements Used for Sharks). Remove its viscera and most of its muscle mass from the pectoral fin bases to the second dorsal and anal fins with a knife, leaving a long dorsal strip of skin connecting the head to the first dorsal fin, second dorsal, caudal peduncle and caudal fin. Leave also a short ventral strip of skin connecting the pelvic-fin bases with the anal fin and caudal peduncle. Strip the vertebral column of excess flesh and cut it off at the head and caudal peduncle, cut it into sections if necessary, tie labels to it and the rest of the shark before fixing it. Wide and very large batoids are often a problem because of their awkward shape. Their size can be reduced by skinning and removing muscle from the pectoral fins, cutting off the pectoral fins and cutting them into sections, and preserving the head, body and tail either intact or divided into pieces.

For best results sharks should be fixed with formalin as soon after death as possible, though they can be frozen or even covered with ice to halt or retard putrefaction until the specimen can be fixed or delivered to a museum or other facility for fixation and preservation. Excess freezing will dehydrate unprotected specimens, and sharks that are to be frozen for considerable periods should be sealed with some water in plastic bags. In hot climates it is especially important to fix or freeze specimens quickly, as they can deteriorate in a matter of hours after being caught. Tropical markets are excellent places to collect inshore and sometimes offshore and deep-water sharks, as fishers often land most of their catch including oddities, but market specimens should be processed as soon as possible as they may not be in the most fresh condition after capture. Specimens should be kept cool, in the shade, and iced or covered with wet cloth or fibrous sack material if they cannot be immediately fixed or frozen. Fast blast-freezing to -40°C is preferable to slower and higher-temperature freezing methods where putrefaction may proceed apace during the freezing process. Some deepwater sharks with large livers and high squalene content may not properly freeze in higher-temperature low-capacity freezing units. Frozen specimens are ideal for skeletal preparations (see Compagno, 1988), but after thawing and fixation as whole specimens they often do not look quite as good as those that were formalin-preserved in the field while fresh.

Containers for fixing and preserving sharks. Containers are necessary to fix sharks in formalin, and include jars, plastic buckets and boxes with lids, small metal barrels, the ubiquitous and durable plastic industrial barrels with tight-sealing lids, cardboard waterproof drums ('liquipaks'), elongated rectangular tanks, garbage cans or whatever waterproof containers are available locally. Formalin will quickly corrode ordinary steel containers, so these should be either stainless or should have acid-proof coatings if used for fixation or long-term storage. Ideally a long tank or deep tray, or, for wide animals, a long and broad tank of wood, plastic, fibreglass, stainless steel or other formalin-resistant material should be used for preserving sharks in a straight, spread-out position, but it may be possible only to fix and store specimens in cylindrical containers in a curled position. Large, heavy plastic bags have been used to fix sharks quite successfully when other containers were not available, and very large specimens could be fixed in a temporary container made from a liner of heavy plastic sheeting and a box or even a hole in the ground. Containers for fixation and temporary storage should have tight-fitting lids to prevent escape of toxic formalin fumes.

Small sharks or their parts can be stored permanently in alcohol in glass bottles in sizes from about 300 ml to 4 or 5 l. Plastic bottles are better for fixation and field storage of small specimens but are not as good as glass for permanent storage. Larger glass bottles and tanks from 10 to 20 l are presently difficult to obtain, but plastic pails or buckets up to about 20 l and small commercial barrels over 20 l are the modern substitutes. Lids on all containers with preservatives should be tight-fitting to retard evaporation. Plastic lids for screw-top bottles with full-turn threads work well, as do glass lids with wire bails and rubber gaskets on special preserving jars for fruit and vegetables; screw-top lids will allow evaporation, and metal ones will corrode, unless provided with a good plastic liner.

The larger sharks, 1.5 m or more in length or width, present special problems for long-term preservation in alcohol. They require facilities with large durable rectangular or square tanks of fibreglass, composite wood and fibreglass, polyethylene, or stainless steel. Large preservation tanks are often custom-built, but less expensive industrial tanks for transport or storage of wet and corrosive materials can be readily substituted for them. Tight-fitting covers for tanks are necessary to minimize evaporation.

Tools and materials needed for fixation and preservation. Basic tools and materials that are useful for fixing and preserving sharks include 40% aqueous (concentrated) formaldehyde, 95% alcohol (ethyl or isopropyl), scalpels, a selection of good knives ranging from small ones with 10 cm blades to large butcher knives with 30 cm blades, a sharpening steel, forceps, pointed metal probes, large needles with large eyes for tying tags or suturing up large specimens, 20 to 50 ml hypodermic syringes (preferably plastic and having locking collars to keep the needles from coming off while injecting specimens), large syringe needles (size 16 or larger), protective clothing including rubber or plastic gloves (including some heavy gloves with long sleeves for 'tank diving' to retrieve specimens in large containers), aprons, lab coats, rubber boots and safety glasses, good quality label paper or card of high rag content that will not tear easily or disintegrate when wet, plastic-impregnated paper that can be written on with pencil, tough tag paper or tie-tags with holes for string, linen, cotton or synthetic string, cheesecloth, mutton-cloth, or ordinary, non-dyed cloth including old bedsheets and pillowcases, polyethylene plastic bags of various sizes and shapes, pencils, and technical pens with indelible India ink.

Recommended fixation and preservation procedures. To fix sharks, prepare a 10% formalin solution by adding 1 part concentrated formaldehyde to 9 parts of water, in a volume enough to at least cover the sharks in the container selected. Formalin is quite toxic, and should be handled with great care in a well-ventilated place, either outside in the shade or in a facility with a fume hood or a room with powerful extractor fans. Gas masks with formalin-specific filters should be used when ventilation is inadequate.

Syringes should be used to inject a quantity of formalin into the body cavity (including the stomach and intestine) and also the muscle masses of the body, tail, and fin bases, and the head to preserve the brain. For injection of large numbers of large specimens pressure garden sprayers or even mortuary suffusion equipment can be adapted for injecting sharks. Dilute 10% formalin can be used for injection, though higher strength formalin, 1:4, 1:2 or even undiluted concentrated formaldehyde is very effective in preventing putrefaction in hot climates. If a syringe is unavailable make several small holes or slits on sides of abdomen through to the body cavity of the shark with a knife, scalpel or probe, preferably on the right side (the left side is generally used for illustration); even when injecting the shark make at least one small slit on the left side of the abdomen. Position the shark flat on its abdomen with fins spread in the preserving container and add enough dilute formalin to cover it. Fins can be pinned out on pieces of styrofoam or other soft material if necessary. Deepwater sharks and some other species may have large and extremely oily livers, which generally leak oil into fixatives and preservatives. Some plastics, including coated label-paper, may have chemical problems with such oil, and it may be desirable to wash out excess oil from the body cavity before fixation and preservation.

With larger sharks in hot climates it may be necessary to use stronger formalin, up to 1:4, for initial fixation, or add more concentrated formaldehyde to 10% solution if outgassing from putrefaction is evident. Small sharks below 1.5 m should be fixed for at least two weeks to a month, while larger specimens should be fixed for a month or more. Volume of the shark should not exceed half of the volume of the preserving fluid. Specimens are then preserved in ethyl or isopropyl alcohol after fixation, with a brief wash in water to remove excess formalin, and stored in suitable containers.

Labels, field numbers and field notes. All specimens should have good-quality labels attached or associated with them that will survive wetting, movement, transportation, and long-term storage. Make a field label for the shark in pencil on plasticized paper or with a technical pen on high quality, high rag content label paper or card (making sure the ink is dry before wetting the label. The field label should include a field number, cruise and station numbers if relevant, date of collection, locality, collector, species (if known), specimen data including total length, precaudal length, weight, sex and maturity stage when available. The label should be tied to the shark or placed inside its mouth or inside a gill slit before fixation. Perforated tag labels with attached string or line should be securely fastened by threading their line through small holes in the bases of the pectoral fins or other fins. Tags using synthetic string such as nylon, dacron, or polypropylene should be tied with secure knots as synthetics are often more slippery than natural fibre.

Field numbers of individual collectors serve to link specimens to collectors, expeditions, research vessels, and various types of data sheets. The writer uses the notation ***LJVC-YYYY-MM-ddX***, using a year/month/day and sometimes letters to make unique field numbers for individual specimens or batches of specimens caught or collected in the same place and time. These field numbers are added to field locality data sheets or field notebook entries, morphometric and other datasheets, and other material pertinent to the specimens (including photographs), and are kept with specimens that are given institutional catalogue numbers. Data including the species, field accession number, specimen data (including length, weight, maturity and sex), station and cruise numbers if relevant, collection date, collector, locality (including coordinates if available), and habitat data as available (including water temperature, depth, bottom conditions, turbidity, salinity, and oxygen level) should be entered in a field notebook or on a field locality data sheet under the field number.

Transport. Specimens can be transported wet over long distances in barrels, liquipaks, cardboard boxes, wooden boxes or other containers if they are properly packed. Each specimen should be wrapped in cloth with a label wrapped with it or attached to it or placed inside the specimen, and the cloth secured with string or elastic bands. It is important to wrap any structures that can puncture plastic bags, such as fin spines, stingray stings, protruding oral teeth, sawshark and sawfish rostra, and extremely rough, thorny specimens with extra cloth or other protective material such as cork or dense plastic foam. Wrapped specimens are conventionally kept moist by soaking them in formalin or alcohol, bagging them in three or more layers of plastic bags, and cushioning them with packing material from newspapers and shredded paper to plastic bubble-wrap and Styrofoam packing material. Quite recently (2000) airlines have refused to transport such wet specimens in alcohol, formalin, or even propylene phenoxcetol in ordinary airmail, but now charge exorbitant fees for transport of ‘dangerous’ cargo. Specimens may have to be washed of fixatives or preservatives and shipped soaked in water by air, provided airfreight or courier services guarantee fast delivery. Surface freight carriers, including ships, still permit specimens to be transported in fixatives or preservatives.

Documentation. If it is not possible to preserve any parts of a shark or even if the animal is preserved intact take black and white or, preferably, colour photographs of the entire specimen in lateral view, dorsal and ventral view, and the underside of its head and pectoral fins, using film cameras with slide or print film, digital still cameras, or video cameras (digital video is particularly effective). For sharks that will be discarded, remove and dry a strip of teeth or the entire dentition from the upper and lower jaws. At minimum, record the date, locality, depth, collector and any other significant data for the specimen and take the following measurements with a metre stick or tape measure as indicated in the Plan of the Catalogue: total length (TL), precaudal length (PCR), fork length (FL), preoral length (POR); head length (HDL); eye length (EYL); mouth width (MOW); pectoral-fin anterior margin (P1A); pelvic-fin anterior margin (P2A); first dorsal-fin height (D1H); second dorsal-fin height (D2H); anal-fin height (ANH); and dorsal caudal margin (CDM). With specimens that have expanded pectoral fins, including angel sharks, wobbegongs and batoids, measure the disk width (DWI), the extreme distance across the pectoral-fin apices. Take other measurements if possible, including the full set of measurements for non-batoid sharks listed here. The writer has additional datasheets with sets of full measurements for various batoids and for chimaeroids, which will eventually be listed as datasheets on the Shark Research Centre web site (http://shark.museums.org.za).

The writer is quite willing to help any readers who have shark identification problems, time allowing; and photos, measurements and tooth samples or small whole sharks can be sent to him care of FAO.

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6. INDEX OF SCIENTIFIC AND VERNACULAR NAMES

Explanation of the System

Italics : Valid scientific names (genera and species).

Italics : Synonyms (genera and species, misidentifications and other combinations).

ROMAN : Family names.

ROMAN : Names of orders.

Roman : Suborders, subfamiles, tribes, and FAO and local names.