

Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes

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Part B: Batomorphii 4c: Order Rajiformes – Suborder Myliobatoidei – Superfamily Dasyatoidea – Family Dasyatidae – Subfamily Dasyatinae – Genus: *Urobatis*, Subfamily Potamotrygoninae – Genus: *Paratrygon*, Superfamily Plesiobatoidea – Family Plesiobatidae – Genus: *Plesiobatis*, Superfamily Myliobatoidea – Family Myliobatidae – Subfamily Myliobatinae – Genera : *Aetobatus*, *Aetomylaeus*, *Myliobatis* and *Pteromylaeus*, Subfamily Rhinopterinae – Genus: *Rhinoptera* and Subfamily Mobulinae – Genera: *Manta* and *Mobula*. Addendum 1 to 4a: erratum to Genus *Pteroplatytrygon*.

by J. HERMAN, M. HOVESTADT-EULER, D.C. HOVESTADT and M. STEHMANN

Abstract

Part B of this series, the Batomorphii, is continued with the remaining taxa of the dasyatoid family Dasyatidae and the plesiobatoid family Plesiobatidae (additional material) and the supraspecific taxa of the Myliobatidae (including some doubtful taxa). The tooth morphology of their representatives, as specified in the title, is described and illustrated by SEM-photographs. A differential diagnosis and systematic interpretations for the supraspecific taxa of the Myliobatoidei are presented as a result of the odontological examinations described here and in the previous two issues 4a and 4b.

Key words: Elasmobranchii - Rajiformes - Myliobatoidei - Dasyatidae - Plesiobatidae - Myliobatidae - Odontology.

Résumé

L'étude de l'odontologie des Batomorphii à laquelle est dévolue la partie B de cette série se poursuit en ce fascicule par l'examen de la dentition des derniers taxa des familles Dasyatidae et Plesiobatidae, ainsi que des taxa supraspécifiques des Myliobatidae (y compris taxa controversés). La morphologie dentaire de leurs représentants est

décrite et figurée (clichés MEB). Une diagnose différentielle et une interprétation systématique de l'ensemble des taxa supraspécifiques des Myliobatoidei sont proposées. Celles-ci résultent des observations odontologiques déjà présentées dans les fascicules 4a et 4b.

Mots-clés: Elasmobranchii - Rajiformes - Myliobatoidei - Dasyatidae - Plesiobatidae - Myliobatidae - Odontologie.

Kurzfassung

Teil B dieser Serie für die rajiformen Taxa der Batomorphii wird fortgesetzt mit den restlichen supraspezifischen Taxa der dasyatoiden Familie Dasyatidae und der plesiobatoiden Familie Plesiobatidae (ergänzendes Material) sowie mit Taxa der Myliobatidae (einschl. einiger unklarer Taxa). Die Zahnmorphologie ihrer im Titel spezifizierten Vertreter wird beschrieben und mit REM-Photos illustriert. Eine odontologische Differentialdiagnose und systematische Interpretationen für alle supraspezifischen Taxa der Unterordnung Myliobatoidei fassen die Ergebnisse dieser Ausgabe und beiden vorherigen, 4a und 4b, zusammen.

Schüsselwörter: Elasmobranchii - Rajiformes - Myliobatoidei - Dasyatidae - Plesiobatidae - Myliobatidae - Odontologie.

**Part B: Batomorphii - 4c: Order: Rajiformes -
Suborder: Myliobatoidei**

General introduction

The rajiform part B of this series (HERMAN, HOVESTADT-EULER, HOVESTADT & STEHMANN, 1994-1999) is continued with the present issue 4c as the third and last contribution on the tooth morphology of supraspecific myliobatoid taxa, which is the sixth in total on rajiforms.

The large number of supraspecific taxa within this suborder, its families and subfamilies had to be published in three issues of this series due to technical limitations. The sequence of publication does not reflect any certain classification or taxonomic ordering but merely depends on availability of study material and progress made in its investigation. The present and last issue, dealing with myliobatoid rays, will also provide the summarizing discussion, final conclusion, and differential diagnosis for each higher taxonomic category of the Myliobatoidea.

The supraspecific classification and nomenclature of the myliobatoids follows NELSON (1994).

This issue deals with the dasyatine genus *Urobatis*, the potamotrygonine genus *Paratrygon*, the plesiobatid genus *Plesiobatis*, the myliobatine genera *Aetobatus*, *Aetomylaeus*, *Myliobatis* and *Pteromylaeus*, the rhinopterine genus *Rhinoptera* and the mobuline genera *Ceratobatis*, *Manta* and *Mobula*. Many authors questioned the validity of the only known specimen of *Ceratobatis robertsii*. Although the specimen was redescribed by BIGELOW & SCHROEDER (1953), it was not treated as a valid species by NOTARBARTOLO DI SCIARI (1987), NISHIDA (1990) and NELSON (1994) and is considered as a senior synonym of *Mobula hypostoma* by NOTARBARTOLO DI SCIARI (1987). The latter author illustrated teeth of several taxa in his revisional work, amongst which were those of *Mobula japonica*. However, the tooth morphology of the latter species exhibits a remarkable similarity with that of *Manta birostris*. He noted also the close relationship of *M. japonica* and *M. mobular* and illustrated the principally different tooth morphology of the remaining mobulids. Therefore, *M. mobular* and one of the species with a non-*Manta*-like tooth morphology, *M. rochebrunei*, are described and illustrated here. The validity of the genus *Urobatis* was doubtful to BIGELOW & SCHROEDER (1953), and it was not mentioned as a valid taxon by NISHIDA (1990) and NELSON (1994). The tooth morphology of both taxa is presented here to provide additional arguments for clarifying their final status. Although, no arguments were given, the genus *Pteromylaeus* was not incorporated in the phylogenetic study of NISHIDA (1990). However, given its distinguishing tooth morphology this genus is treated here as a valid taxon.

Unlike previous issues of this series, listings of all the nominal species cannot always be given due to the lack of recent revisions dealing with the validity of nominal species and genera of the myliobatoids (except for NISHIDA, 1990). Instead, an estimated number of species will only be given for the genera concerned.

The authors will not draw any nomenclatorially valid conclusions. Being aware of dealing with one complex of characters only, they will present their odontological results and leave it to following revising authors to incorporate also odontological points of view in a full systematic review with eventual taxonomic and nomenclatorial changes. The full bibliographical reference for each species will be given in the descriptive section and not be repeated under literature references.

Along with the description of the tooth morphology, the vascularization of the teeth will be described and illustrated.

Superfamily: Dasyatoidea - Family: Dasyatidae

Subfamily: Dasyatinae

Introduction

Male and female tooth material of the genus *Urobatis* was lacking for the previous issue (Part B, 4b), which are now described and illustrated here. Nominal species formerly assigned to *Urobatis* were synonymised with various nominal species of *Urolophus* (CASTRO-AGUIRRE & ESPINOSA PEREZ, 1996). The type species *Urobatis sloani* was synonymised with *Urolophus jamaicensis* by CASTRO-AGUIRRE & ESPINOSA PEREZ (1996).

Material

The following 3 specimen of 1 genera were examined:

<i>Urobatis sloani</i> (= <i>Urobatis jamaicensis</i>)			
ISH 69-1984	♀	147 mm	DW
ISH 69-1984	♂	105 mm	DW
Coll. Herman	♀	310 mm	TL

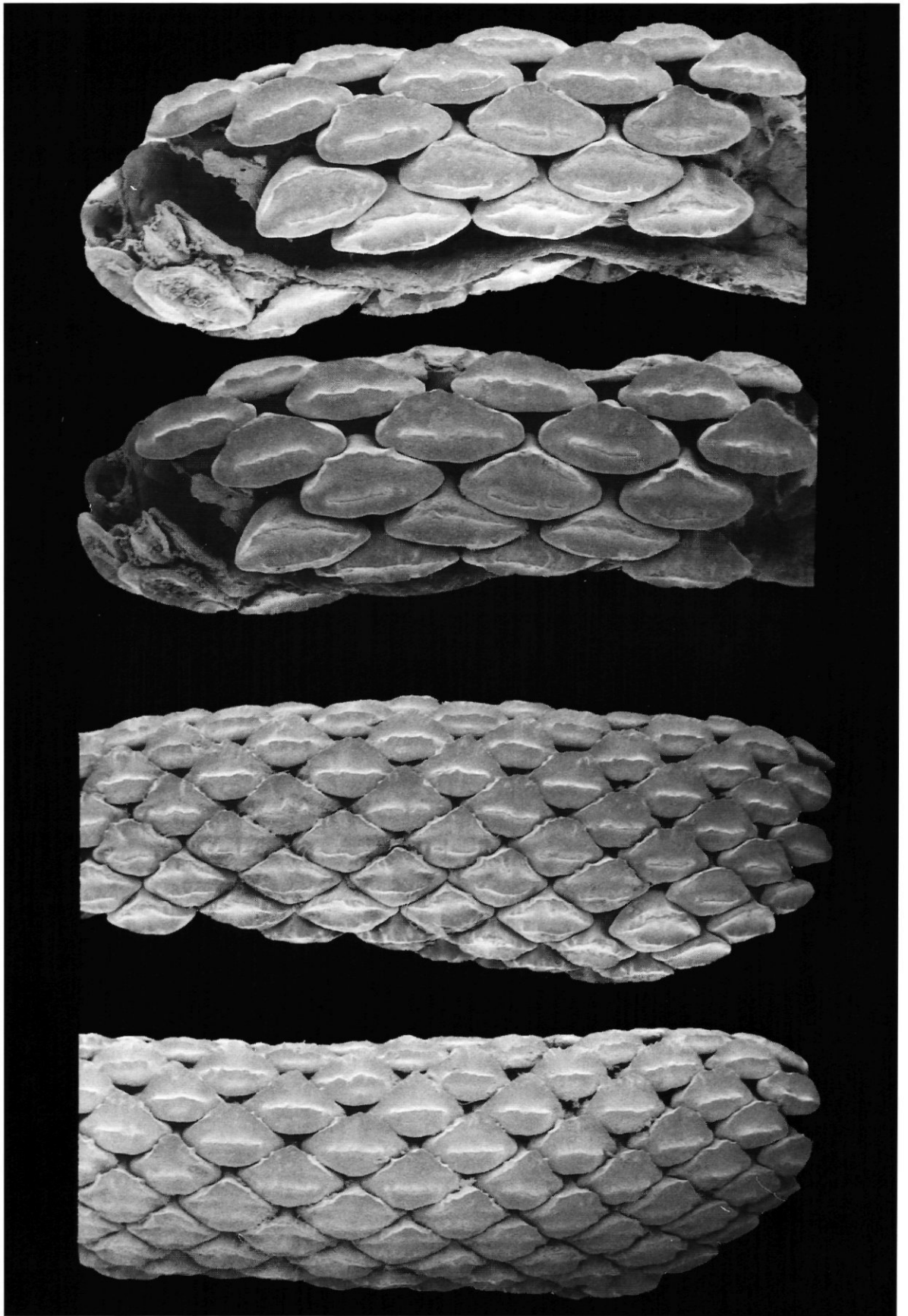
Description of the odontological characters

Genus *Urobatis* GARMAN, 1913

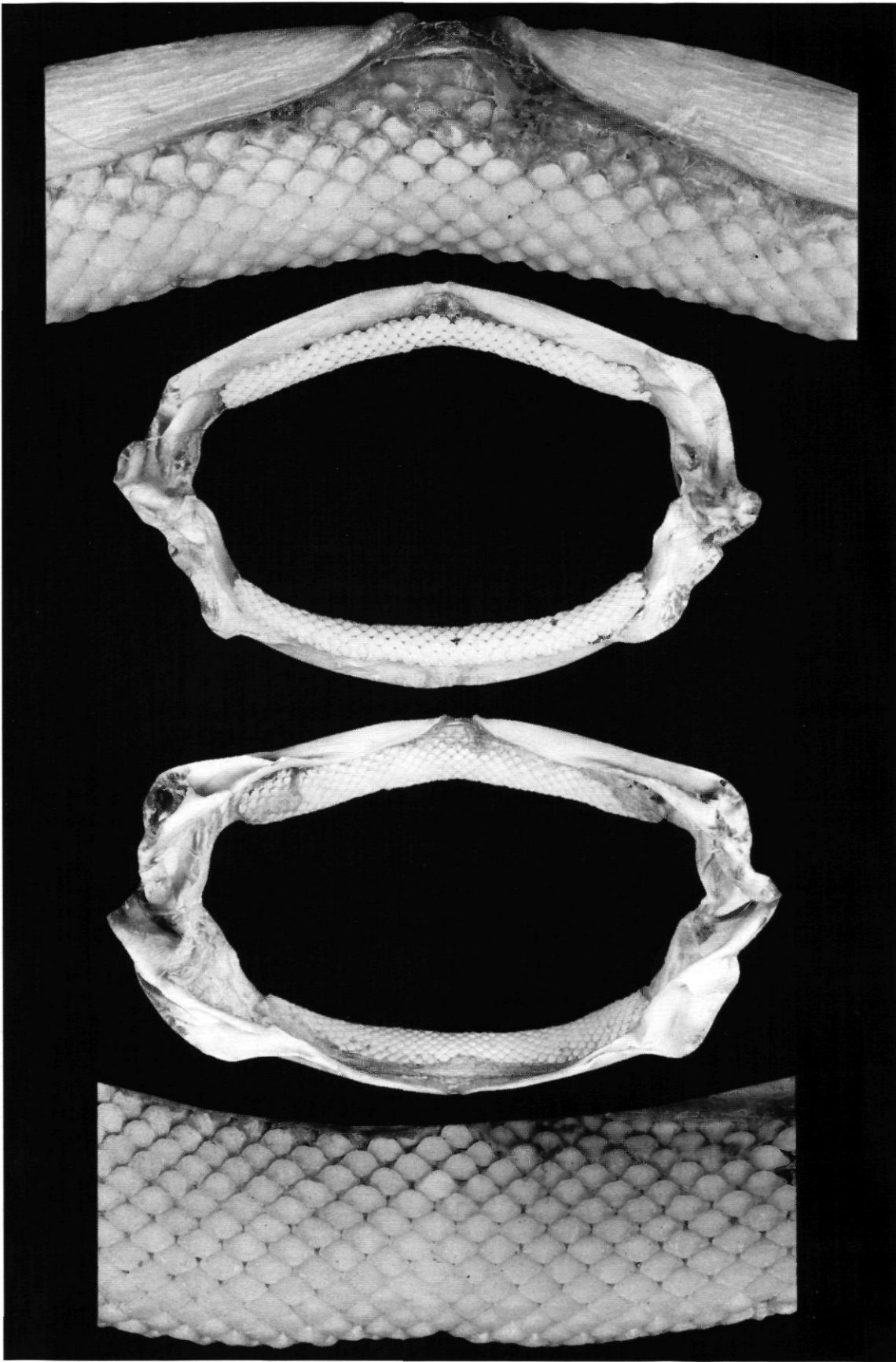
This genus comprises, after GARMAN (1913), the species *U. maculatus*, *U. halleri*, *U. nebulosus*, *U. vermiculatus* and the type species *U. sloani*. The genus *Urobatis* is now considered as a synonym of the genus *Urolophus* and the type species *U. sloani* as synonym of *U. jamaicensis* CASTRO-AGUIRRE & ESPINOSA PEREZ, 1996). Teeth of *U. jamaicensis* will be described and illustrated to provide information from the odontological point of view.

Urobatis sloani (BLAINVILLE, 1816)
= *Urolophus jamaicensis* (CUVIER, 1817)
(Plates: 1 to 4; Textplate: 1)

Leiobatis sloani BAINVILLE, 1816. Prodrôme d'une nouvelle distribution systématique du règne animal. *Bulletin de la Société Phylomatique Paris*, 8: 105-124.



Textplate 1. – *Urobatis sloani* (BLAINVILLE, 1816). Female 31 cm t.l., Belize, British Honduras. Right parts of the upper and lower jaws. SEM pictures, magnification of 17.



Textplate 2. – *Plesiobatis daviesi* (WALLACE, 1967). Female 230 cm t.l., off New Caledonia. Outer and inner views of the jaws, magnification of 0.75. Details of symphyseal parts.

HETERODONTY

The dentition is gradient monognathic heterodont with lateral and posterior teeth becoming lower toward the commissure.

Neither sexual, nor ontogenetic heterodonty are given.

VASCULARIZATION

Although the external morphology of the teeth shows a holaulacorhizid root type, a pulp cavity is absent in the root, but the corresponding space filled by osteodentine. The vascular tubes of the orthodentine in the crown region radiate from the osteons into crown and root. Inner lateral foramina are absent. (See textfigure 1).



Textfigure 1.

Urobatis sloani tooth histological cross section.

MALES AND FEMALES

In occlusal view, the crown has an arched, high, irregularly shaped transverse keel, dividing the crown into an inner and outer part. A second transverse keel is present on the outer surface, the mesial and distal margins do not reach those of the crown. The crown is as high as broad in anterior teeth and diminishing in height and size toward the commissure. In occlusal view, the outer and inner margins of the crown are arched, and both margins join in relatively sharp mesial and distal marginal angles. An inner central ridge is absent. The lower inner surface is slightly concave and slopes toward the rounded inner crown rim. The concave surface in front of the second transverse keel exhibits a poorly developed ornamentation, sometimes hardly perceptible in females, but better developed in males. In basal view of the crown shows a rather, broad, slightly convex crown rim at the outer part, gradually narrowing to half its width at the inner part. The crown-root junction lies in a shallow depression in the centre of the crown's basal surface.

The holaulacorhizid narrow, moderately high root is more or less oval to circular in cross-section, obliquely shaped inward in profile, and slightly diverges at the root base. The root base presents a well-developed, deep median groove with one or two central foramina. Inner and outer foramina, as well as root coating are absent.

Subfamily: Potamotrygoninae

INTRODUCTION

The lacking material of a male and female *Paratrygon aiereba* for the previous issue (4b) is described and illustrated below. Only juveniles were available for examination.

Material

The following 2 specimen of 1 species were examined:

<i>Paratrygon aiereba</i>			
UFPB 3524	♂	211 mm	DW
UFPB 3478	♀	275 mm	DW

Description of the odontological characters

Genus *Paratrygon* ROSA, CASTELLO & THORSON, 1987

After ROSA, CASTELLO & THORSON (1987) the genus is monotypic with *Paratrygon aiereba*. The genus was not incorporated in the phylogenetic study of NISHIDA (1990) without any discussion. Also NELSON (1994) synonymised this genus with *Disceus* without any argumentation.

Paratrygon aiereba (MÜLLER & HENLE, 1841)
(Plates: 5 to 8 ; Textplate:..)

Trygon aiereba MÜLLER & HENLE, 1841 Systematische Beschreibung der Plagiostomen. Verlag Von Veit und Comp. Berlin: 1-200.

HETERODONTY

The dentition is gradient monognathic heterodont with lateral and posterior teeth becoming lower and slightly inclined toward the commissure.

Sexual heterodonty is absent in juveniles and is assumed to be absent in adults as well.

Usually, the ontogenetic heterodonty in dasyatid taxa is presented by low crowns, having a transverse keel in females, versus a high cusp in males only (e.g. *Dasyatis pastinaca*) or sometimes even in both, males and females (e.g. *Amphotistius kuhlii*). However, juveniles of *Paratrygon aiereba* already possess a relatively high cusp in anterior teeth and a low cusp in lateral teeth. This suggests, that ontogenetic heterodonty will hardly be present, or maybe given by higher cusps, particularly in lateral teeth.

VASCULARIZATION

The teeth possess a holaulacorhizid root type with a pulp cavity extended upward in the root. The vascular tubes of the orthodentine in the crown region radiate from the pulp cavity into crown and root. Inner lateral foramina are absent. (See textfigure 2).



Textfigure 2.

Paratrygon aiereba tooth histological cross section.

MALES AND FEMALES

In occlusal view, the crown has an inward inclined, massive cusp. The crown is as high as broad in anterior teeth, slightly inclining distally and diminishing in height in lateral, and transformed into a transverse keel in posterior teeth. The outer and inner margins of the crown are arched, and both margins join in blunt mesial and distal marginal angles. The inner central ridge at the smooth inner face is poorly developed. The lower mid-section and the mesial and distal regions are slightly concave and slope toward the rounded inner crown rim. The slightly concave outer part is smooth. In basal view the crown shows a rather, broad, slightly convex crown rim at the outer part, gradually narrowing to half its width at the inner part. The crown-root junction lies in a shallow depression in the centre of the crown's basal surface.

The holaulacorhizid narrow, moderately high root is more or less oval in cross-section, obliquely shaped inward in profile, and slightly diverges at the root base. The root base presents a well developed, deep median groove with one or two central foramina. Inner and outer foramina, as well as root coating are absent.

Family: Plesiobatidae

INTRODUCTION

Adult males and females and juveniles of *Plesiobatis daviesi* are now described and illustrated below.

Material

The following 3 specimen of 1 species were examined:

<i>Plesiobatis daviesi</i>			
CSIRO CA4238	♂	376 mm	DW
Coll. Seret	♀	1260 mm	DW
Coll. Seret	♂	610 mm	DW

Description of the odontological characters

Plesiobatis daviesi (WALLACE, 1967)
(Plates: 9 to 14; Textplate: 2)

Urotrygon daviesi WALLACE, 1967. The batoid fishes of the east coast of southern Africa. Part II: Manta, eagle, duckbill, cownose, butterfly and sting rays. *Oceanographic Research Institute Investigational Report, Durban* (16): 1-56.

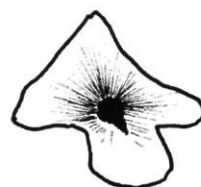
HETERODONTY

The dentition is gradient monognathic heterodont with lateral and posterior teeth becoming lower toward the commissure in males.

Sexual heterodonty is documented by a high crown in anterior and antero-lateral teeth in males, *versus* a high, transverse keel across the crown in females. Ontogenetic heterodonty is present in juvenile males, having adult female tooth morphology with low cusps.

VASCULARIZATION

The teeth possess a holaulacorhizid root type with a large pulp cavity in the root. The vascular tubes of the orthodontine radiate from the pulp cavity into crown and root. Inner lateral foramina are absent. (See textfigure 3).



Textfigure 3.
Plesiobatis daviesi tooth histological cross section.

MALES

In occlusal view, the broad-based crown has an inwardly inclined high cusp with irregularly shaped cutting edges at both sides. The crown is as high as broad in anterior and lateral teeth, not inclining distally and diminishing in height toward the commissure. The outer margins of the crown are arched, the inner one is more or less trapezoid, and both margins join in very blunt mesial and distal marginal angles. The inner central ridge at the inner face is poorly developed. The lower mid-section and the mesial and distal regions are slightly concave and slope toward the rounded inner crown rim. The inner surface possess a coarse costules mainly positioned along the cutting edges. The slightly concave outer part presents a fine, reticulated ornamentation. In basal view the crown shows a rather, broad, slightly convex crown rim at the outer part, gradually narrowing to half its width at the inner part. The crown-root junction lies in a shallow depression in the centre of the basal surface of the crown.

The holaulacorhizid narrow, moderately high root is more or less oval to circular in cross-section, obliquely shaped inward in profile, and slightly diverges at the root base. The root base presents a well-developed, deep median groove with one or two central apertures. Inner and outer foramina, as well as root coating are absent.

FEMALES

In occlusal view, the broad based crown has a relatively high transverse keel, generally flattened by abbrasion through working. The crown is as high as broad in anterior and lateral teeth, broadening and diminishing in size toward the commissure. The outer and inner margins of the crown are strongly arched, attaining an almost semi-oval shape in posterior teeth. The inner central ridge on the inner face is poorly developed. The inner surface possess a coarse costules mainly positioned along the cutting edges. The lower mid-section and the mesial and distal regions are slightly concave and slope toward the rounded inner crown rim. The slightly concave outer part presents a fine, reticulated ornamentation. In basal view the crown shows a rather, broad, slightly convex crown rim at the outer part, gradually

narrowing to half its width at the inner part. The crown-root junction lies in a shallow depression in the centre of the basal surface of the crown.

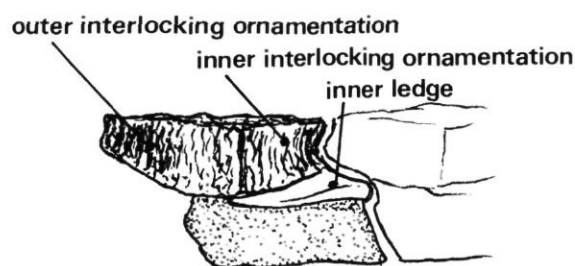
The holaulacorhizid narrow, moderately high root is more or less oval to circular in cross-section, obliquely shaped inward in profile, and slightly diverges at the root base. The root base presents a well developed, deep median groove with one or two central apertures. Inner and outer foramina, as well as root coating are absent.

Superfamily: Myliobatoidea

According to NELSON (1994), the Myliobatoidea include the families Gymnuridae (see previous issues 4a and 4b), and Myliobatidae.

Family: Myliobatidae

This family is subdivided (NELSON, 1994) into the subfamilies Mobulinae (*Manta* and *Mobula*), Myliobatinae (*Aetobatus*, *Aetomylaeus*, *Myliobatis* and *Pteromylaeus*) and Rhinopterinae (*Rhinoptera*). The tooth morphology of all these genera is significantly different from that of other batoids. The taxa of the subfamilies Myliobatinae and Rhinopterinae present odontological characters being different from those described in previous rajiform issues. Their terminology is presented in textfig. 4 below.



Textfigure 4.
Myliobatis tooth terminology.

Inner and outer ornamentation serves for interlocking the teeth of a row in mesio-distal direction, whilst the inner ledge locks the teeth in vertical direction to form crushing plates.

Material

The following 51 specimen of 13 species were examined:

Aetobatus narinari

AMS D4054	♀	550 mm	DW
ZMH 10392	♀	1941 mm	TL
ISH 2-1993	♂	890 mm	TL
ZMH 8865	♂	720 mm	TL
Coll. Herman	♀	1020 mm	TL

Aetomylaeus maculatus

ZMH 1390	♀	1009 mm	TL
ISH 13-1961	♂	1035 mm	TL

ISH 14-1961	♂	280 mm	DW
CSIRO H 4426-15	♀	1548 mm	TL
IRSNB uncat.	♂	520 mm	TL

Ceratobatis robertsii

BMNH 1897.7.1.40	♀	770 mm	DW (holotype)
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Cephaloptera giorno

MNH uncat.	♀	4800 mm	DW
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Manta birostris

Coll. Herman	♀	4700 mm	DW
Coll. Herman	♀	2500 mm	DW

Mobula mobular

Coll. Cigala Fulgosi	♂	1240 mm	DW
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Mobula rochebrunei

Coll. Herman	♂	1200 mm	DW
Coll. Herman	♀	1100 mm	DW
Coll. Herman	♂	990 mm	DW
Coll. Herman	♀	1070 mm	DW

Myliobatis aquila

Coll. Hovestadt	♂	500 mm	DW
Coll. Hovestadt	♂	960 mm	DW
Coll. Hovestadt	♀	1040 mm	DW
Coll. Hovestadt	♀	650 mm	DW
Coll. Hovestadt	♂	530 mm	DW
Coll. Hovestadt	♀	480 mm	DW
Coll. Hovestadt	♀	440 mm	DW
Coll. Hovestadt	♂	530 mm	DW
Coll. Hovestadt	♂	550 mm	DW
Coll. Hovestadt	♂	750 mm	DW
Coll. Hovestadt	♀	400 mm	DW
Coll. Hovestadt	♂	600 mm	DW
Coll. Herman	♀	1200 mm	DW
Coll. Herman	♀	560 mm	DW
Coll. Herman	♂	520 mm	DW

Myliobatis australis

Coll. Hovestadt	♂	740 mm	DW
Coll. Hovestadt	♂	795 mm	DW
Coll. Hovestadt	♀	940 mm	DW
Coll. Hovestadt	♂	1000 mm	DW
Coll. Herman	♀	660 mm	DW

Myliobatis fremenvillei

Coll. Hovestadt	♀	810 mm	DW
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Pteromylaeus bovinus

Coll. Bor	♂	472 mm	DW
Coll. Bor	♂	425 mm	DW
Coll. Bor	?	? mm	DW
Coll. Bor	?	? mm	DW
ISH 1348-1964	♂	520 mm	DW

Rhinoptera bonasus

Coll. Hovestadt	♂	520 mm	DW
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Coll. Hovestadt	♀	390 mm	DW
Coll. Hovestadt	♀	390 mm	DW
<i>Rhinoptera brasiliensis</i>			
Coll. Herman	♀	370 mm	DW
<i>Rhinoptera marginata</i>			
ISH 86-1977	♀	421 mm	DW
<i>Rhinoptera peli</i>			
Coll. Herman	♀	700 mm	DW

Subfamily: Mobulinae

The subfamily Mobulinae comprises after NELSON (1994) the genera *Manta* and *Mobula*. The tooth morphology of the doubtful genus *Ceratobatis* is described and illustrated with its type species *C. robertsii* to provide its odontological features. Two significantly different odontological morphotypes are represented by *M. mobular* and *M. rochebrunei*.

Genus: *Ceratobatis* BOULENGER, 1897

The genus is monotypic. The type species *C. robertsii* has only teeth in the upper jaw.

Ceratobatis robertsii BOULENGER, 1897
(Plate: 25)

Ceratobatis robertsii BOULENGER, 1897. Description of a new ceratopteryn eagle-ray from Jamaica. *Annals and Magazine of natural History, London*, (6): 1-20.

HETERODONTY

This genus has mesio-distally enlarged, flat crowned, anterior teeth, and smaller lateral and posterior teeth in the upper jaw only. Because only the female holotype is known, neither sexual nor ontogenetic heterodonty could be examined.

VASCULARIZATION

The teeth show an adapted, holaulacorhizid or, depending on its position in the jaw, polyaulacorhizid root type with a broad pulp cavity in the lower part of the crown. The vascular tubes of the circumpulpar dentine radiate from the pulp cavity into crown and root. The root is osteodont. Inner lateral foramina are absent. (See textfigure 5)



Textfigure 5.
Ceratobatis robertsii tooth histological cross section.

FEMALES

The teeth are mesio-distally enlarged. In occlusal view, the anterior teeth are mesio-distally approximately twice as large as in inner-outer direction, the posterior teeth even up to three times larger than lateral teeth. Because the crown is directed extremely inward, the occlusal view shows only the outer surface with a broad, straight transverse ridge at the inner margin and the outer ornamentation. This particular ornamentation is represented by coarse, vertically arranged costules. The inner view shows the inner surface completely overhung by the transverse ridge. An inner ornamentation is represented by depressions in the surface of the crown's inner part. The root is irregularly polyaulacorhizid, with two or three, irregularly positioned grooves in basal view. The outer view shows several irregularly sized foramina, lined along the crown-root junction. Inner foramina are absent. The maximum size of the teeth is approximately 2 mm wide.

Genus: *Manta* BANCROFT, 1828

The genus has only teeth in the lower jaw and comprises four nominal species. The type species is *M. birostris*.

Manta birostris (DONNDORFF, 1798)
(Plates: 15 to 18 ; Textplate: 3)

Raia birostris DONNDORFF, 1798. Zoologische Beiträge zur 13ten Ausgabe des Linnéschen Natursystems. Leipzig. Vol. 3, Ichthyologische Beiträge: 876.

HETERODONTY

This species has teeth with high, flat crowned, anterior teeth, of which some are mesio-distally enlarged. This last phenomenon is more obvious on the jaw of the smallest specimen examined (female 250 cm d.w.). Neither sexual heterodonty nor ontogenetic heterodonty could be examined due to lack of material.

VASCULARIZATION

The teeth show an adapted holaulacorhizid to sometimes anaulacorhizid root type. Root and crown are completely osteodont, with a coarse reticulated vascular canal system connecting various osteons. (See textfigure 6)



Textfigure 6.
Manta birostris tooth histological cross section.

FEMALES

The crown is high and circular to semi-oval in cross-section. The top is flat to slightly concave with a surface, that is obliquely shaped inward in profil. The surface shows a well-developed reticulated ornamentation. The inner margin of the crown slightly overhangs the inner surface. Inner and outer surfaces are smooth. The root strongly widens from the level of crown base into all directions to attain a maximum width of one and a half times that of the crown, and then basally narrows abruptly to become bulb-shaped. Several foramina are randomly scattered over the root surface. Some teeth possess a median groove with a central foramen. The maximum size of the teeth is approximately 2 mm wide.

Genus: *Mobula* RAFINESQUE, 1810

The genus comprises 13 nominal species (NOTARBARTOLO DI SCIARI, 1987). The type species is *Mobula mobular*. *M. mobular* and *M. rochebrunei* are described and illustrated.

Mobula mobular (BONNATERRE, 1788)
(Plate: 24)

Raia mobular BONNATERRE, 1788. Tableau encyclopédique et méthodique des trois règnes de la nature. Ichthyologie: 5.

HETERODONTY

This specis has teeth with high, flat-crowned, anterior teeth. Neither sexual heterodonty nor ontogenetic heterodonty could be examined due to lack of material.

VASCULARIZATION

The teeth show an adapted holaulacorhizid to sometimes anaulacorhizid root type. The teeth are orthodont with one or two pulp cavities in the root, from which the vascular tubes of the orthodontine radiate into root and crown. (See textfigure 7)



Textfigure 7.
Mobula mobular tooth histological cross section.

MALES

The crown is high and circular to semi-oval in cross-section. The top is flat to slightly concave with a surface, that is obliquely shaped inward in profil. The surface shows a well-developed reticulated ornamentation. The inner margin of the crown slightly overhangs the inner surface. Inner and outer surfaces are smooth. The root strongly widens from the

level of crown base into all directions to attain a maximum width of one and a half times that of the crown, and then basally narrows abruptly to become bulb-shaped. Several foramina are randomly scattered over the root surface. Some teeth possess a median groove with a central foramen. The maximum size of the teeth is approximately 2 mm wide.

Mobula rochebrunei (VAILLANT, 1879)
(Plates: 19 to 23; Textplates: 4 and 5)

Cephaloptera rochebrunei VAILLANT, 1879. Note sur une nouvelle espèce d'élasmobranche hypotrème, le *Cephaloptera rochebrunei*. *Bulletin de la Société Philomatique, Paris*, 7(3): 187-188.

HETERODONTY

The dentition is gradient monognathic heterodont with mesio-distally slightly enlarged anterior teeth becoming smaller in lateral and posterior teeth. Sexual heterodonty is documented by an inward inclined crown with an irregularly shaped cutting edge in females, but a cutting edge with mostly one to six or even more defined cusps in males. Ontogenetic heterodonty is shown by juvenile teeth being not mesio-distally enlarged. The dentition is rather unstable and varies to a degree as described above.

VASCULARIZATION

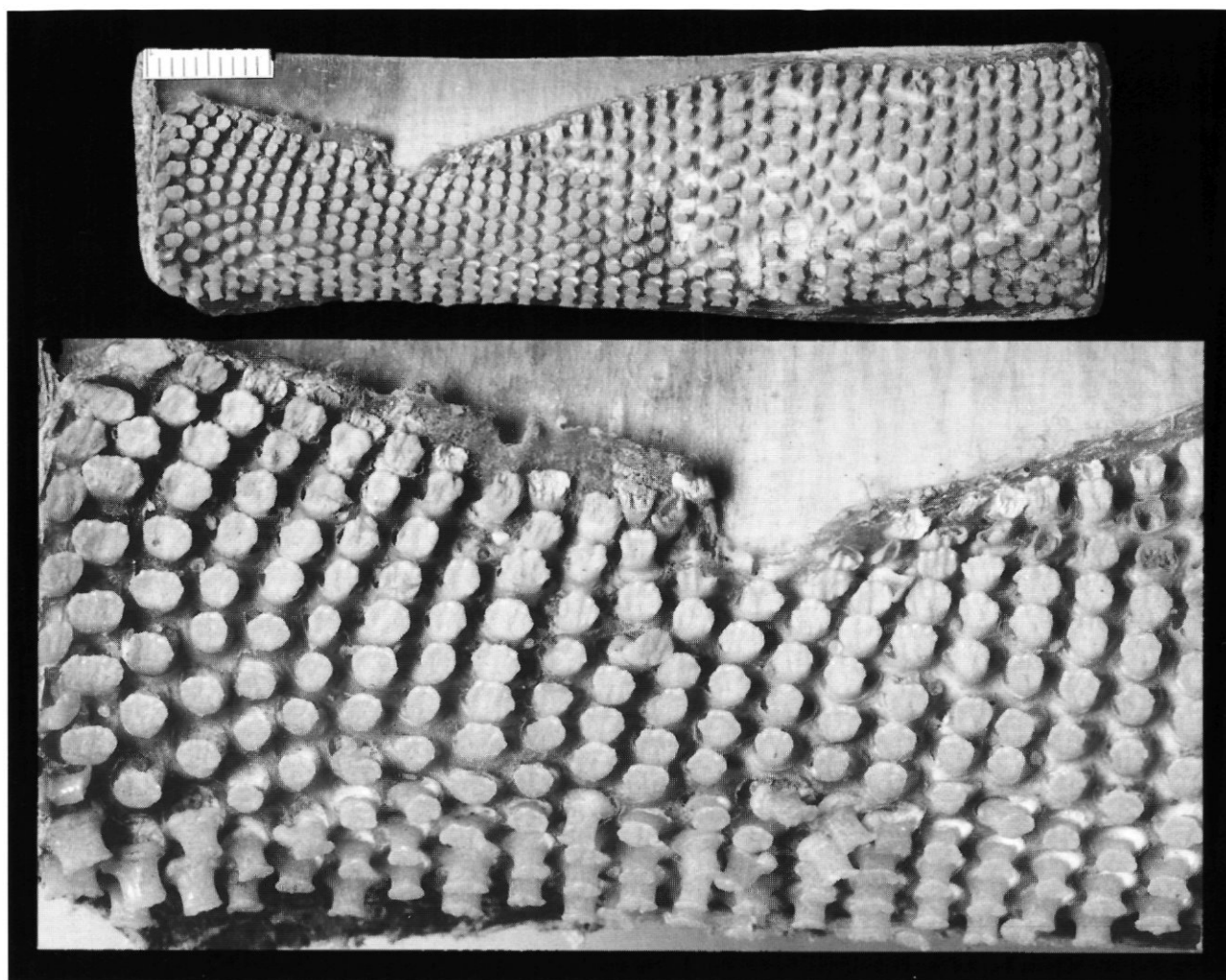
The teeth show an adapted, holaulacorhizid or, depending on their position in the jaw, polyaulacorhizid root type with a broad pulp cavity in the lower part of the crown. The vascular tubes of the circumpulpar dentine radiate from the pulp cavity into crown and root. The root is osteodont. Inner lateral foramina are absent. (See textfigure 8)



Textfigure 8.
Mobula rochebrunei tooth histological cross section.

FEMALES

The anterior teeth are mesio-distally enlarged and approximately twice as wide as broad, the posterior ones upto three times as wide as lateral teeth. Because of the extremely inward directed crown, the occlusal view only shows an outer surface with a broad, angled to coarsely serrated transverse ridge at the inner margin and an outer ornamentation varying



Textplate 3. – *Manta birostris* (DONNDORFF, 1798). Female 250 cm d.w., Gorea, Senegal. Male 470 cm d.w., Somone, Senegal.
Part of the right side of the lower jaw.

from hardly perceptible to well developed. If present, this particular ornamentation is formed by coarse, vertically arranged costules. The inner surface is completely overhung by the transverse ridge. An inner ornamentation is not always present, but if present, it is only in the surface of the crown's inner part. The root is irregularly polyaulacorhizid, with two or three, irregularly positioned grooves in basal view. The outer view shows several foramina of various sizes, lined along the crown-root junction. Inner foramina are absent. The maximum size of the teeth is approximately 2 mm. wide.

MALES

The teeth are mesio-distally approximately twice as wide as broad. The crown is directed inward, presenting one to three cusplets and remains of an outer ornamentation consisting of large, irregular undulations. An inner ornamentation is lacking. The root is irregularly polyaulacorhizid, with two or three, irregularly positioned grooves in basal view. The outer view shows several scattered foramina of irregular size. Inner foramina are absent. The maximum size of the teeth is approximately 1 1/2 mm wide.

Subfamily Myliobatinae

The Myliobatinae comprise the genera *Aetobatus*, *Aetomylaeus*, *Myliobatis* and *Pteromylaeus*. To allow SEM-photographing of these species' large teeth, juveniles were selected only.

Genus: *Aetobatus* BLAINVILLE, 1816

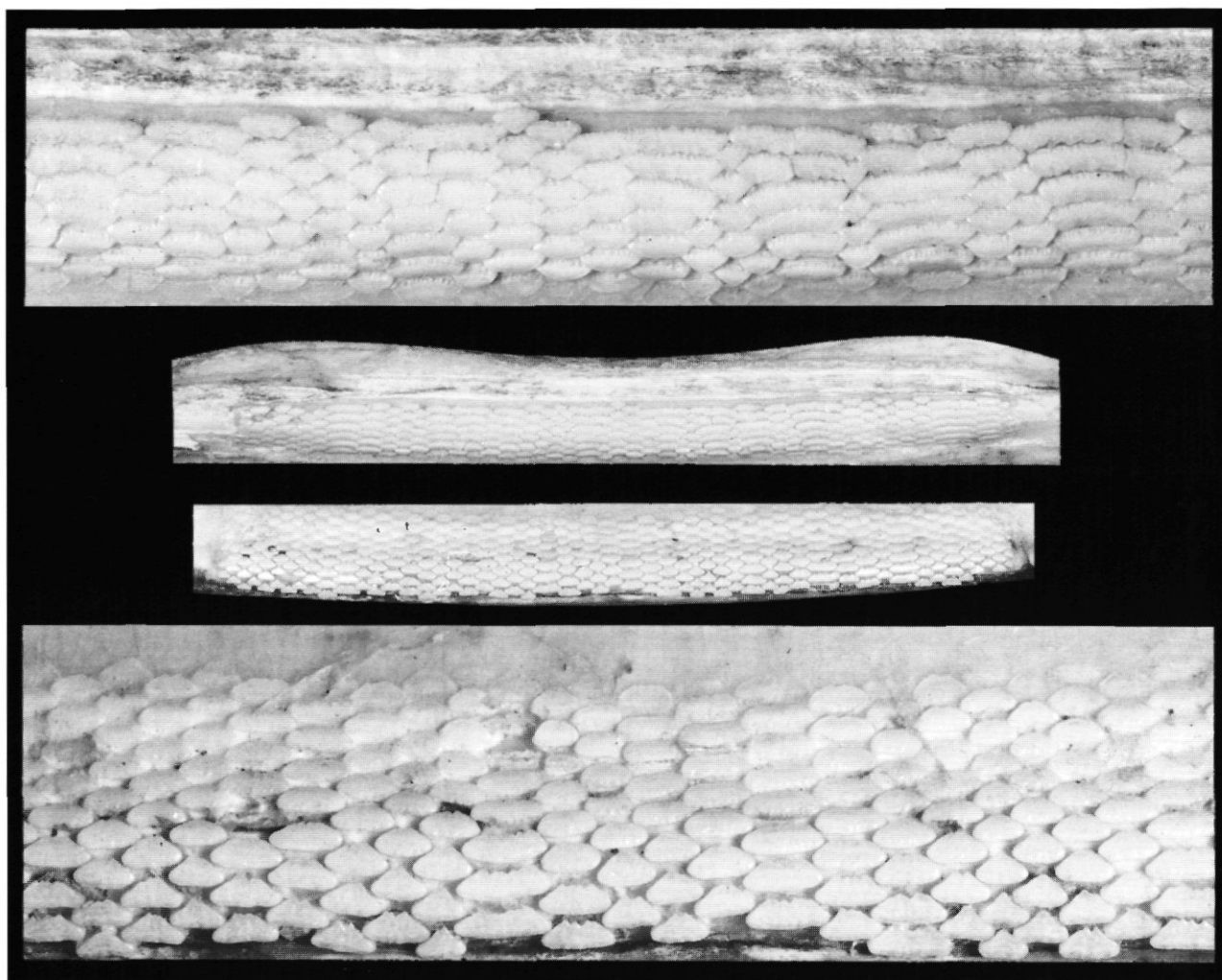
This genus is monotypic with *A. narinari*.

Aetobatus narinari (EUPHRASEN, 1790)
(Plate: 26; Textplate: 6)

Raja narinari EUPHRASEN, 1790. Raja beskrifven. Handlingar Kungliga Svenska Vetenskapsakademiens 2: 217-219.

HETERODONTY

The low-crowned dentition of this genus consists of a single symphyseal tooth row in both upper and lower jaws.



Textplate 4. – *Mobula rochebrunei* (VAILLANT, 1879). Female 110 cm. d.w., Gorea, Senegal. Upper and lower dentitions, magnification of 1.5. Details of the symphyseal parts of both jaws.

Dignathic heterodonty is documented in occlusal view by mesio-distally V-shaped lower and mesio-distally straight upper teeth. Convex upper and lower teeth in inner and outer view and a wider angled V-shape in lower teeth of juveniles show a weak ontogenetic heterodonty. Sexual heterodonty was not found.

VASCULARIZATION

The teeth have a polyaulacorhizid root type with an adapted type of osteodentine, with mesio-distally enlarged canals above the root lobes. These canals are connected to the vertical ones of the root lobes, as well as to a narrow band of osteodentine above them, from which densely packed, parallel canals arise and pierce vertically into the crown. (See textfigure 9)

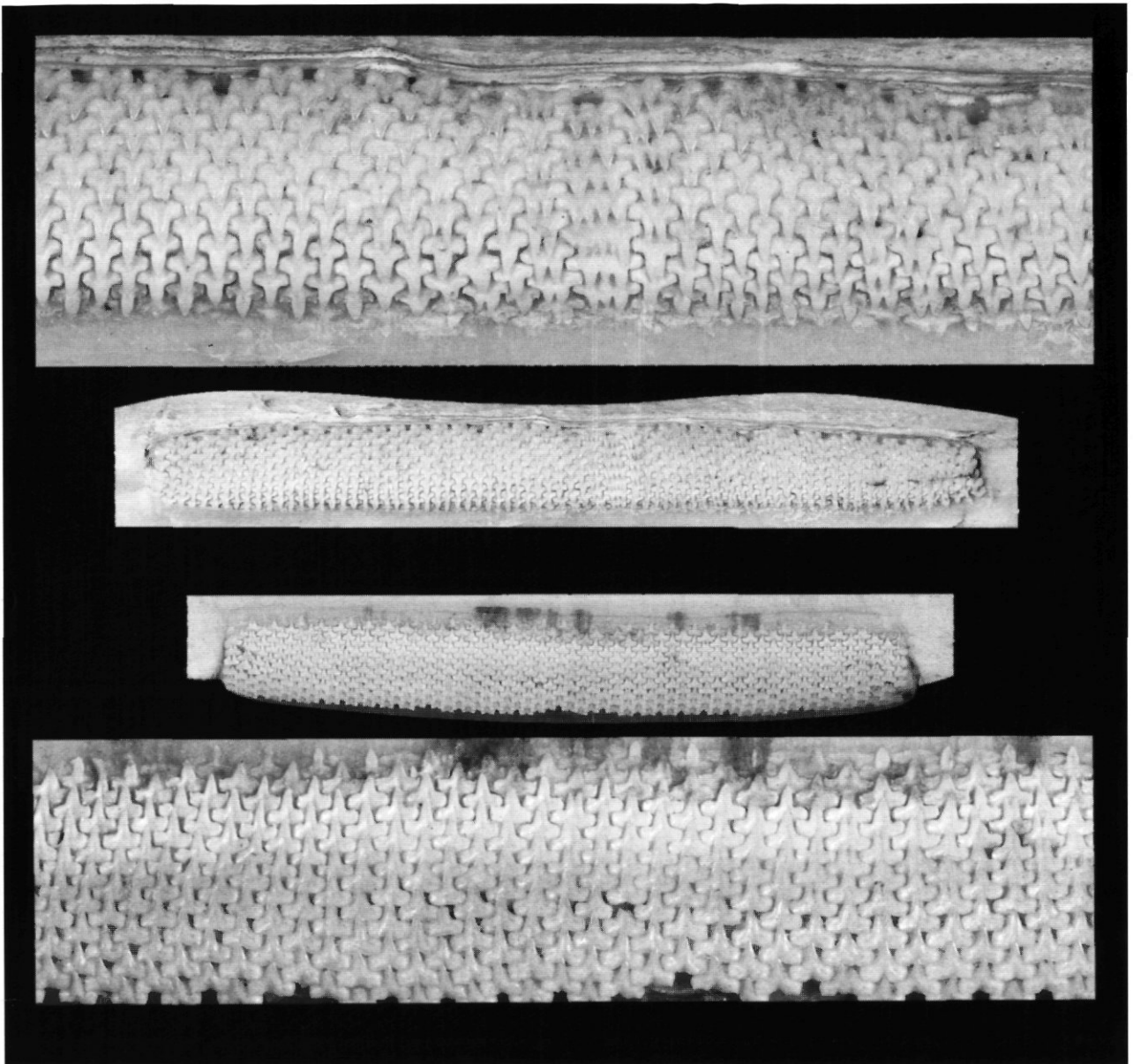


Textfigure 9.
Aetobatus narinari tooth histological cross section.

MALES AND FEMALES

Teeth of the single upper jaw row are extremely enlarged, with a flat top in occlusal view. A tooth is mesio-distally arched outward, with a convex crown top surface in juveniles, but mesio-distally straight with a flattened crown top surface in adults. The lower teeth are V-shaped with the pointed end outward at an angle of approximately 150 degrees in juveniles but narrower at 110 degrees in adults, with a flat crown top surface. Disregarding abrasion marks, the crown top surface is always smooth.

An inner and outer interlocking ornamentation is absent. However, adult teeth exhibit relatively fine vertical costules on inner and outer surfaces. A narrow inner ledge is present. The root is shifted inward from the crown in profil, so that the outer crown overhangs the outer root edge. This feature interlocks the teeth, in that the outer crown edge rests on the inner root edge of the tooth in front and the outer crown edge of the previous tooth on the protruding inner root edge. The root is polyaulacorhizid with numerous evenly shaped basal grooves, each with scattered foramina along the groove's centre.



Textplate 5. – *Mobula rochebrunei* (VAILLANT, 1879). Male 120 cm. d.w., Gorea, Senegal. Upper and lower dentitions, magnification of 1.5. Details of the symphyseal parts of both jaws.

Genus: *Aetomylaeus* GARMAN, 1908

This genus is monotypic with *A. maculatus*.

Aetomylaeus maculatus (GRAY, 1834)
(Plates: 27 and 28; Textplate: 7)

Myliobatus maculatus GRAY, 1834. Illustrations of Indian zoology; chiefly selected from the collection of Major-General Hardwicke, London. vol. 2: pl. 101.

HETERODONTY

The low-crowned dentition is disjunct monognathic heterodont through mesio-distally very much enlarged symphyseal

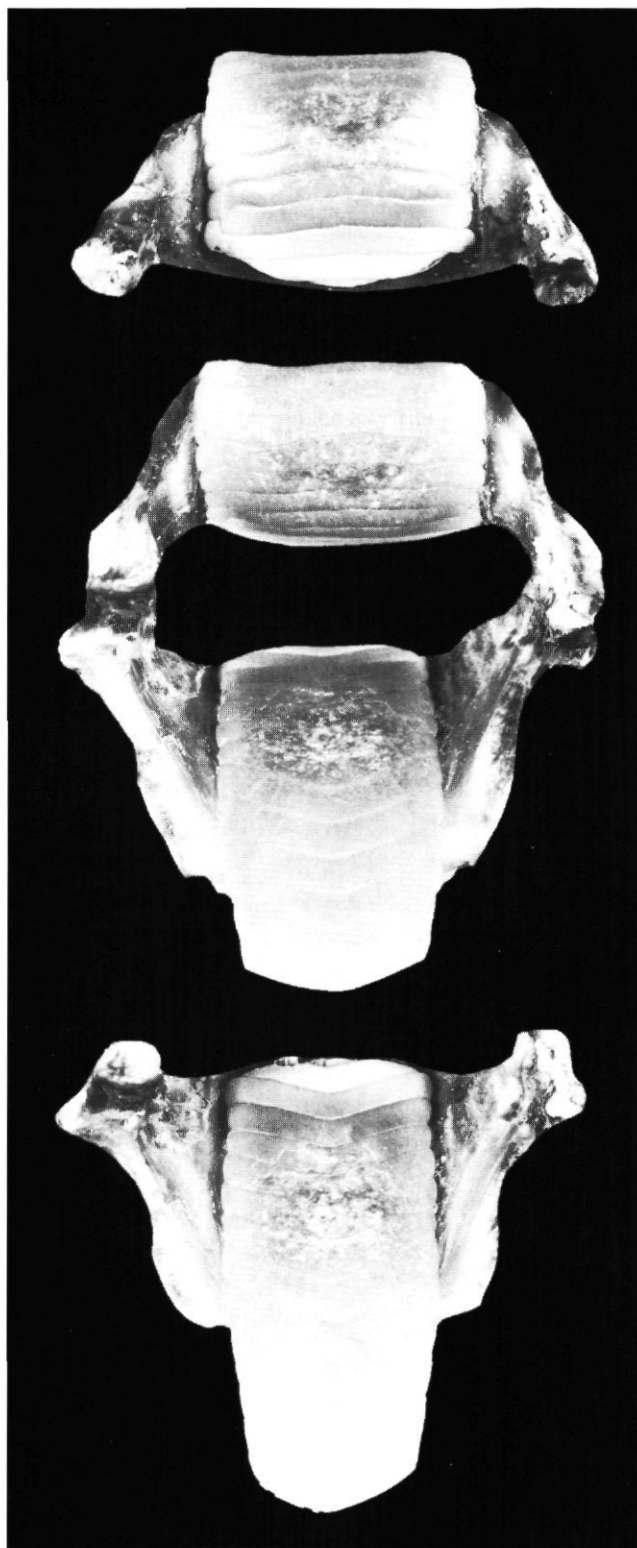
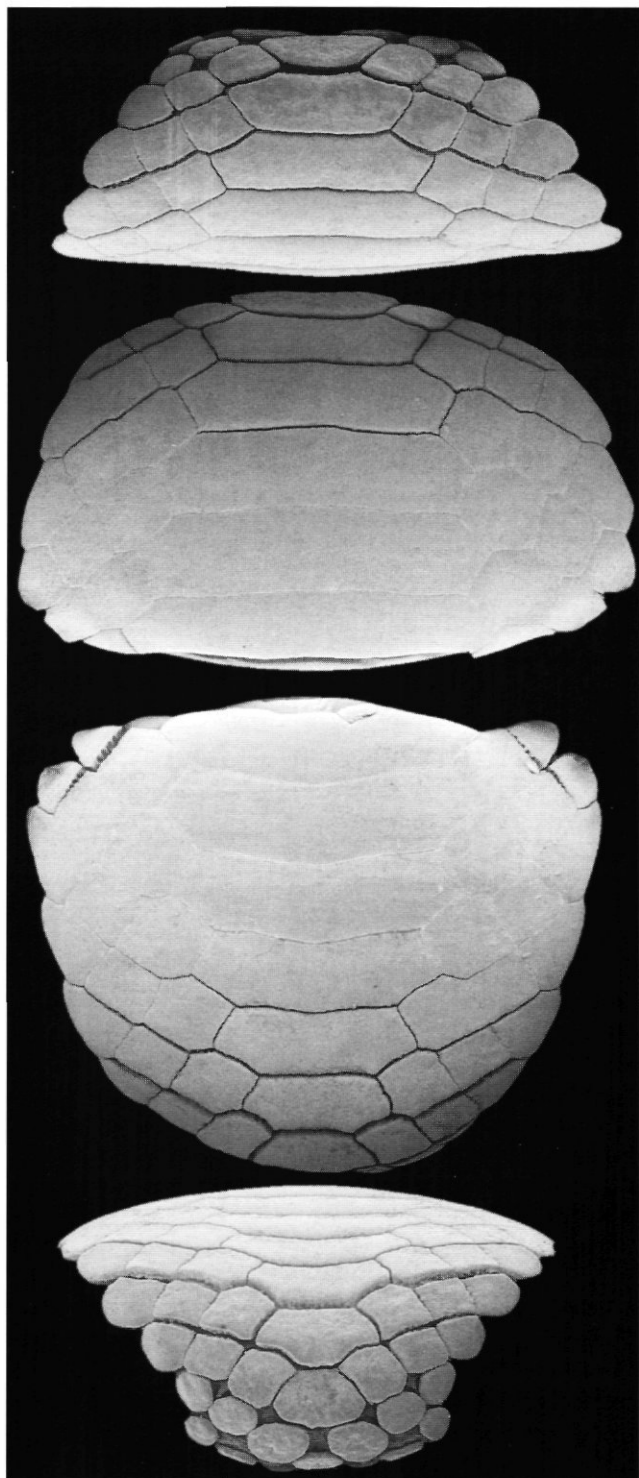
teeth and not enlarged, square-shaped lateral teeth. Neither sexual nor ontogenetic heterodonty was found. The enlargement of the symphyseals is not stable and may vary within the species. The lateral teeth are positioned in an imbricated manner, in that half of the tooth width of one row is shifted mesially and distally over the neighboring rows.

Textfigure 10.
Aetomylaeus maculatus tooth histological cross section.



VASCULARIZATION

The teeth have a holaulacorhizid to polyaulacorhizid root type (depending on their jaw position) with an adapted type of osteodentine, that shows mesio-distally enlarged canals above the root lobes. These canals are connected to the vertical ones of the root lobes, as well as to a narrow band of osteodentine above them, from which irregularly shaped semi-parallel canals arise, that run vertically into the crown. (See textfigure 10)



Textplate 6. – *Aetobatus narinari* (EUPHRASEN, 1790). Female 102 cm t.l., 38 cm d.w., Rio de Janeiro, Brasil. Jaws, magnification of 2.

Textplate 7. – *Aetomylaeus maculatus* (GRAY, 1834). Male 52 cm t.l., Indonesia. Upper and lower dental plates, magnification of 8.5.

MALES AND FEMALES

Teeth of the upper symphyseal row are hexagonal in occlusal view and extremely enlarged, with a flat top surface. These teeth are slightly arched inward in juveniles but straight in adults. Teeth of the lower symphyseal row are similar and straight in both, juveniles and adults. Disregarding abrasion marks, the crown's top surface of upper and lower teeth is always smooth.

An inner and outer interlocking ornamentation is provided by relatively fine, reticulated, merely vertically arranged costules. A narrow inner ledge is present. The root is shifted inward from the crown in profile, so that the outer crown edge overhangs the outer root edge. This feature interlocks the teeth, in that the outer crown edge rests on the inner root edge of the tooth in front and the outer crown edge of the previous tooth on the protruding inner root edge. The root is polyaulacorhizid with numerous evenly shaped basal grooves, each with scattered foramina along the groove's centre.

The lateral teeth are square-shaped in occlusal view, with a flat, smooth crown top surface. An inner and outer interlocking ornamentation is similar to that of the symphyseal teeth. Inner and outer ledges are present. The root is shifted inward from the crown in profile, so that the outer crown edge overhangs the outer root edge. This feature interlocks the teeth, in that the outer crown edge rests on the inner root edge of the tooth in front and the outer crown edge of the previous tooth on the protruding inner root edge. The root is polyaulacorhizid with numerous evenly shaped basal grooves, each with scattered foramina along the groove's centre. The root of posterior teeth is asymmetrical, and the inner and outer interlocking ornamentation, as well as inner and outer ledges are absent at the distal part.

Genus: *Myliobatis* CUVIER, 1816

This comprises ca. 10 nominal species (BIGELOW & SCHROEDER, 1953). The type species is *M. aquila*.

Myliobatis aquila (LINNAEUS, 1758)
(Plate: 29; Textplate: 8)

Raia aquila LINNAEUS, 1758. Systema naturae, ed.X: p.232.

HETERODONTY

The low-crowned dentition is disjunct monognathic heterodont through mesio-distally very much enlarged symphyseal teeth and not enlarged, quadrate-shaped lateral teeth. Neither sexual nor ontogenetic heterodonty was found. The enlargement of the symphyseals is not stable and varies within the species. The lateral teeth are positioned in an imbricated manner, in that half of the tooth width of one row is shifted mesially and distally over the neighbouring rows.

VASCULARIZATION

The teeth have a holaulacorhizid to polyaulacorhizid root type (depending on their jaw position) with an adapted type of osteodentine, that shows mesio-distally enlarged canals above the root lobes. These canals are connected to the vertical ones of the root lobes, as well as to a narrow band of osteodentine above them, from which irregularly shaped semi-parallel canals arise, that run vertically into the crown. (See textfigure 11)



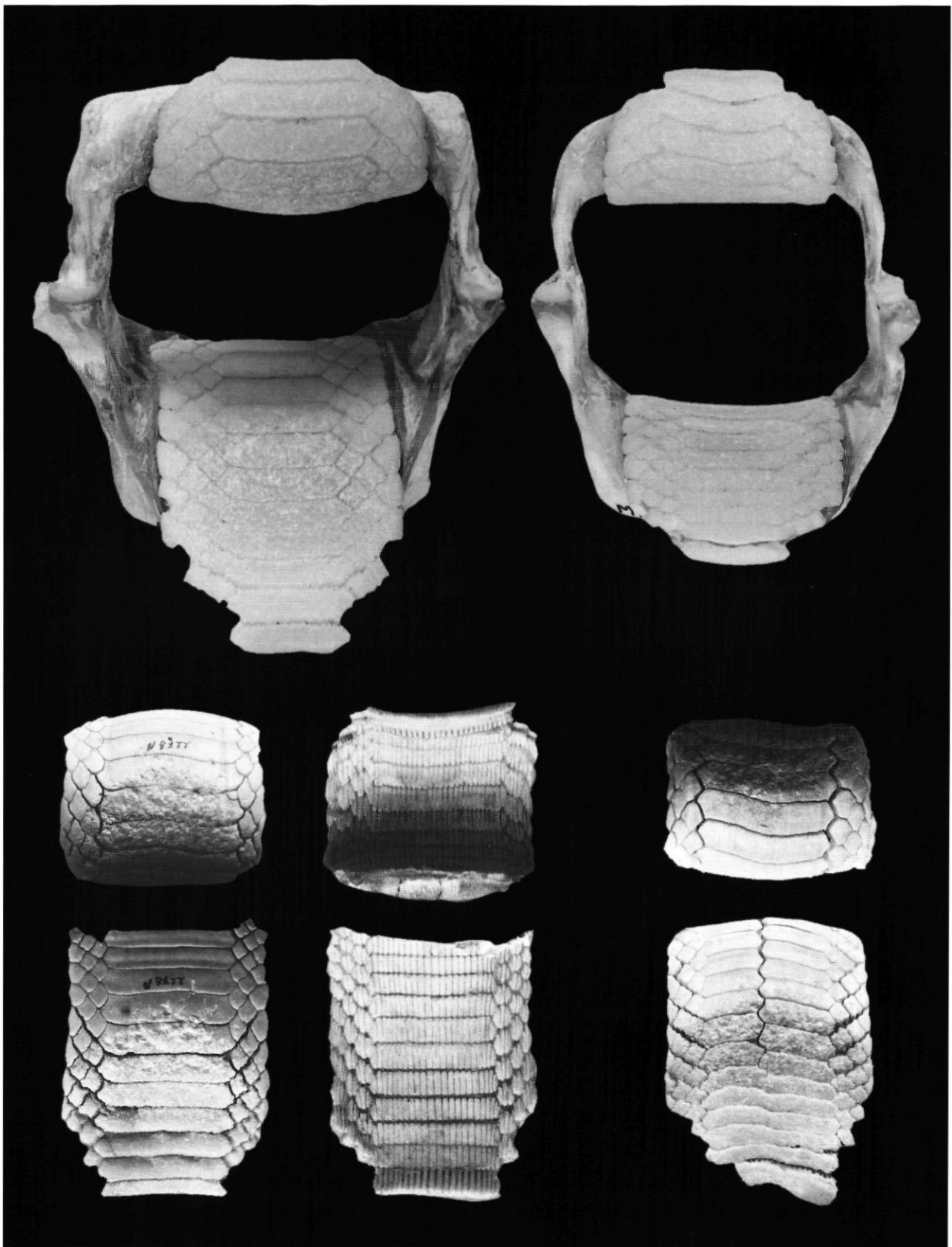
Textfigure 11.
Myliobatis aquila tooth histological cross section.

MALES AND FEMALES

Teeth of the upper symphyseal row are hexagonal in occlusal view and extremely enlarged, with a flat top surface. These teeth are slightly arched inward in juveniles, but straight in adults. Teeth of the lower symphyseal row are similar and straight in both, juveniles and adults. Disregarding abrasion marks, the crown's top surface of upper and lower teeth is always smooth.

An inner and outer interlocking ornamentation is provided by relatively coarse, reticulated, merely vertically arranged costules. A narrow inner ledge is present. The root is shifted inward from the crown in profile, so that the outer crown edge overhangs the outer root edge. This feature interlocks the teeth, in that the outer crown edge rests on the inner root edge of the tooth in front and the outer crown edge of the previous tooth on the protruding inner root edge. The root is polyaulacorhizid with numerous evenly shaped basal grooves, each with scattered foramina along the groove's centre.

The lateral teeth are square-shaped in occlusal view with a flat, smooth crown top surface. An inner and outer interlocking ornamentation is similar to that of the symphyseal teeth. Inner and outer ledges are present. The root is shifted inward from the crown in profile, so that the outer crown edge overhangs the outer root edge. This feature interlocks the teeth, in that the outer crown edge rests on the inner root edge of the tooth in front and the outer crown edge of the previous tooth on the protruding inner root edge. The root is polyaulacorhizid with numerous evenly shaped basal grooves, each with scattered foramina along the groove's centre. The root of posterior teeth is asymmetrical, and the inner and outer interlocking ornamentation, as well as inner and outer ledges are absent at the distal part.



Textplate 8. – *Myliobatis aquila* CUVIER, 1816. **a.** Jaws of a female 60 cm t.l., Nice, France. **b.** Jaws of a male 52 cm t.l., La Rochelle, France. **c.** Dental plates, occlusal and radicular views of a female circa 50 cm t.l., Nice, France. **d.** Dental plates of a female circa 60 cm t.l. showing a dental traumatic anomaly. Nice, France. All approximatively natural size.



Textplate 9. – *Pteromylaeus bovinus* (GEOFFROY SAINT HILAIRE, 1817), no data. Venice, Italy. Jaws, magnification of 0.7. Details of dental plates, circa natural size.

Genus: *Pteromylaeus* GARMAN, 1913

This genus comprises 3 nominal species (GARMAN, 1913). The type species is *P. asperrimus* but was not available. Teeth of *P. bovinus* were studied instead.

Pteromylaeus bovinus (E. GEOFFROY SAINT HILAIRE, 1817)
(Plate: 30; Textplate: 9)

Myliobatis bovina E. GEOFFROY SAINT HILAIRE, 1817. Histoire naturelle des poissons de le mer Rouge et de la Méditerranée. France. Commission d’Egypte. Vol. 1: p.26, fig. 1.

HETERODONTY

The low crowned dentition is disjunct monognathic heterodont through mesio-distally very much enlarged symphyssial teeth and not enlarged lateral teeth. Sexual heterodonty was found. Ontogenetic heterodonty is shown in adults through outward arched upper and lower symphyssial teeth (the lowers more arched than the upper ones), with the mesial and distal margins shifted inward by abrupt curving of the mesial and distal part of the inner and outer margin. The lateral teeth are positioned in an imbricated manner, in that half of the tooth width of a row is shifted mesially and distally over the neighbouring rows.

VASCULARIZATION

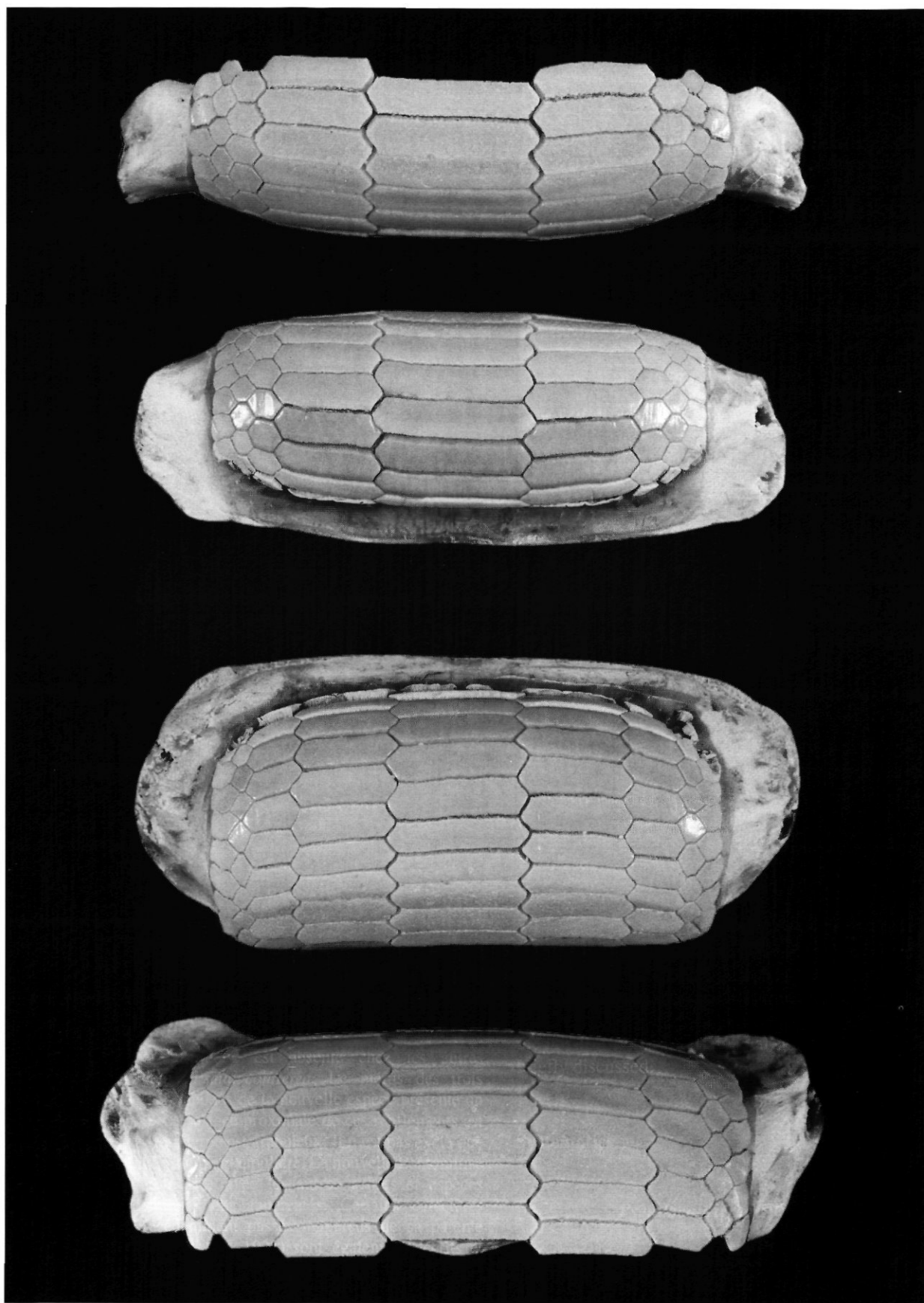
The teeth have a holaulacorhizid to polyaulacorhizid root type (depending on their jaw position) with an adapted type of osteodentine, that shows mesio-distally enlarged canals above the root lobes. These canals are connected to the vertical ones of the root lobes, as well as to a narrow band of osteodentine above them, from which irregularly shaped semi-parallel canals arise, that run vertically into the crown. (See textfigure 12)



Textfigure 12.
Pteromylaeus bovinus tooth histological cross section.

MALES AND FEMALES

Teeth of the upper symphyssial row are hexagonal in occlusal view and extremely enlarged, with a flat top surface. These teeth are slightly arched inward in juveniles but straight in adults. The teeth of the lower symphyssial row are similar and straight in both, juveniles and adults. Disregarding abbrasion marks, the crown’s top surface of upper and lower teeth is always smooth.



Textplate 10. – *Rhinoptera peli* BLEEKER, 1863. Female 70 cm d.w., Joal, Senegal. Upper and lower jaws occlusal and light oblique views of the dental plates, magnification of 1.5.

An inner and outer interlocking ornamentation is provided by relatively coarse, reticulated, merely vertically arranged costules. A narrow inner ledge is present. The root is shifted inward from the crown in profil, so that the outer crown edge overhangs the outer root edge. This feature interlocks the teeth, in that the outer crown edge rests on the inner root edge of the tooth in front and the outer crown edge of the previous tooth on the protruding inner root edge. The root is polyaulacorhizid with numerous evenly shaped basal grooves, each with scattered foramina along the groove's centre.

The lateral teeth are rhomboid in occlusal view, with a flat, smooth crown's top surface. Inner and outer interlocking ornamentation is similar to that of the symphysial teeth. Inner and outer ledges are present. The root is shifted inward from the crown in profil, so that the outer crown edge overhangs the outer root edge. This feature interlocks the teeth, in that the outer crown edge rests on the inner root edge of the tooth in front and the outer crown edge of the previous tooth on the protruding inner root edge. The root is polyaulacorhizid with numerous evenly shaped basal grooves, each with scattered foramina along the groove's centre. The root of posterior teeth is asymmetrical, and the inner and outer interlocking ornamentation, as well as inner and outer ledges are absent at the distal part.

Subfamily Rhinopterinae

This subfamily is presented by the single genus *Rhinoptera*.

Genus *Rhinoptera* CUVIER, 1829

The genus comprises about 6 nominal species (BIGELOW & SCHROEDER, 1953). Type species is *R. marginata*. Dentition of a female of *Rhinoptera peli* BLEEKER, 1863 is illustrated on Textplate 10.

Rhinoptera marginata
(E. GEOFFROY SAINT HILAIRE, 1817)
(Plate: 31)

Myliobatis marginata GEOFFROY SAINT HILAIRE, 1817. Histoire naturelle des poissons de la mer Rouge et de la Méditerranée. France. Commission d'Égypte. Vol. 1: pl. 25, figs. 3-4.

HETERODONTY

The low-crowned dentition is gradient monognathic heterodont through mesio-distally very much enlarged symphysial teeth and less enlarged teeth toward the commissure. The lateral teeth are positioned in an imbricated manner, in that half of the tooth width of one row is shifted mesially and distally over the neighbouring rows. Neither sexual nor ontogenetic heterodonty was found.

VASCULARIZATION

The teeth have a polyaulacorhizid root type with an adapted type of osteodentine with mesio-distally enlarged canals above the root lobes. These canals are connected to the vertical ones of the root lobes, as well as to a narrow band of osteodentine above them, from which densely packed, semi-parallel canals arise and pierce vertically into the crown. (See textfigure 13)



Textfigure 13.
Rhinoptera marginata tooth histological cross section.

MALES AND FEMALES

Teeth of the upper symphysial row are hexagonal in occlusal view and enlarged, with a flat crown's top surface. These teeth are slightly arched inward in juveniles but straight in adults. Teeth of the lower symphysial row are similar but straight in both, juveniles and adults. Disregarding abrasion marks, the crown's top surface of both, upper and lower teeth is always smooth. The lateral teeth become less enlarged and show a regular hexagonal shape. The posteriors are irregularly square-shaped due to their straight distal margin. An inner and outer interlocking ornamentation and ledges are absent. A central depression along the inner surface and a protrusion along the outer surface provide interlocking. The root is slightly shifted inward from the crown in profil, so that the outer crown edge overhangs the outer root edge. This feature interlocks the teeth, in that the outer crown edge rests on the inner root edge of the tooth in front and the outer crown edge of the previous tooth on the protruding inner root edge. The root is polyaulacorhizid with numerous evenly shaped basal grooves, each with scattered foramina along the groove's centre. The posterior teeth are asymmetrical, with one or two basal grooves.

Differential diagnosis (See Tables 1 and 2)

Teeth of representatives of the following supraspecific taxa of the myliobatoid superfamilies Dasyatoidea, Plesiobatoidea and Myliobatoidea were so far examined, described and illustrated in the issues 4a, 4b and the present one of part B of this series and are listed under their families, respectively: Dasyatidae: *Amphotistius*, *Dasyatis*, *Disceus*, *Himantura*, *Paratrygon*, *Pastinachus*, *Plesiotrygon*, *Potamotrygon*, *Pteroplatytrygon*, *Taeniura*, *Trygonoptera*, *Urobatis*, *Urogymnus*, *Urolophoides*, *Urolophus* and *Urotrygon*, Hexatrygonidae: *Hexatrygon*, Plesiobatidae: *Plesiobatis*, Gymnuridae: *Aetoplatea* and *Gymnura*, Myliobatidae: *Aetobatus*, *Aetomylaeus*, *Manta*, *Mobula*, *Myliobatis*, *Pteromylaeus* and *Rhinoptera*.

Selection of the odontological characters

The odontological characters of living Myliobatoidei were never before defined with regards to their phylogenetic significance. The following odontological characters were observed during our examinations:

1. Four types of crown morphology:
 - 1a. With single cusp or multiple cusps. Single cusp with mesial and distal cutting edges, or two or more cusps present.
 - 1b. Single cusp absent, but instead
 - 1b1. With single arched transverse keel.
 - 1b2. With arched transverse keel, and a second one on the outer surface of the crown.
 - 1c. Without a cusp or transverse keel, crown with flat top surface.
 - 1c1 Inner and outer interlocking ornamentation and inner ledge present.
 - 1c2 Inner ledge present only.
 - 1c3 Without interlocking ornamentation and inner ledge.
2. Two root types:
 - 2a. Holaulacorhizy.
 - 2b. Polyaulacorhizy.
3. Shape and height of root
4. Cusp shape
5. With uvula.
6. With inner central ridge.
7. With outer ornamentation.
8. Sexual heterodonty.
9. Three types of tooth vascularization:
 - 9a. Orthodonty.
 - 9b. Osteodonty.
 - 9c. Modified osteodonty
10. Lappet-shaped mesial and distal crown base extensions
11. With numerous scattered foramina over the root and crown base in basal view

See also textfigure 4.

Primary odontological characters

The morphology of crown and root, combined with the type of vascularization, divides the Myliobatoidei into four suprageneric groups.

In the first group, a cusp with mesial and distal cutting edges, or multicuspidity (1a), or a single or double transverse keel are given (1b1 and 1b2), the root is always holaulacorhizid (2a) and the vascularization is orthodont (9a) or osteodont (9b). This combination of features applies to: *Amphotistius*, *Dasyatis*, *Disceus*, *Himantura*, *Paratrygon*, *Plesiotrygon*, *Potamotrygon*, *Pteroplatytrygon*, *Taeniura*, *Trygonoptera*,

Urobatis, *Urogymnus*, *Urolophoides*, *Urolophus*, *Urotrygon*, *Hexatrygon*, *Plesiobatis*, *Aetoplatea* and *Gymnura*.

In the second group, the crown lacks a cusp or transverse keel, has a flat top surface (1c1, 1c2 and 1c3), the root is polyaulacorhizid (2b), and the vascularization type is modified osteodont (9c). This combination of features applies to: *Aetobatus*, *Aetomylaeus*, *Myliobatis*, *Pastinachus*, *Pteromylaeus* and *Rhinoptera*.

In the third group, a cusp or transverse keel is always absent, the crown has a flat surface (1c3), no inner and outer interlocking ornamentation nor an inner ledge, the root is sometimes polyaulacorhizid (2b), and the vascularization type is orthodont or osteodont (9a and 9b). This combination of features applies to *Manta* and *M. mobular*-type.

In the fourth group the cusp has mesial and distal cutting edges, or multiple cusps are present (1a), roots are sometimes polyaulacorhizid (2b) and the vascularization type is orthodont (9a). This combination of features applies to the *M. rochebrunei*-type and *Ceratobatis*.

All groups are defined by character complexes of suprageneric significance, i.e. by the morphology of the crown (1a, 1b1, 1b2, 1c1, 1c2, 1c3), root (2a, 2b) and by vascularization (9a, 9b, 9c).

Vascularization

Some of the genera examined showed orthodonty (9a), having a pulp cavity surrounded by orthodontine. This is found in *Aetoplatea*, *Amphotistius*, *Gymnura*, *Hexatrygon*, *Himantura*, *Mobula mobular*-type, *Paratrygon*, *Plesiobatis*, *Trygonoptera*, *Urobatis*, *Urolophoides*, *Urolophus* and *Urotrygon*.

Several other genera showed osteodonty to a degree through replacement of the pulp cavity by interconnected osteons, however, always surrounded by orthodontine. The degree of osteodontid development varies between the genera. This was found in *Ceratobatis*, *Dasyatis*, *Disceus*, *Mobula rochebrunei*-type, *Plesiotrygon*, *Potamotrygon*, *Pteroplatytrygon*, *Taeniura* and *Urogymnus*.

Normal osteodonty (9b) was found in *Manta*.

A very distinct type of osteodontine (9c), in which the osteons in the crown are always vertically oriented, is characteristic for *Aetobatis*, *Aetomylaeus*, *Myliobatis*, *Pastinachus*, *Pteromylaeus* and *Rhinoptera*.

The myliobatid genera *Aetobatis*, *Aetomylaeus*, *Myliobatis*, *Pastinachus*, *Pteromylaeus* and *Rhinoptera* and the mobulid genera *Manta*, *Mobula mobular*-type and the *Mobula rochebrunei*-type (including *Ceratobatis*) develop mesio-distally enlarged teeth up to one single tooth row (*Aetobatis*). This phenomenon is particularly illustrated in plate 17. CASIER (1947) suggested that this phenomenon had resulted from fusion of different dental germina.

Secondary odontological characters

Secondary odontological characters of the above list are more significant details to distinguish between the subgroups and their genera within the various groups, i.e. characters as 3, 4, 5, 6, 7, 8, 10 and 11.

GROUP 1

Within the first group, *Aetoplatea* and *Gymnura* are separated as a subgroup from the other taxa by the presence of lappet-shaped mesial and distal extensions at the crown base (10). *Aetoplatea* is distinguished from *Gymnura* by its broad base and slender, narrow cusp, whilst *Gymnura* has a narrow base and a semi-triangular cusp (4)

Himantura, *Trygonoptera*, *Urobatis*, *Urolophus* and *Urobatis* are distinguished from the other taxa by the presence of a second transverse keel.

An inner central ridge (6) is definitely present in the genera *Urogymnus* and *Disceus*. This character is shown also on several single teeth of a jaw in other taxa, however, poorly developed only and not taken into consideration. An uvula is found in *Disceus* and *Paratrygon* only (5), however with reservation that only juveniles were available of the latter taxon (5). Particular abundance of foramina scattered over the root's surface in basal view is characteristic for *Urogymnus* (11).

The shape of the crown's outer margin in occlusal view, being angled or arched, is not stable enough to provide a reliable character. The shape varies not only within the genera or species, but is even inconsistent within one and the same jaw. However, the lateral teeth of *Hexatrygon* can be distinguished by a semi-trapezoid front margin in occlusal view, mesio-distally enlarged, and a relatively low root.

Several taxa exhibit to a degree an ornamentation on the crown's outer surface. However, examination of different species of e.g. the genus *Dasyatis* revealed that some species possess a very well developed ornamentation (some with a coarse, and some with a fine reticulated ornamentation), whereas others hardly showed any ornamentation at all. The character complex is probably useful for interspecific distinction rather.

GROUP 2

Within the second group, the presence of an inner and outer interlocking ornamentation distinguishes *Aetomylaeus*, *Myliobatis*, *Pteromylaeus* and *Pastinachus* from *Aetobatus* and *Rhinoptera*. *Aetomylaeus*, *Myliobatis* and *Pteromylaeus* have a mesio-distally broad symphyseal tooth, versus *Pastinachus* with a narrow one. *Pteromylaeus* is separated from *Aetomylaeus* and *Myliobatis* by symphyseal teeth with the mesial and distal margins shifted to the rear and more elongated lateral teeth in inner-outer direction. *Aetomylaeus* possesses a finer inner and outer interlocking ornamentation

than *Myliobatis*. *Aetobatus* is distinguished from *Rhinoptera* by its single symphyseal tooth row.

GROUP 3

The *Mobula mobular*-type of tooth morphology applies to *Mobula mobular* and *Mobula japonica* (see also NOTAR-BARTOLO DI SCIARI, 1987). Their teeth appeared to be very similar to *Manta*, but can be distinguished by their orthodont tooth vascularization, versus osteodont in *Manta*.

GROUP 4

The *Mobula-rochebrunei*-type of tooth morphology applies to the remaining taxa of the genus *Mobula*, including *Ceratobatis*.

Sexual heterodonty

Only four taxa of the first group present sexual heterodonty, in that mature males possess a tooth cusp: *Dasyatis*, *Himantura*, *Pteroplatytrygon*, *Taeniura* and *Urolophus*. *Amphotis-tius* shows only slight sexual heterodonty with a cusp in anterior teeth in males.

Sexual homodonty is presented by a transverse keel, as a typical female character.

Sexual heterodonty is absent in all taxa of the second group. Due to lack of material sexual heterodonty could not be determined in the groups 3 and 4.

Conclusions

The supraspecific taxa of the Myliobatoidea are divided into four groups by extreme differences in their tooth morphology and vascularization.

GROUP 1

Dasyatis, *Disceus*, *Himantura*, *Paratrygon*, *Plesiotrygon*, *Potamotrygon*, *Pteroplatytrygon*, *Taeniura*, *Trygonoptera*, *Urobatis*, *Urogymnus*, *Urolophoides*, *Urolophus*, *Urotrygon*, *Hexatrygon*, *Plesiobatis*, *Aetoplatea* and *Gymnura*.

Within this group, two subgroups can be separated from the third subgroup as the remaining taxa, which are:

Aetoplatea and *Gymnura* on the one, *Himantura*, *Trygonoptera*, *Urobatis* and *Urolophus* (= *Urobatis*) on the other hand.

Several taxa develop to varying degrees an inner central ridge, sometimes only in one of the sexes or even in a few teeth in the jaw only. Therefore, this character is not taken into consideration for grouping or distinguishing taxa.

The genus *Disceus* was considered as a junior synonym of *Paratrygon* by ROSA, CASTELLO & THORSON (1987). Although only juveniles of *Paratrygon* were available for examination, their tooth morphology seems to support this synonymy.

The numerous foramina scattered over the root surface (basal view) is unique for *Urogymnus*, and distinguishes this taxon from the other dasyatoids.

Urobatis sloani, represented here as *Urolophus jamaicensis*, exhibits a similar type of tooth morphology as found in *Himantura uarnak*. Like the other genera with a second transverse keel as significant odontological character (*Himantura*, *Trygonoptera*, and *Urolophus*), the oval-shaped, low-cusped crown (occlusal view), marks their close interrelationships, versus the semi-square-shaped one, relatively high-cusped crown of *Urolophus cruciata*.

The earliest records of teeth with dasyatoid type of tooth morphology are known from the upper Cretaceous. Considering the low number of dasyatoid species known from the Cretaceous up to the Miocene and, in contrast to the great specific diversity of living dasyatoid taxa, it is very likely that we are witnessing a possible explosive evolutionary development being still in progress to date. Examples of such phenomenon are well known to paleontologists of other early developments in various groups of chondrichthyans. These were often characterized by taxa, which rapidly developed new specific or generic characters, as well as by taxa, in which these characters changed only slow. Odontologically, the large number of living taxa of Dasyatoidea shows relatively little intergeneric differentiation but many intergrades of development, as revealed in the differential diagnosis above. The ongoing evolutionary process of speciation likewise appears to affect many other character complexes of external and internal morphology and thus explains the difficulty of establishing an indisputable systematic classification for the Dasyatoidea.

GROUP 2

Aetomylaeus, *Myliobatis*, *Pteromylaeus*, *Pastinachus*, *Aetobatus* and *Rhinoptera*. Although they can be distinguished as genera, *Aetomylaeus*, *Myliobatis* and *Pteromylaeus* also form an odontological subgroup. In contrast, *Aetobatus*, *Pastinachus* and *Rhinoptera* are all separate odontological developments that cannot be grouped.

This particular type of tooth morphology, with the hexagonal shape of the crown in occlusal view and the flat top surface, is an ancient character complex already known from lower Cretaceous records (CAPETTA, 1987). However, the internal and external morphology of the living taxa of this subgroup was not developed earlier than the Miocene (HOVESTADT & HOVESTADT-EULER, 1999). Although their type of tooth morphology was already developed to that of the living taxa, the morphology of earliest known skeletons have similarity to that of *Pastinachus*. (see JAEKEL, 1894, fig.6, FRICKHINGER, 1991, p.215 and HOVESTADT & HOVESTADT-EULER, 1999, figs.1 to 9).

GROUP 3

Manta and the *Mobula mobular*-type must have passed an extraordinary odontological development. A similar development of such tooth morphology is already known from the

upper Paleocene (HERMAN, 1979; Capetta, 1987), and this concept has not changed much until to date. The loss the upper jaw teeth and change to osteodontology of the lower teeth may indicate an intermediate step to total loss of jaw teeth due to filter feeding.

GROUP 4

The *Mobula rochebrunei*-type has developed an extraordinary tooth morphology (described above). This type of tooth morphology is already known from the upper Eocene (MÜLLER, 1999).

The superorder Myliobatoidei comprises (after NELSON, 1994) the three Superfamilies Myliobatoidea, Dasyatoidea and Plesiobatoidea. The results of the odontological study presented in 4a, 4b and the present issue of Part B of this series revealed significant differences in tooth morphology, separating Myliobatoidea from Plesiobatoidea and Dasyatoidea. Gymnuridae and Mobulidae do not share any odontological characters with the supraspecific taxa grouped under the Myliobatoidei. On the other hand, the dasyatid genus *Pastinachus* revealed strong odontological similarity with the myliobatoid taxa. Considering these odontological results, the supraspecific taxa grouped under the Myliobatoidea are *Aetobatus*, *Aetomylaeus*, *Myliobatis*, *Pastinachus*, *Pteromylaeus* and *Rhinoptera*. Amongst these supraspecific taxa, *Pastinachus* is distinguished from the group of the remaining taxa. Within the latter group, *Aetobatis*, *Myliobatis* and *Pteromylaeus* represent a subgroup, in which the latter genus is again separated from the two (see phylogenetic diagram 2).

The odontological differences between the supraspecific taxa of the Dasyatoidea and Plesiobatoidea are marginal and do not support two different Superfamilies. Odontologically, Dasyatoidea are separated into two supraspecific groups with *Himantura*, *Trygonoptera* and *Urolophus* as one group, and another of the remaining taxa. Within the latter group, *Amphotistius*, *Dasyatis*, *Plesiobatis*, *Plesiotrygon*, *Potamotrygon*, *Pteromylaeus*, *Taeniura*, and *Urolophoides* lack significant differentiation and are tentatively grouped. *Hexatrygon* differs significantly from all the rest and suggests its own supraspecific unit.

Several observed odontological differences are only of interspecific significance. From the odontological point of view, the actual classification of subfamilies, as well as the large number of supraspecific taxa cannot be supported.

Material of *Paratrygon* and *Disceus* was insufficient. However, the characteristic uvula on teeth of the examined individuals supports synonymising *Disceus* with *Paratrygon* and distinguishes the latter genus from the other taxa. Its numerous foramina scattered over the root surface (basal view) distinguishes *Urogymnus* from *Hexatrygon*. In general terms, there is a significant similarity in the tooth morphology between the Dasyatoid taxa and supraspecific taxa of the Suborder Rajoidei and - from the odontological point of view - the Dasyatoidea should be ranked under this Subfamily (see also phylogenetic diagram 1).

Group 1

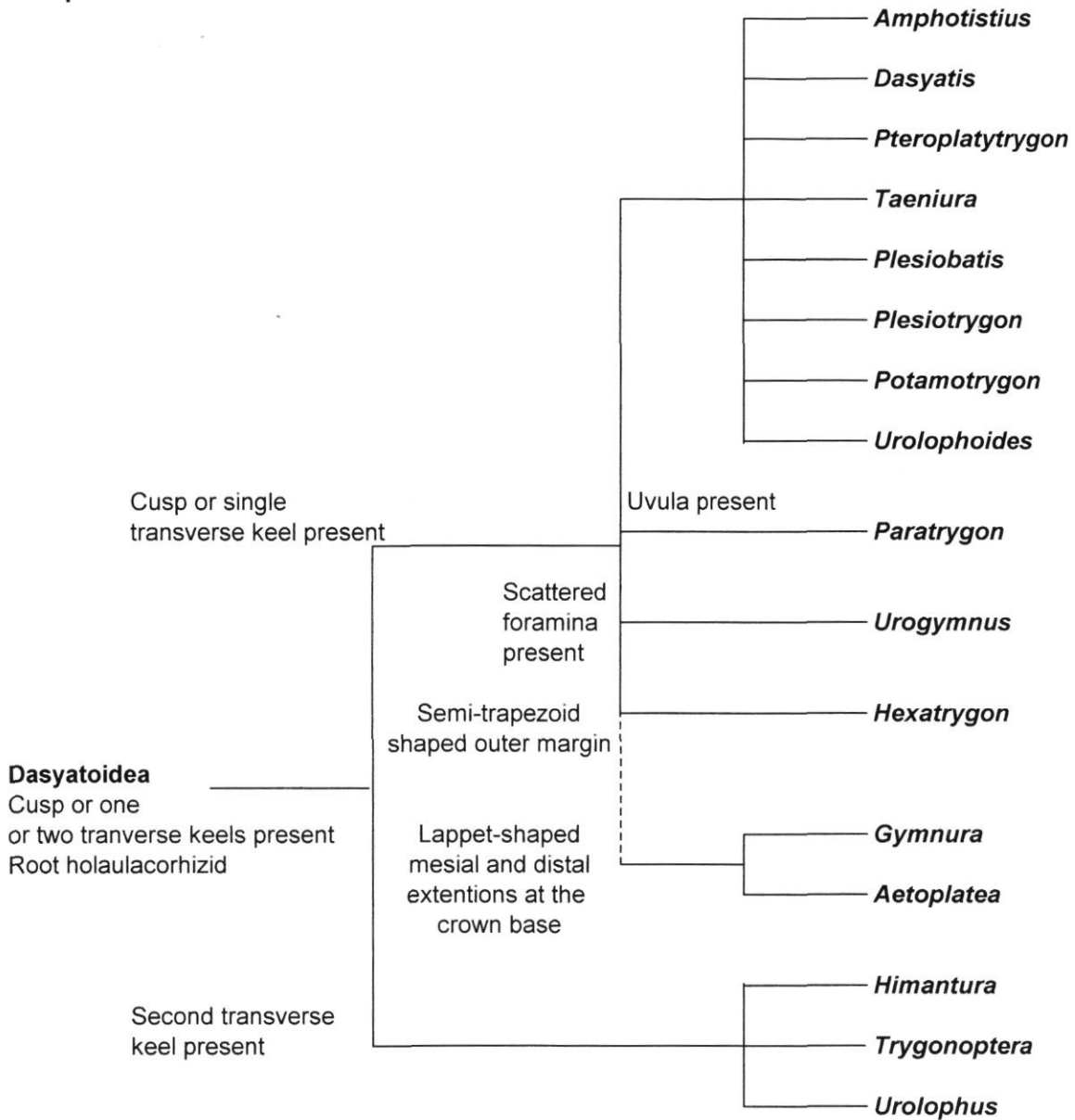


TABLE 1

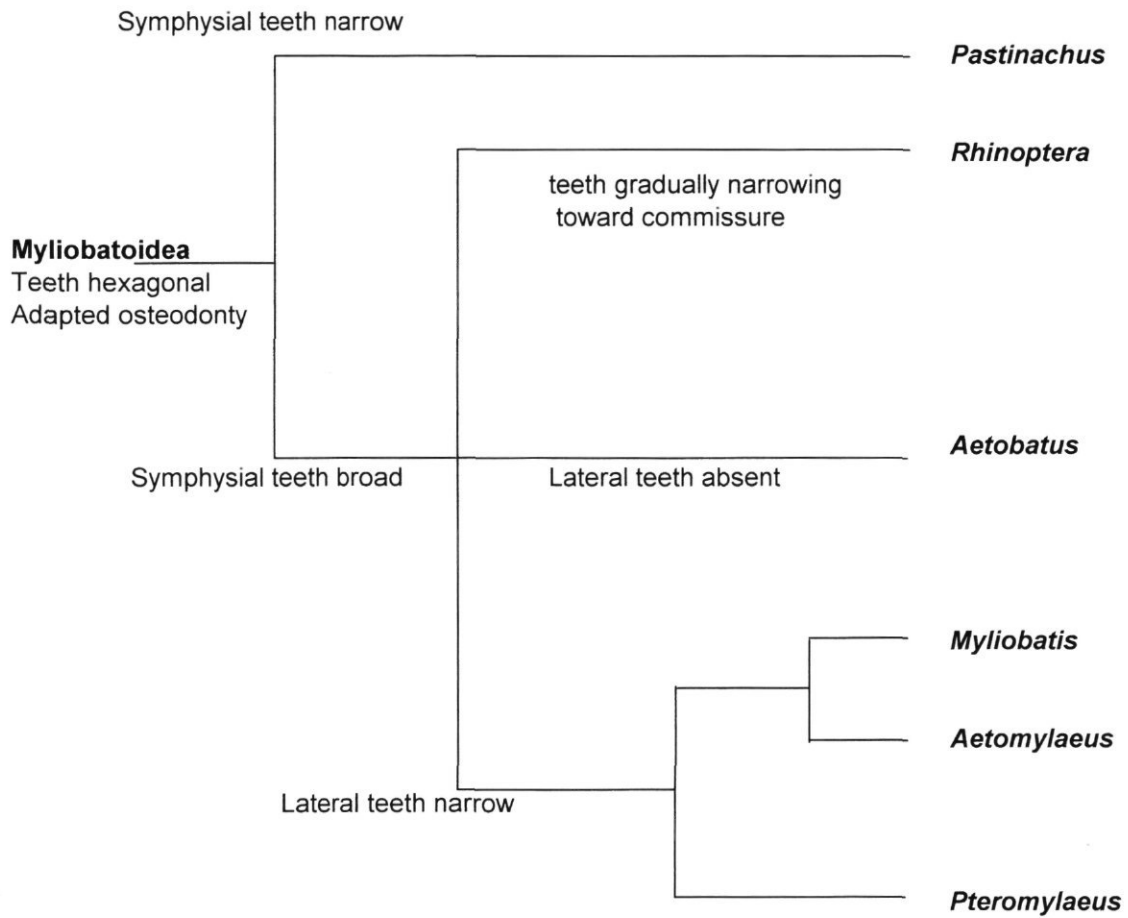
A similar conclusion can be drawn for the Gymnuridae, as they share many characteristic features corresponding with the supraspecific taxa of the Rajoidei, but Gymnuridae are tentatively related to the Dasyatoidea (see phylogenetic diagram 1).

Finally, the extraordinary odontological characters of the Mobulidae separate their supraspecific taxa from those of the Myliobatoidea, but also reveal the difficulty to define their origin. Within the mobulids, two groups can be distinguished, the *M. mobular*-type including *Manta* and the *M. rochebrunei*-type (see phylogenetic diagram 3).

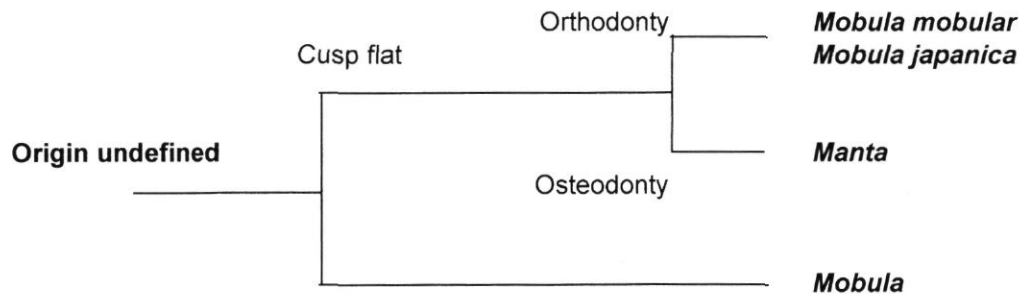
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The authors thank Mr.B.Seret, IRD at MNNH, Paris, Dr.F.Cigala-Fulgosi, Istituto di Geologia, Paleontologia e Geographia, Parma, Italia, Mr.T.Bor, Sliedrecht (The Netherlands), Dr.D.Nolf, Institut Royal des Sciences naturelles de Belgique, Brussels, Dr.R.S.Rosa, Universidade Federal da Paraiba, João Pessoa, Brasil, Dr.P.Last, Commonwealth Scientific and Industrial Ressearch Organisation (CSIRO), Hobart, Australia, Dr. J.Paxton and Mr.M. McGrouther, Australian Museum, Sydney, Australia, Mr. J. Johnson, Queensland Museum, Brisbane, Australia, Prof. Dr. H. Wilkins, Zoologisches Museum Hamburg/Institut für Seefischerei Hamburg, Germany, for permission to examine specimens at their disposal. J.Cillis, Institut Royal des Sciences naturelles de Belgique, Brussels took the SEM-photographs.

Group 2



Group 3



Cusp strongly directed inwardly, multicuspid

TABLE 2

Part B: Batomorphii Addendum 1 to 4a: Order Rajiformes – Suborder Myliobatoidei – Superfamily Dasyatoidea – Family Dasyatidae – Subfamily Dasyatinae – erratum to Genus: *Pteroplatytrygon*.

Abstract

In part B, 4a, the jaw of what is probably a male *Dasyatis centroura* was described and illustrated erroneously as a male *Pteroplatytrygon violacea*. This error is corrected in this addendum with the description and illustration of a male jaw of indeed the latter species.

Key words: Elasmobranchii - Rajiformes - Myliobatoidei - Dasyatidae.

Résumé

Dans le fascicule 4a de la partie B de cette série, la mâchoire décrite et figurée comme appartenant à un mâle de *Pteroplatytrygon violacea* s'est avérée être celle d'un mâle de *Dasyatis centroura*. Dans cet addendum, la description et l'illustration de la dentition d'un mâle de l'espèce concernée viennent corriger cette erreur.

Mots-clés: Elasmobranchii - Rajiformes - Myliobatoidei - Dasyatidae.

Kurzfassung

In Teil B, 4a, ein wahrscheinlich zu einem männlichen *Dasyatis centroura* gehörender Kiefer war beschrieben und illustriert als *Pteroplatytrygon violacea*. Dieser Irrtum ist korrigiert in diesem Addendum mit der Beschreibung und Illustration eines männlichen Kiefers der tatsächlich zu den letzten gehörenden Spezies.

Schlüsselwörter: Elasmobranchii - Rajiformes - Myliobatoidei - Dasyatidae.

Introduction

In part B, 4a, the jaw of what is probably a male *Dasyatis centroura* was described and illustrated erroneously as a male *Pteroplatytrygon violacea* (discovered by Dr. H. CAPPETTA). This error is corrected in this addendum with the description and illustration of a male jaw of indeed the latter species.

Superfamily: Dasyatoidea - Family: Dasyatidae

Subfamily: Dasyatinae

Material

The following specimen was examined:

<i>Pteroplatytrygon violacea</i>			
Col. Herman	♂	445 mm	DW
Coll. Cappetta	♂	? mm	DW

Description of the odontological characters

Genus *Pteroplatytrygon* FOWLER, 1910

Pteroplatytrygon violacea (BONAPARTE, 1832)
(Plates:... and.. ; Textplate:..)

Trygon violacea BONAPARTE, 1832 Iconografia della fauna italica per le quattro classi degli animali vertebrati. Tomo III, Pesci: fasc. I. punta 6, plate 155.

HETERODONTY

The dentition is gradient monognathic heterodont with lateral and posterior teeth becoming lower and inclined toward the commissure.

Sexual heterodonty is documented by a high cusp on anterior and antero-lateral teeth in males, *versus* a transverse keel across the crown in females. The posteriors teeth of both males and females have a transversal keel. Lacking teeth of male juveniles, ontogenetic heterodonty could not be determined. However, it is assumable, that juvenile males have an adult female tooth morphology with low cusps.

VASCULARIZATION

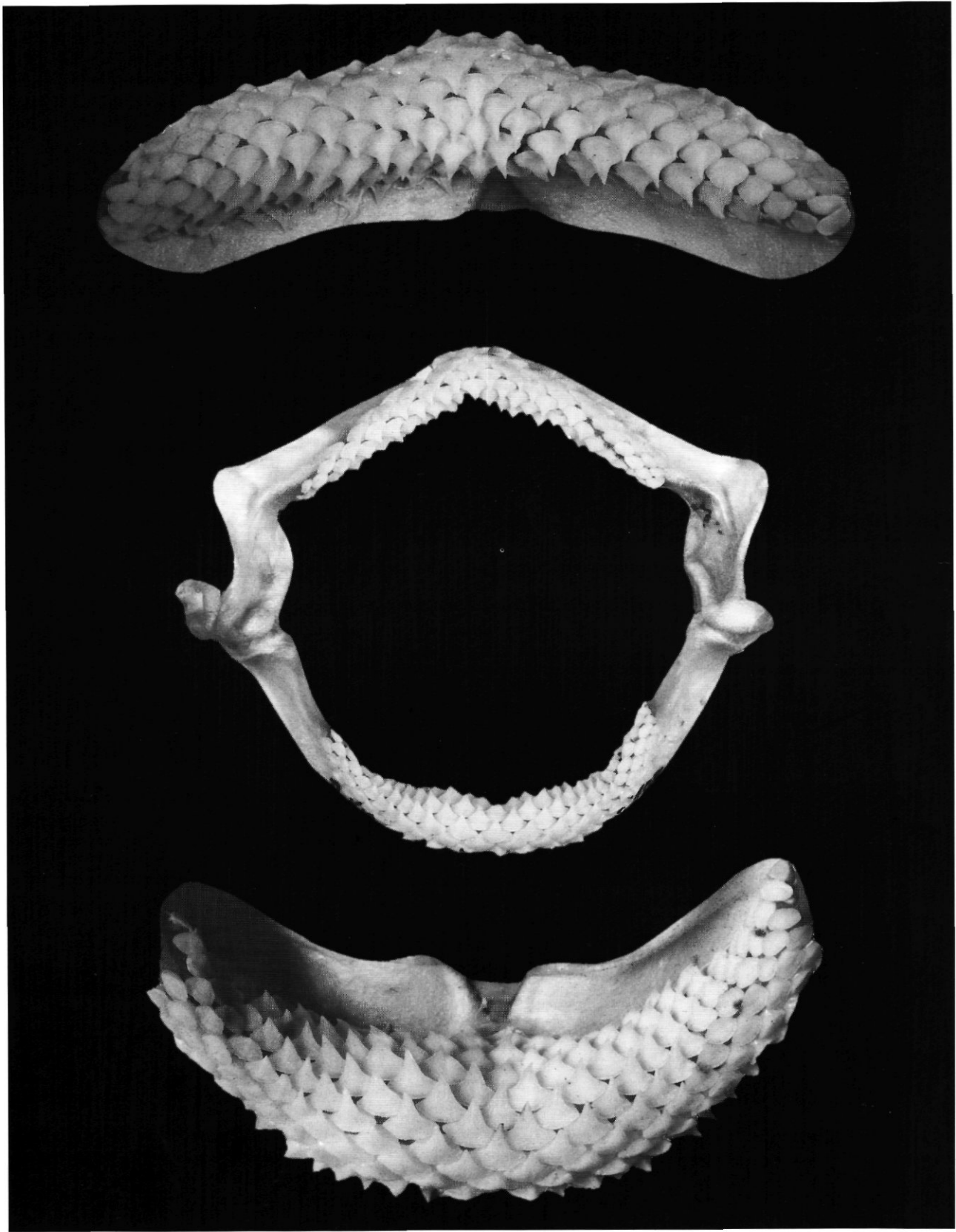
Although the external morphology of the teeth shows a holaulacorhizid root type, a pulp cavity is absent in the root area, but the place is filled with osteodentine instead. An enlarged osteon forms a main canal in the crown and several more scattered osteons are present in the rooth. The vascular tubes of the orthodentine in the crown region radiate from the osteons into crown and root. Inner lateral foramina are absent. (See textfigure 14).



Textfigure 14.
Pteroplatytrygon violacea tooth histological cross section.

MALES

The crown of anterior teeth are relatively broad, with a high, triangularly shaped cusp, the lateral teeth become broader with a lower cusp and diminish in size toward the commissure. The posterior teeth possess a transversal keel instead of



Textplate 11. – *Pteroplatytrygon violacea* (BONAPARTE, 1832). Male 44.5 cm d.w., Channel of Sicilia, Italy. Jaws, magnification of 2. Details of upper and lower dentition, magnification of 4.

a cusp. The outer margin of the crown is arched, the inner one is trapezoid, and both margins join in mesial and distal marginal angles. The inner central ridge is absent. The inner face is slightly concave and slopes toward the rounded inner crown rim. The slightly concave outer part presents a well developed reticulated ornamentation, which is formed by deep depressions above the smooth rim, which become slightly shallower toward the apex of the cusp. The basal view of the crown shows a rather, broad, slightly convex crown rim at the outer part, gradually narrowing to half its width at the inner part. The crown-root junction lies in a shallow depression in the center of the basal surface of the crown. The holaulacorhizid narrow, moderately high root is more or less oval to circular in cross-section, oblique toward the rear of the tooth, and slightly diverges at the root base. The root base presents a well developed, deep and broad median groove, that encloses one large aperture. Inner and outer foramina as well as root coating are absent.

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General glossary (applying to all previous issues of this series since 1987).

Concerning the jaw

Anterior

Tooth position close to junction of left and right jaw halves.

Commissural

Tooth position near the end of jaw.

Dignathic

Heterodont by having different tooth morphology in upper and lower jaws.

File

Tooth row from symphysis toward end of jaw.

Heterodonty

Different tooth morphology within a tooth file. There are two types of heterodonty: dignathic and monognathic.

Homodonty

Uniform tooth morphology within a tooth file

Lateral

Tooth positions half way along the jaw.

Longitudinal

Symphysial/commissural direction of a tooth file.

Monognathic

Heterodonty within one jaw only. (this can appear as gradient or disjunct)

Parasymphysial

First anterior tooth row, if a symphysial tooth row is absent.

Posterior

Tooth positions toward the angle of jaws.

Pseudosymphysial

One of the parasymphysial tooth rows placed in the position of the symphysial tooth row (symmetry).

Row

Tooth row from inner face to outer face of jaw.

Symphysial

Teeth at junction of both halves of a jaw.

Transverse

Outer/inner direction of a row.

Concerning the tooth

An-,Hemi-,Hol- and Polyaulacorhizid

Concerning their vascularization, E.Casier(1947) recognized and described four phylogenetically significant root types within the orthodont histotypes of elasmobranch teeth.

Anaulacorhizid

Vascularization through scattered foramina of equal size on both outer and inner faces, (e.g. Hexanchidae).

Hemiaulacorhizid

Vascularization through a median groove and 1 or 2 lateral foramina on inner face, (like in Squatinidae and Orectolobidae)

Holaulacorhizid

Vascularization through many small foramina concentrated in a median groove running from outer to inner face, (e.g. Rajidae)

Polyaulacorhizid

Vascularization through many small foramina concentrated in several grooves running parallel from outer to inner face, (e.g. Myliobatidae)

Apron

Expansion of the central part of the outer crown base.

Basal

Bottom face concerned.

Inner central ridge

Convex protrusion at the upper midsection of the inner crown face.

Costules

Short, vertical ridges sometimes present on inner and/or outer crown base.

Crown

Enamelated tooth part.

Distal

Tooth edge or part toward angle of jaws.

Histotype

Type of internal tooth vascularization.

Inner face

Viewed from inside the mouth.

Longitudinally

Apico-basally directed structuring on a tooth.

Median groove

Groove running from the inner root base to the inner crown-root junction, dividing a holaulacorhizid type of root into two root lobes. It includes the main foramina of the vascularization system.

Mesial

Tooth edge or part toward junction (symphysis) of left and right jaw halves.

Neo-holaulacorhizid

Modification of the holaulacorhizid type of root, combining a shallow median groove and an extremely expanded pulp cavity.

Orthodont

Histotype of vascularization, by which a tooth is supplied primarily by an internal pulp cavity radiating into numerous tiny canals penetrating the orthodontine layer.

Osteodont

Histotype of vascularization, by which a tooth is supplied without any pulp cavity by scattered tiny cavities and canals penetrating the osteodontine layer of the root and the internal crown material.

Outer face

Viewed from outside the mouth.

Pseudo-apron

Apron-like vertical ridges that appear sometimes on lateral and posterior teeth.

Pseudo-osteodont

The former pulp cavity of an originally orthodont histotype of tooth being filled secondarily with osteodontine.

Pulp cavity

Cavity inside the tooth from which the vascularization is spread via canaliculi.

Root

Non-enamelled tooth part, that forms the junction with the jaw gum and provides vascularization of the tooth.

Root coating

Coating on the upper part of the root (probably enamelled)

Root stem

Root part between the crown base and root lobe section.

Secondary anaulacorhizid

Median groove of a holaulacorhizid type of root totally overgrown to form a closed tube internally connected or merged with the pulp cavity

Secondary hemiaulacorhizid

Median groove of holaulacorhizid type of root overgrown to various extent, converting the median groove to an internal tube, which is merged with the pulp cavity.

Striae

Vertical ridges running from crown base toward apex.

Sulcus

Groove developed by the primary vascularization canals leading from root base to the main foramina in anaulacorhizid root type. It differs from the median groove in which several foramina are concentrated of the holaulacorhizid root type and the parallel grooves of the polyaulacorhizid root type, respectively, in that a sulcus lacks foramina.

Transverse

Mesio-distally directed.

Transverse keel

Transverse ridge dividing the crown into inner and outer face.

Uvula

Lobate extension of the inner crown base.

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Composition of the plates

As far as possible plates of isolated teeth of one juvenile (male or female) and of both male and female adults are presented for each supraspecific taxon.

The plates have a consistent composition: upper teeth are presented with their cusps downward and lower teeth with their cusps upward.

The choice of left or right jaw halves illustrated depends on the preservation quality of the specimen's tooth files only.

Legend:

s = symphysial position

a = anterior position

la = latero-anterior

l = lateral position

lp = latero-posterior

p = posterior position

c = commissural position

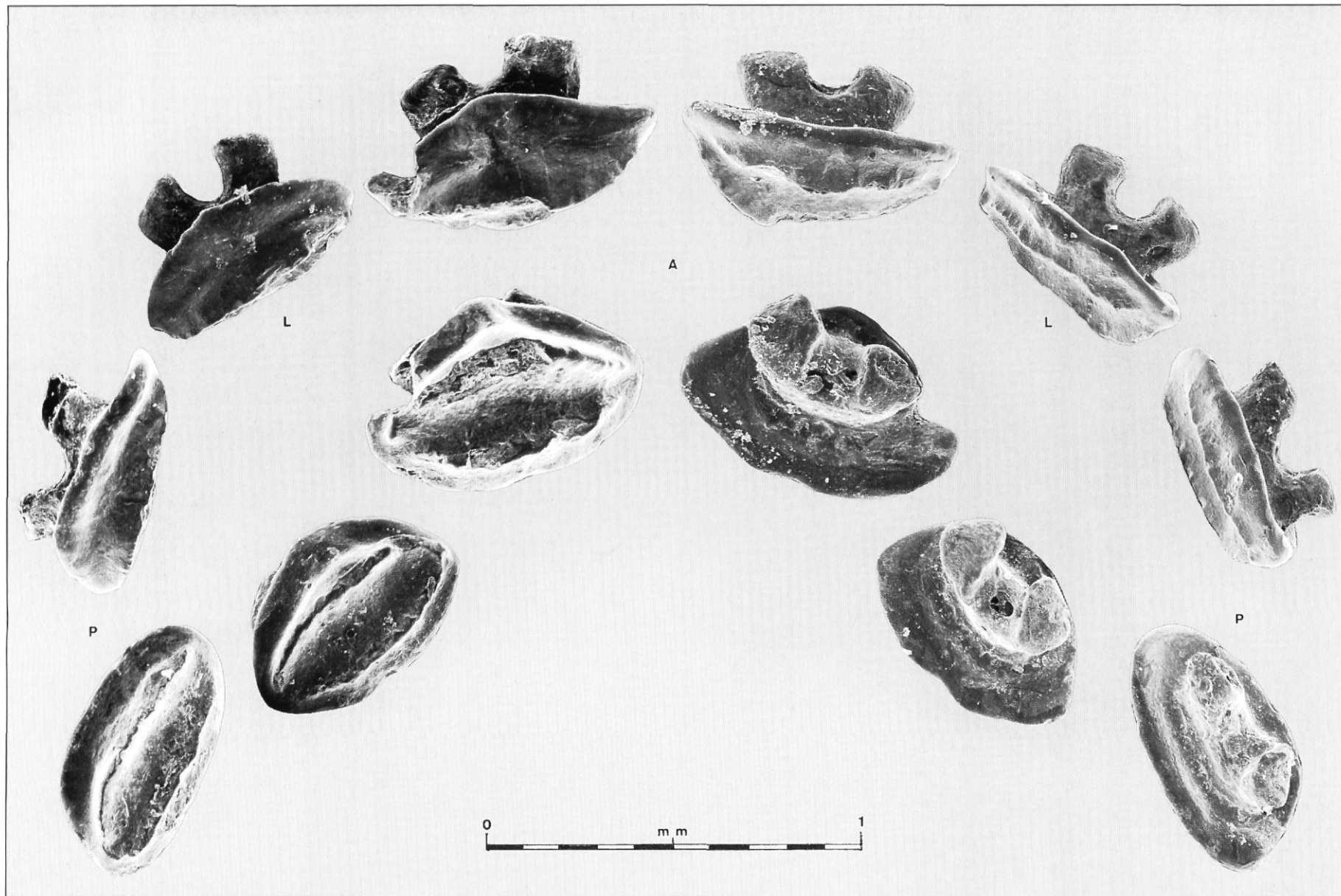


Plate 1. – *Urobatis sloani* (BLAINVILLE, 1816) teeth of synonym *Urolophus jamaicensis* (CUVIER, 1817), female 15 cm d.w., Gulf of Mexico. Upper teeth.



Plate 2. — *Urobatis sloani* (BLAINVILLE, 1816) teeth of synonym *Urolophus jamaicensis* (CUVIER, 1817), female 15 cm d.w., Gulf of Mexico. Lower teeth.



Plate 3. - *Urolophus sloani* (BLAINVILLE, 1816) teeth of synonym *Urolophus jamaicensis* (CUVIER, 1817), male 10.5 cm d.w., Gulf of Mexico. Upper teeth.



Plate 4. - *Urobatis sloani* (BLAINVILLE, 1816) teeth of synonym *Urolophus jamaicensis* (CUVIER, 1817), male 10.5 cm d.w., Gulf of Mexico. Lower teeth.



Plate 5. - *Paratrygon atereba* (MÜLLER & HENLE, 1841). Female 27.5 cm d.w., Ararari, Maranhao, Brasil. Upper teeth.

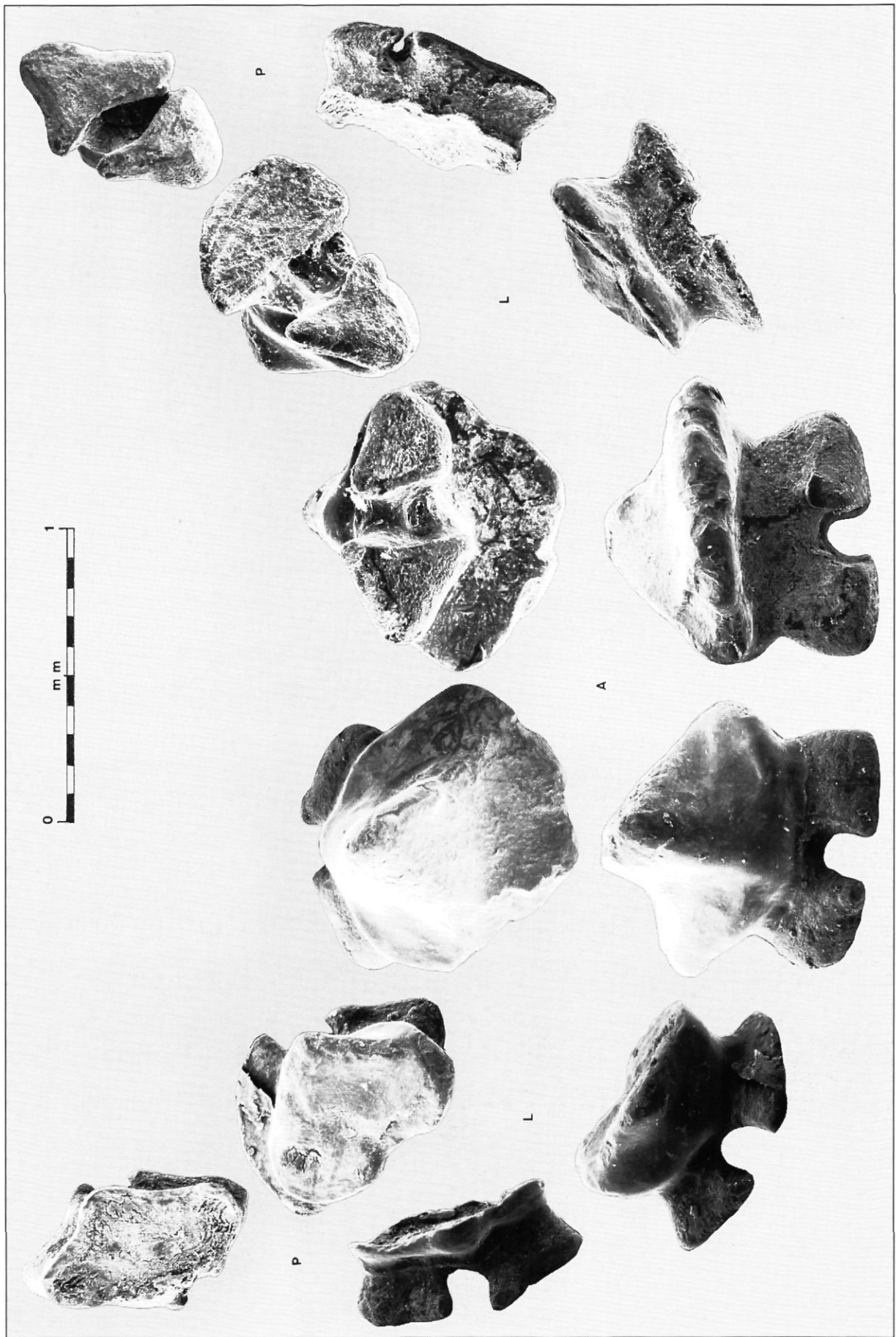


Plate 6. — *Paratrygon aiereba* (MÜLLER & HENLE, 1841). Female 27.5 cm d.w., Ararari, Maranhao, Brasil. Lower teeth.

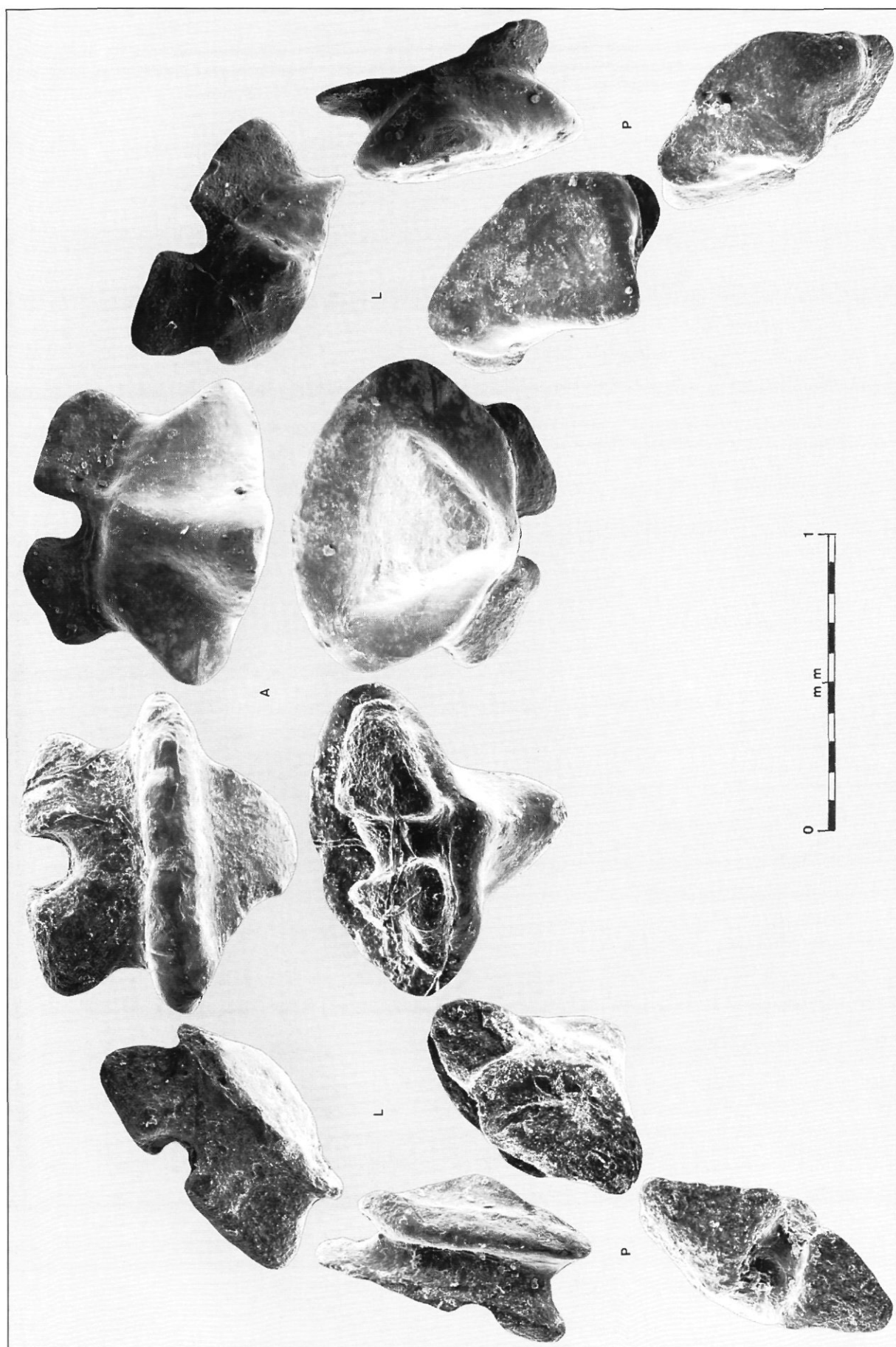


Plate 7. - *Paratrygon aiereba* (MÜLLER & HENLE, 1841). Male 21 cm d.w., Ararari, Maranhao, Brasil. Upper teeth.

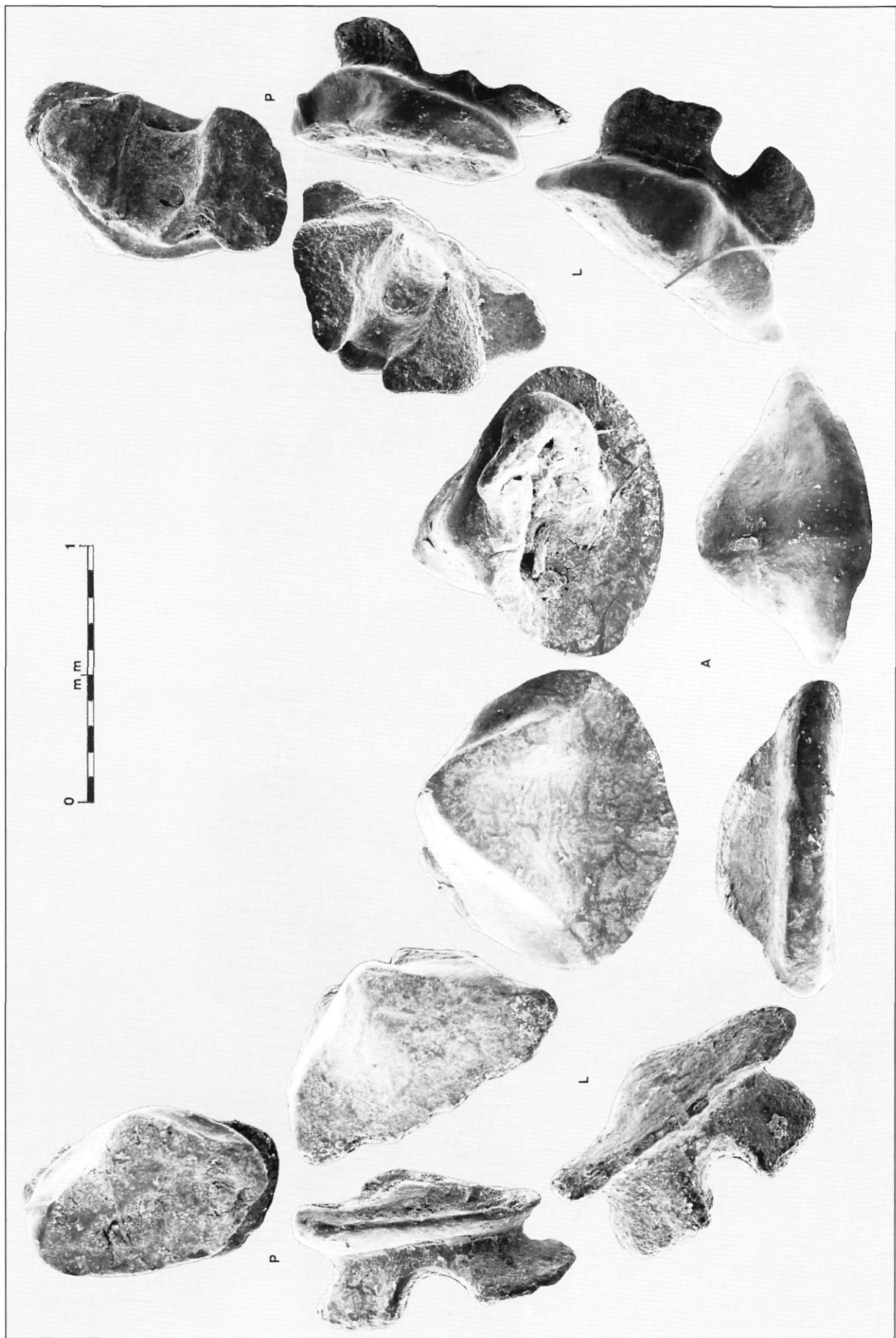


Plate 8. - *Paratrygon aiareba* (MÜLLER & HENLE, 1841). Male 21 cm d.w., Ararari, Maranhao, Brasil, Lower teeth

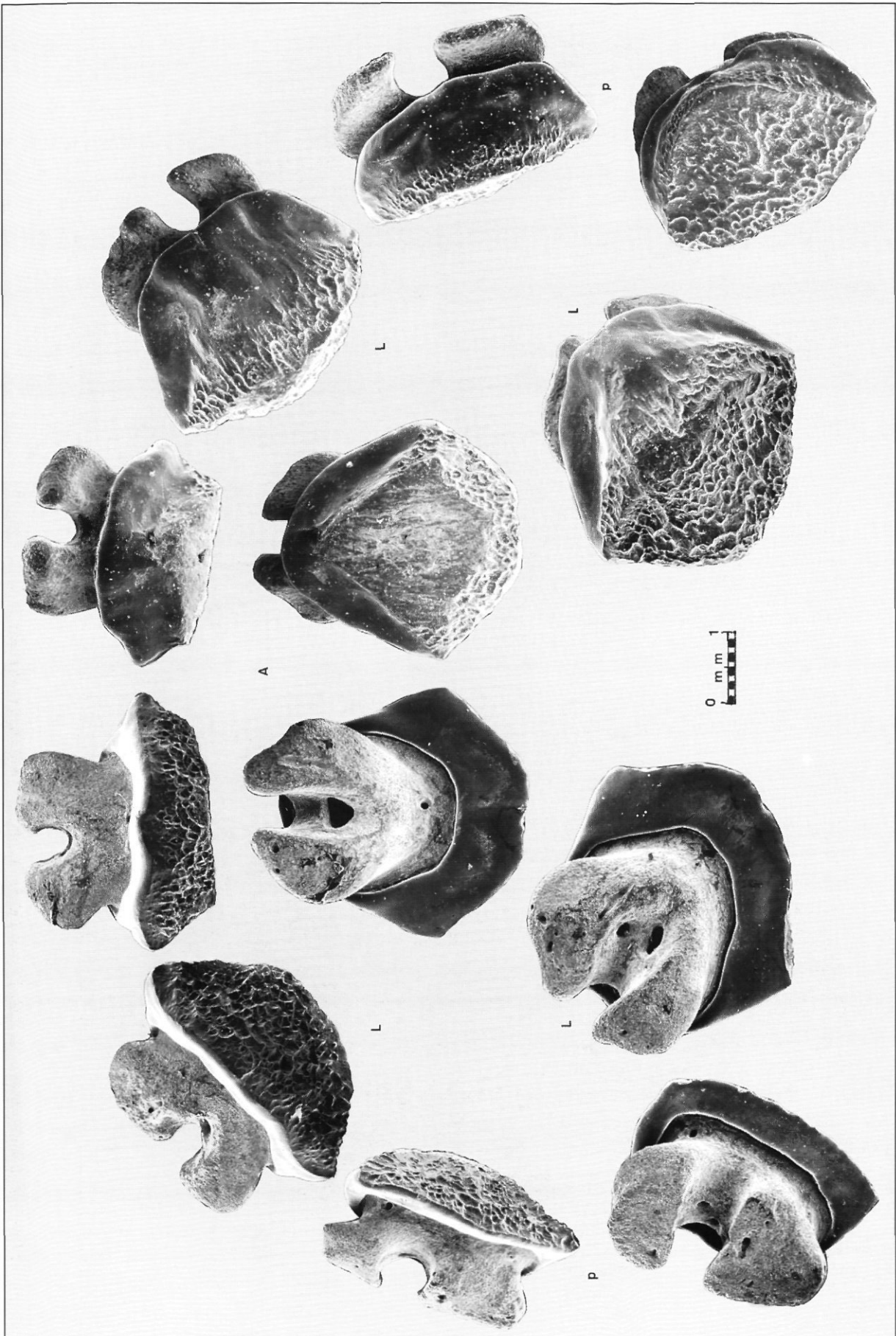


Plate 9. - *Plesiobatis daviesi* (WALLACE, 1967). Female 230 cm t.l., off New Caledonia. Upper teeth.

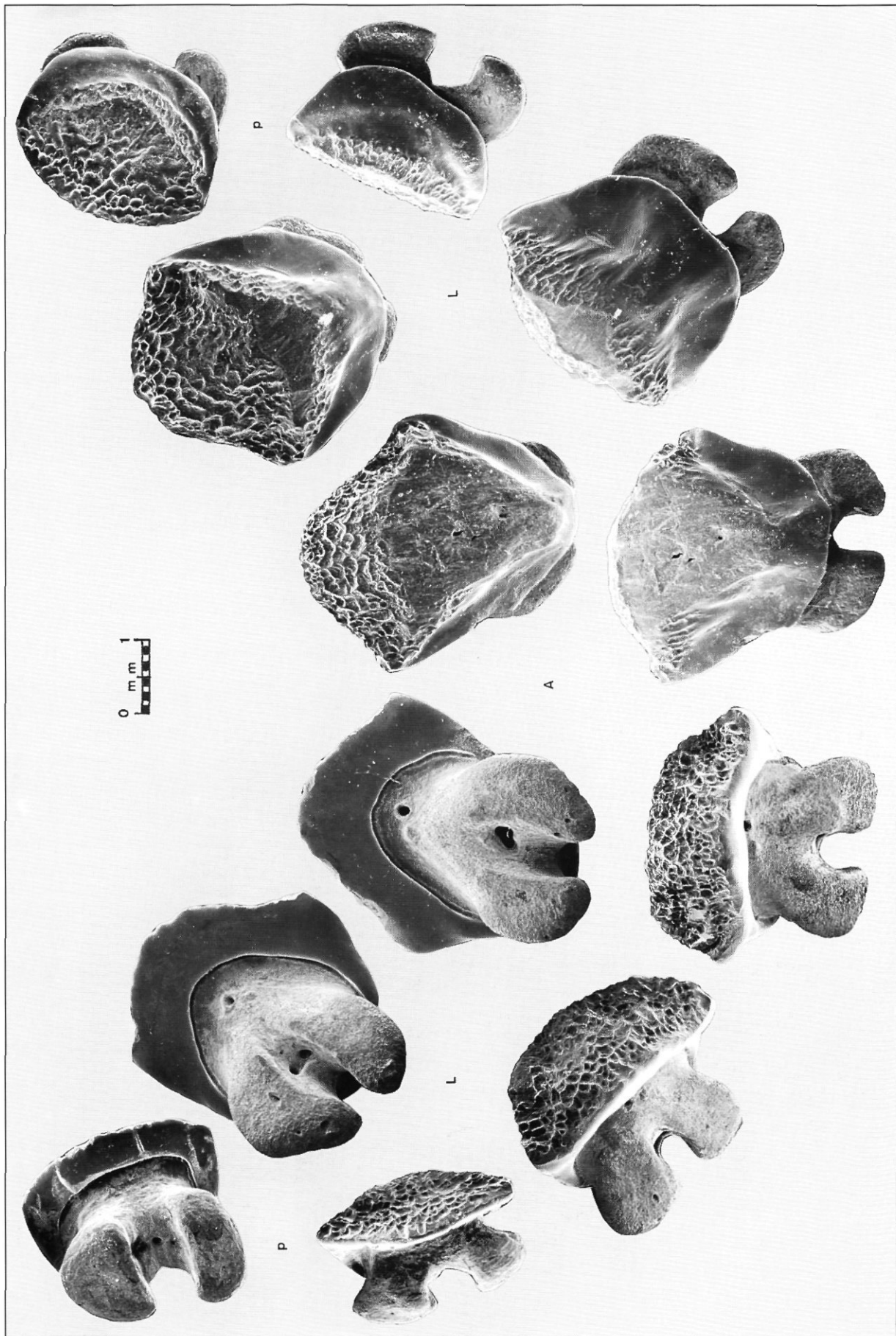


Plate 10. - *Plesiobatis daviesi* (WALLACE, 1967). Female 230 cm t.l., off New Caledonia. Lower teeth.

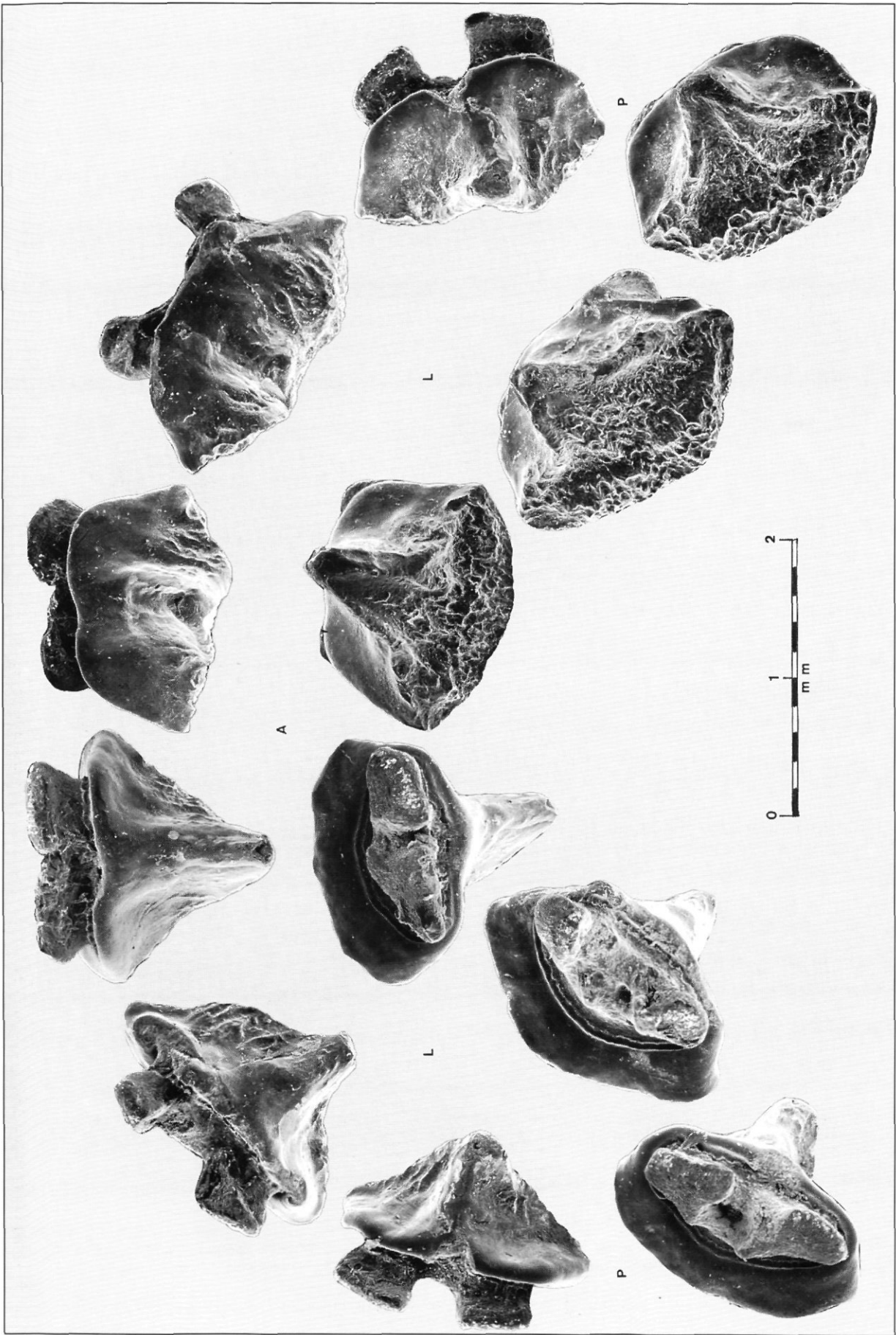


Plate 11. - *Plesiobatis daviesi* (WALLACE, 1967). Male 105 cm d.w., off New Caledonia. Upper teeth.

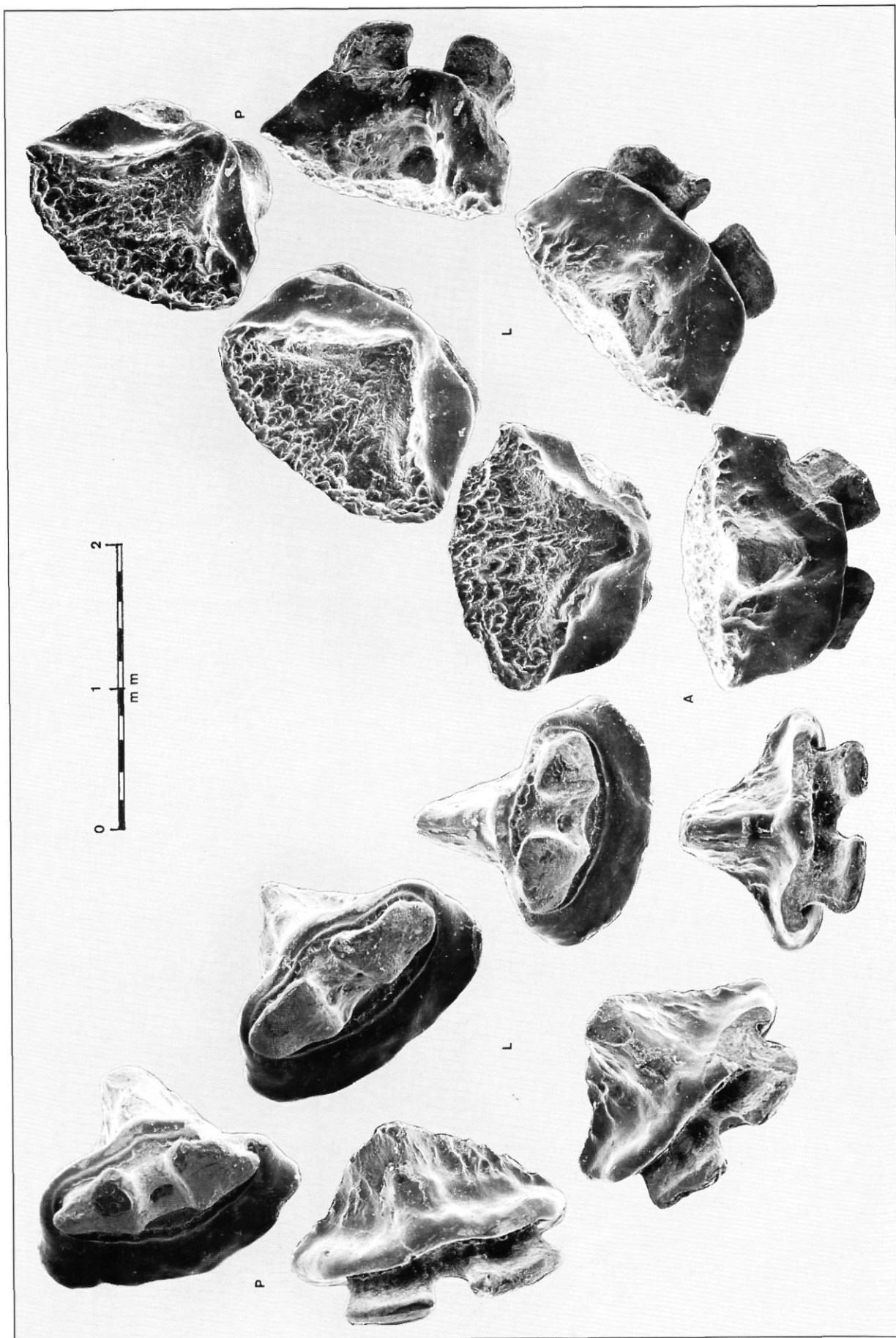


Plate 12. — *Plesiobatis daviesi* (WALLACE, 1967). Male 105 cm d.w., off New Caledonia. Lower teeth.



Plate 13. – *Plesiobatis daviesi* (WALLACE, 1967). Male 37 cm d.w., off Hobart, Tasmania. Upper teeth.



Plate 14. - *Plesiobatis daviesi* (WALLACE, 1967). Male 37 cm d.w., off Hobart, Tasmania. Lower teeth.

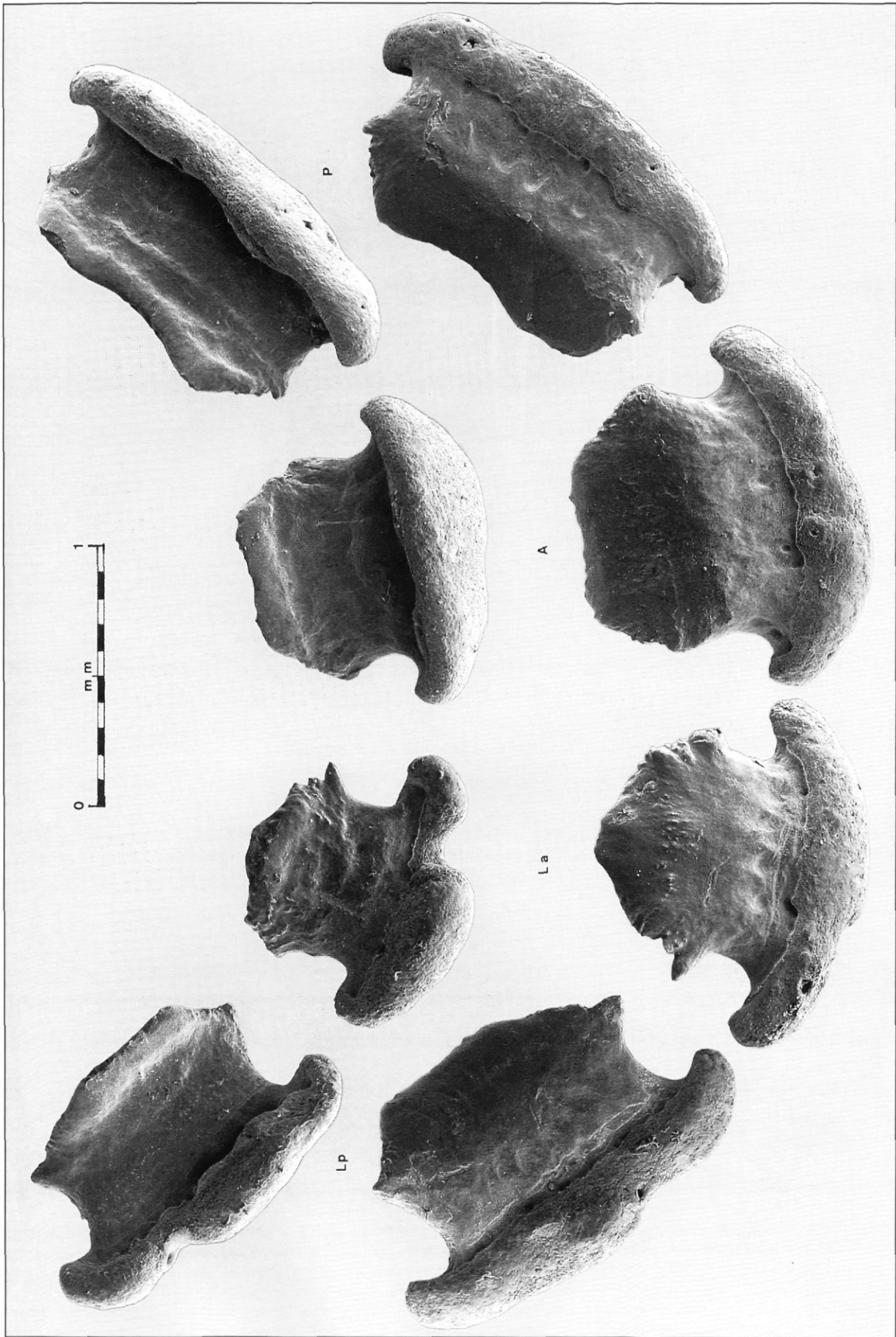


Plate 15. – *Manta birostris* (DONNDORFF, 1798). Female 250 cm d.w., Gorea, Senegal. Lower teeth (only extant).

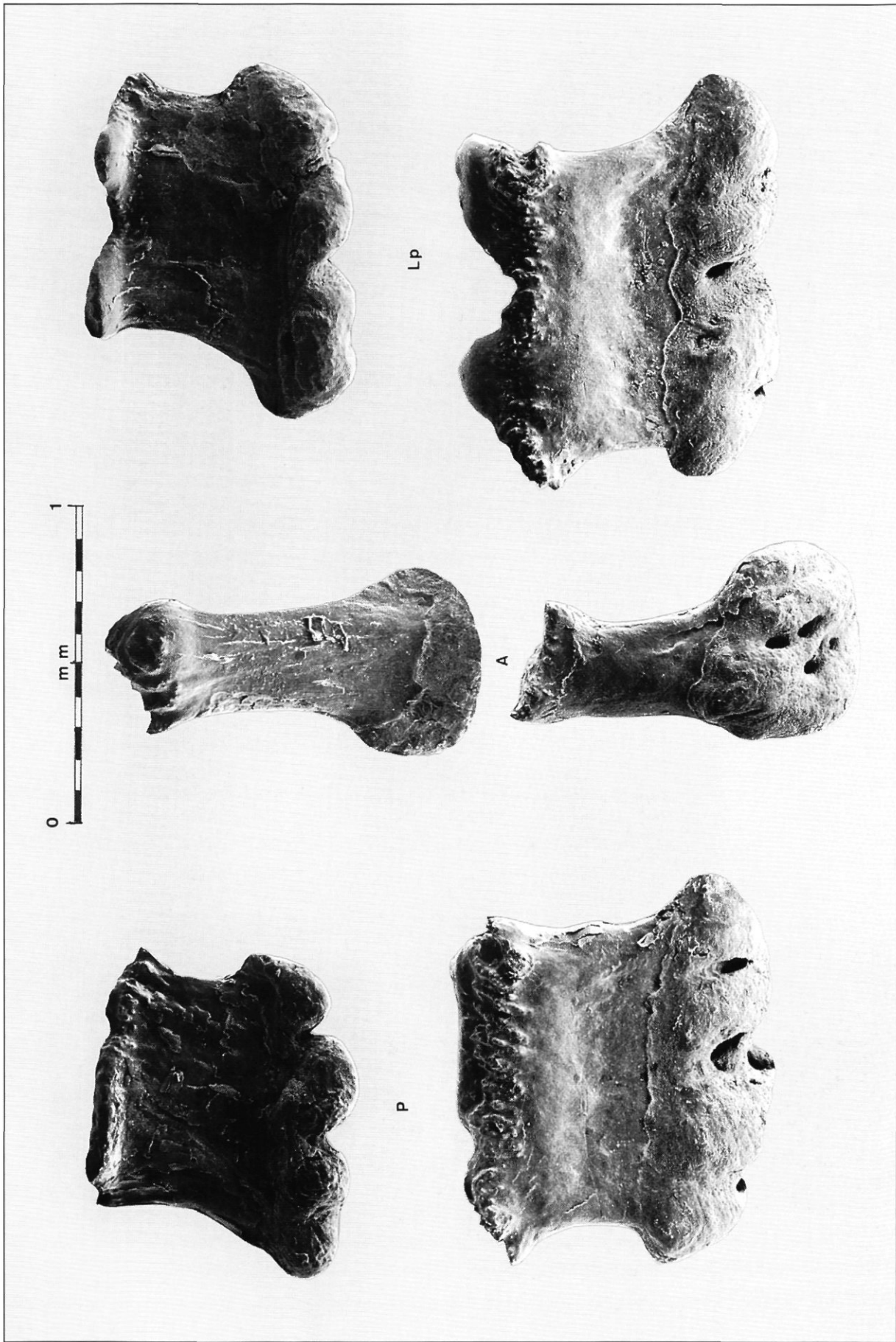


Plate 16. - *Manta birostris* (DONNDORFF, 1798). Female 250 cm d.w., Gorea, Senegal. Teeth suggesting that the larger one of the mobulids or mantids, such like those of myliobatids result of the fusion of different dental germina (theory of E. CASIER 1947).

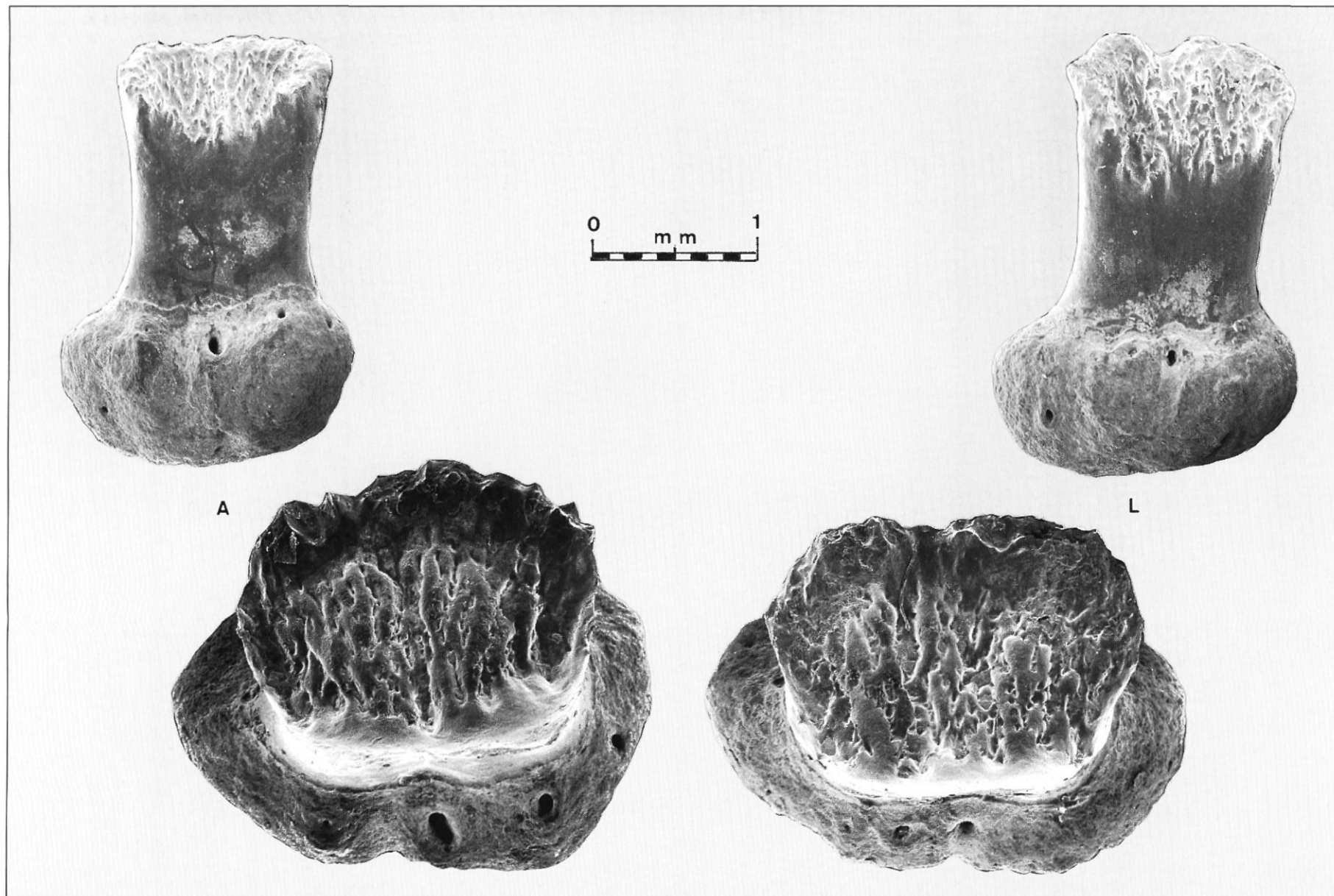


Plate 17. – *Manta birostris* (DONNDORFF, 1798). Female 470 cm d.w., Somone, Senegal. Lower teeth (only extant). Scale bar refers to outer views.

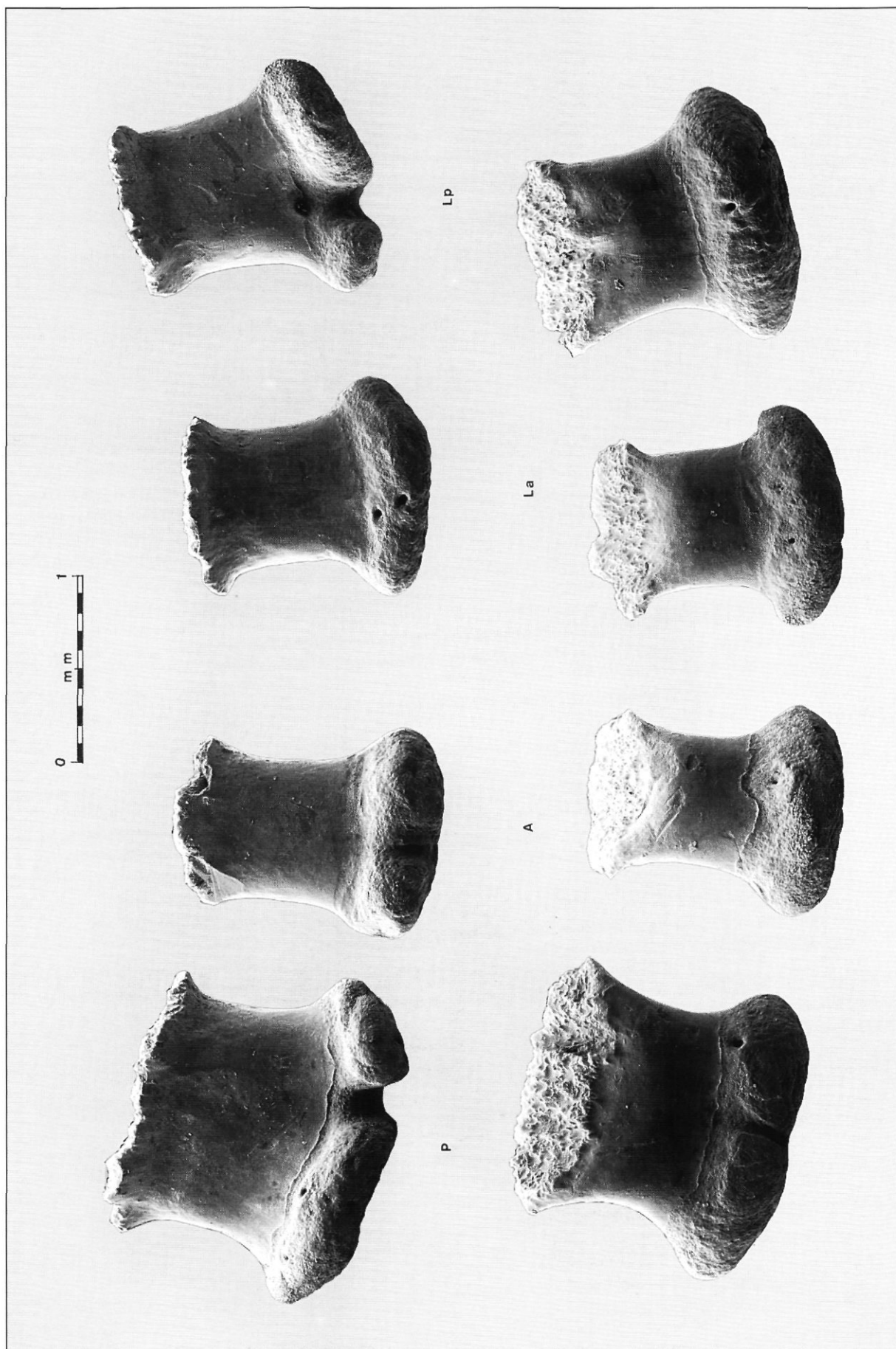


Plate 18. - *Manta birostris* (DONNDORFF, 1798). Teeth of synonym *Cephaloptera giorno* (LACEPEDE, 1802). Female 480 cm d.w., Baia Rosas, Mogador (Essaouira), Morocco. Lower teeth (only extant). Scale bar refers to outer views.

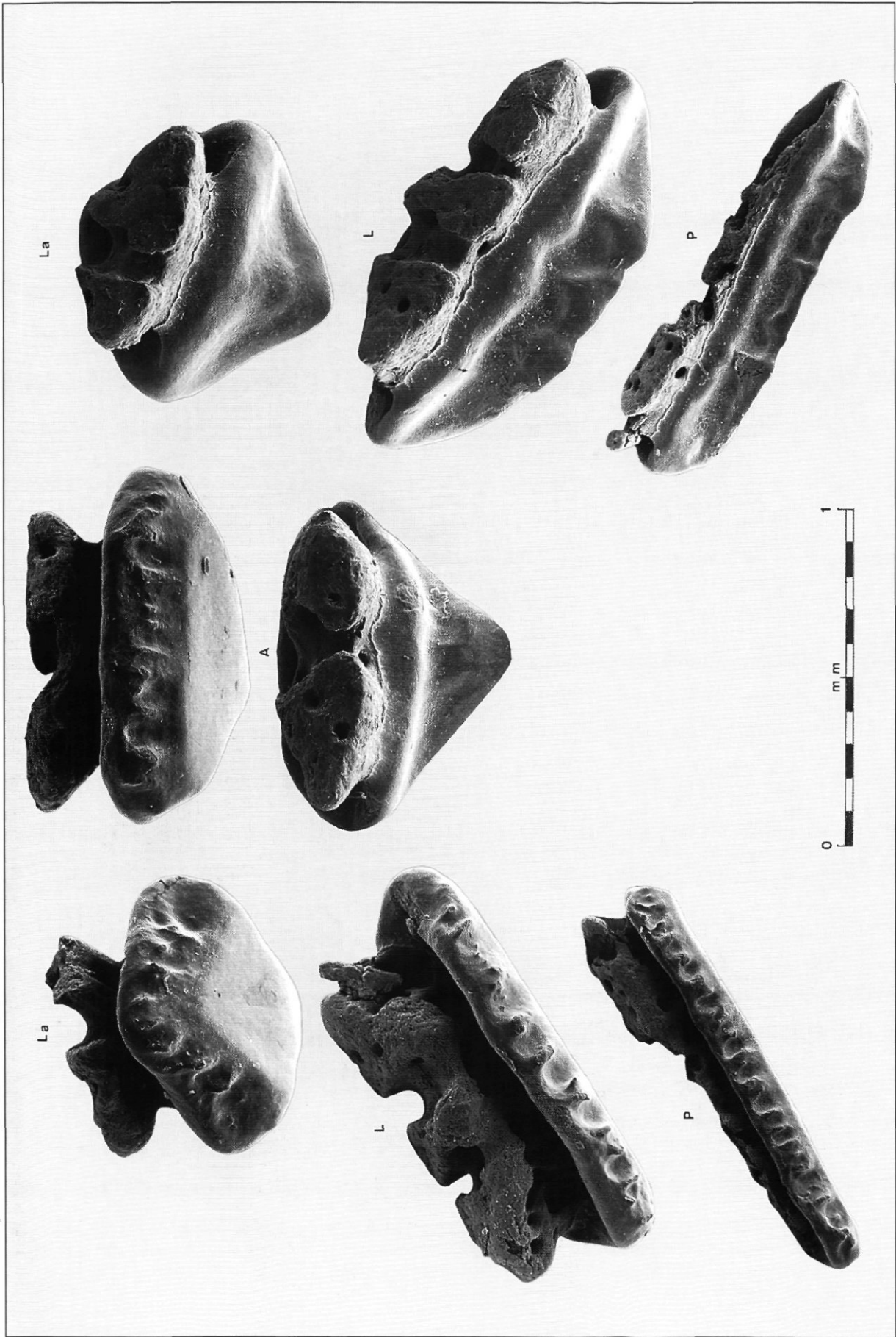


Plate 19. – *Mobula rochebrunei* (VAILLANT, 1879). Female 110 cm. d.w., Gorea, Senegal. Upper teeth.

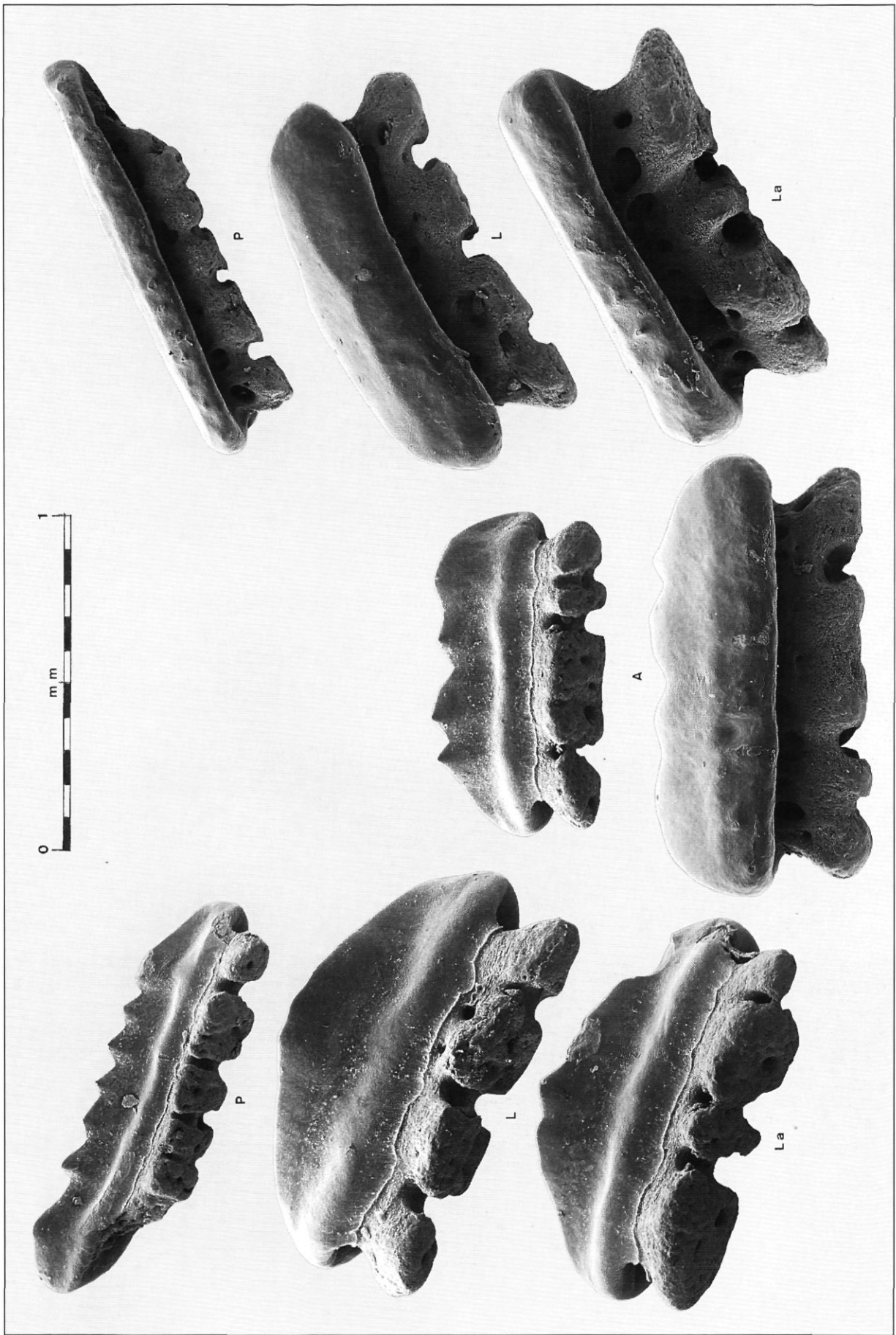


Plate 20. — *Mobula rochebrunei* (VAILLANT, 1879). Female 110 cm. d.w., Gorea, Senegal. Lower teeth.

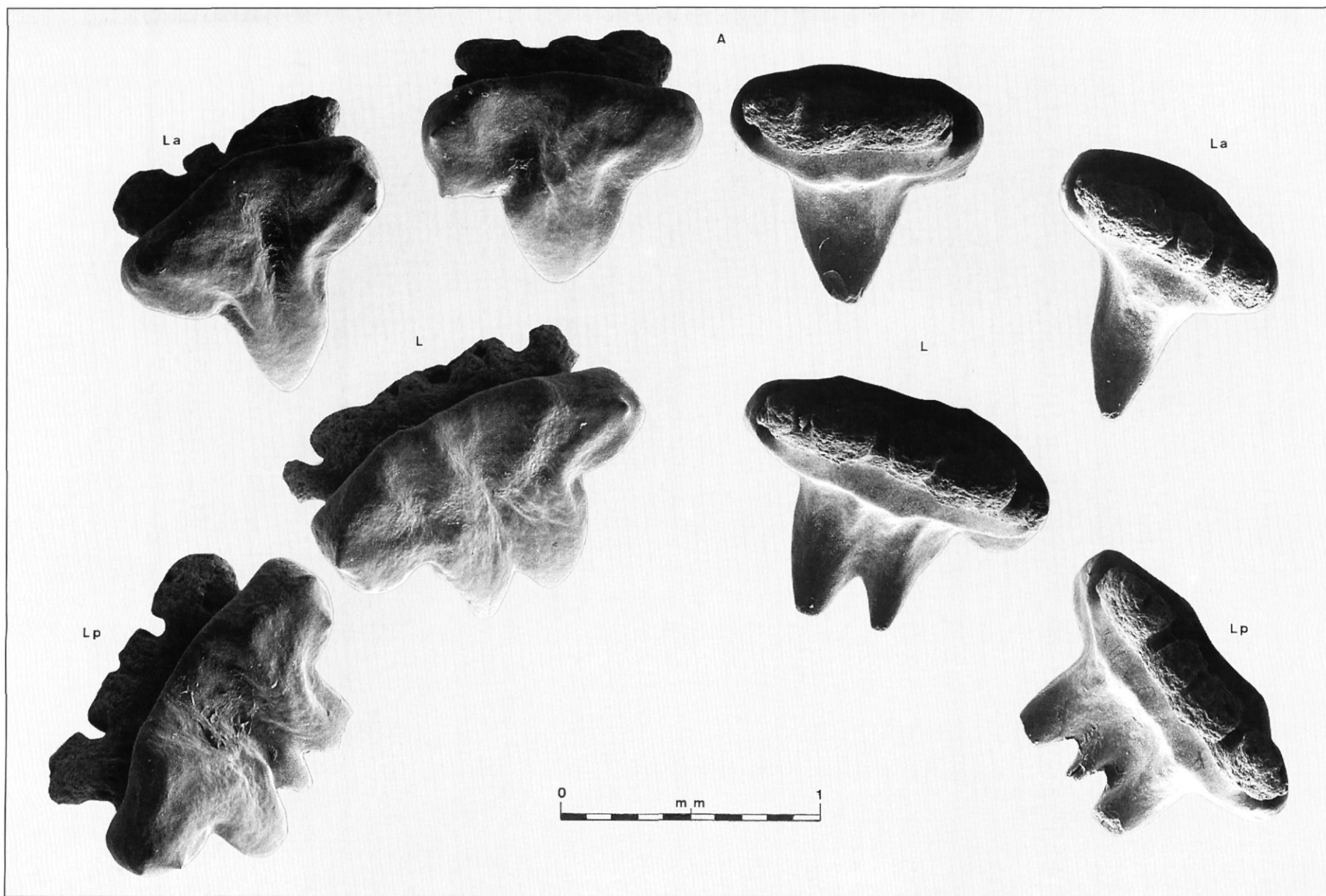


Plate 21. — *Mobula rochebrunei* (VAILLANT, 1879). Male 120 cm. d.w., Gorea, Senegal. Upper teeth. Scale bar refers to outer views.

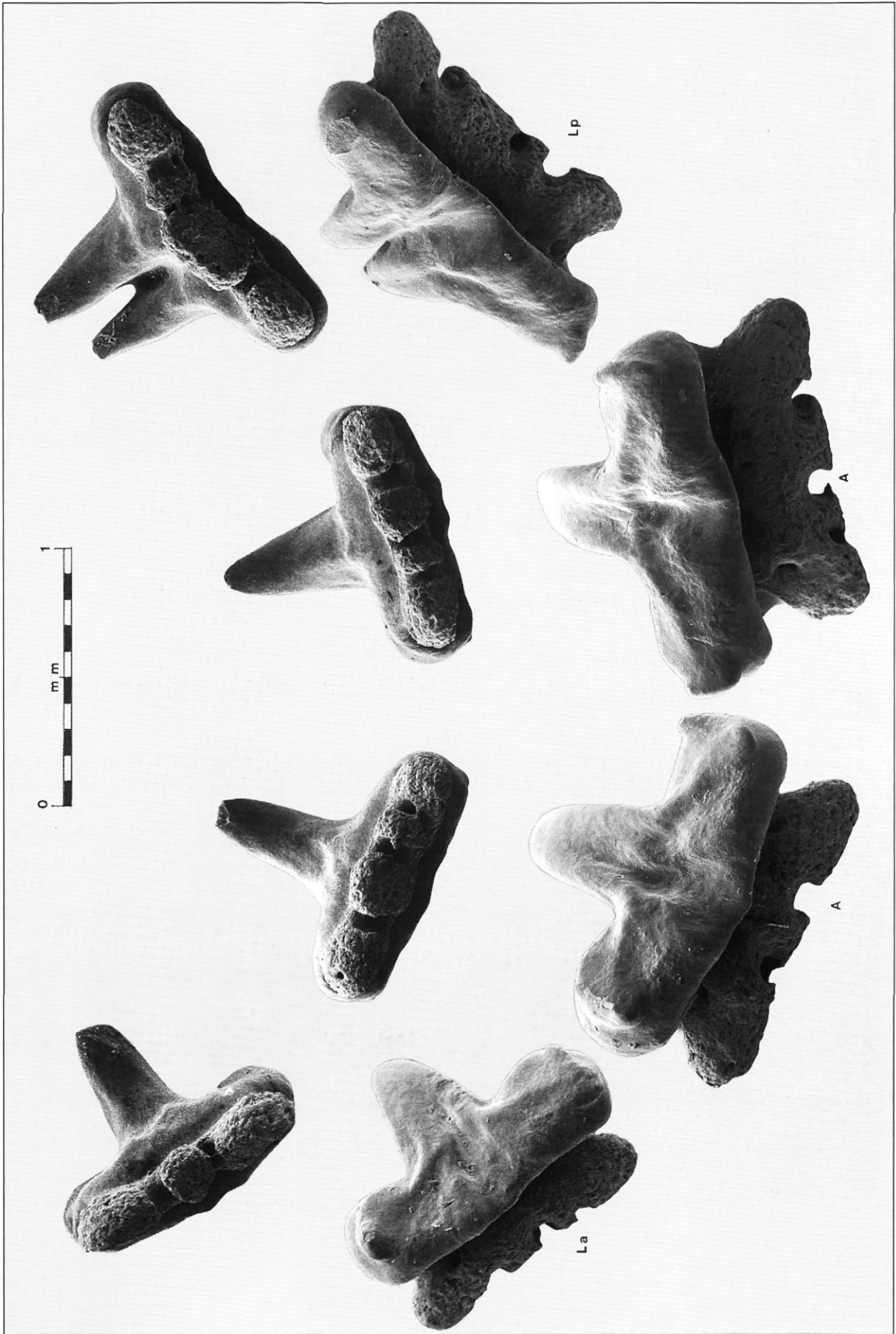


Plate 22. - *Mobula rochebrunei* (VAILLANT, 1879). Male 120 cm. d.w., Gorea, Senegal. Lower teeth. Scale bar refers to outer views.

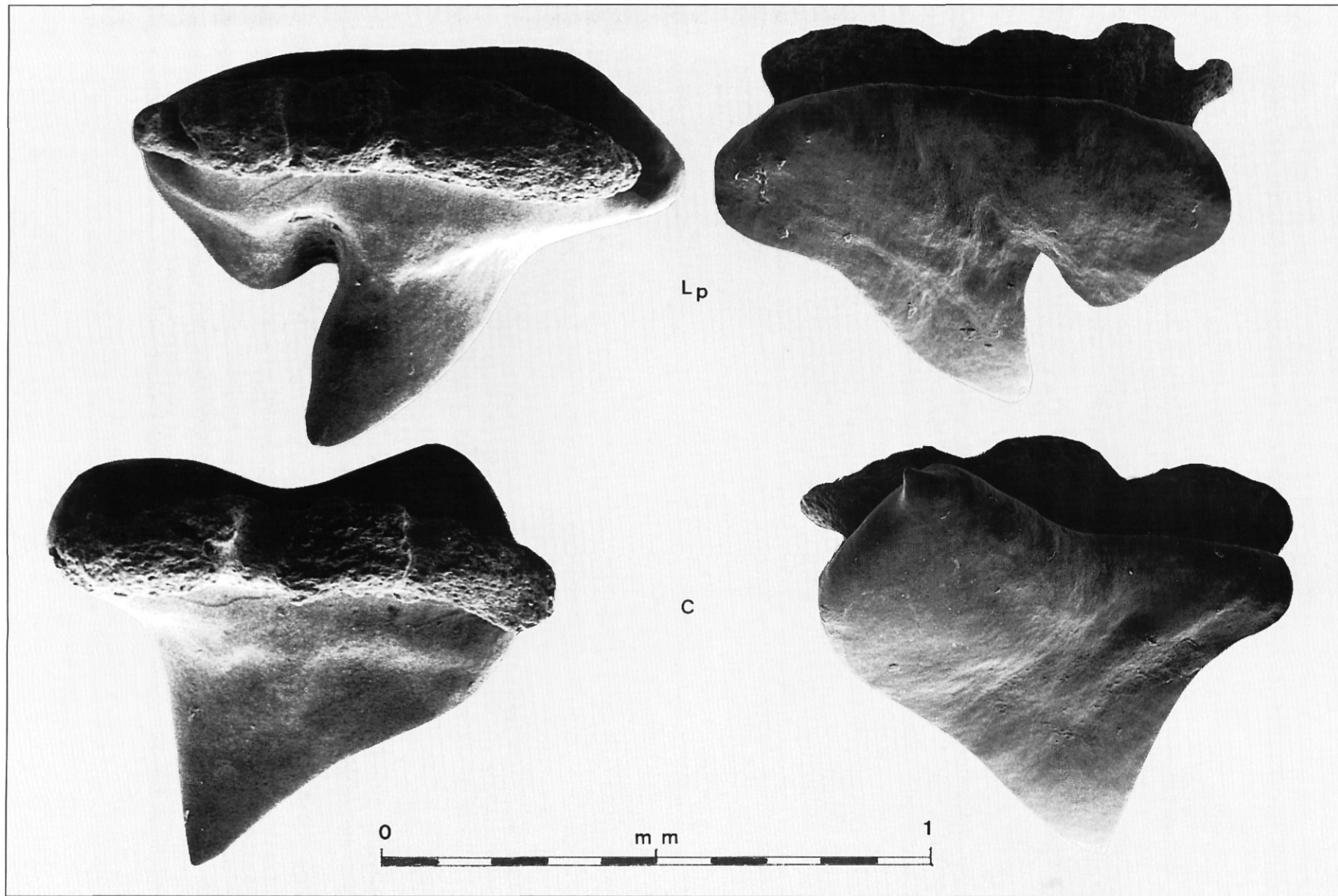


Plate 23. — *Mobula rochebrunei* (VAILLANT, 1879). Male 120 cm. d.w., Gorea, Senegal. Upper commissural teeth.

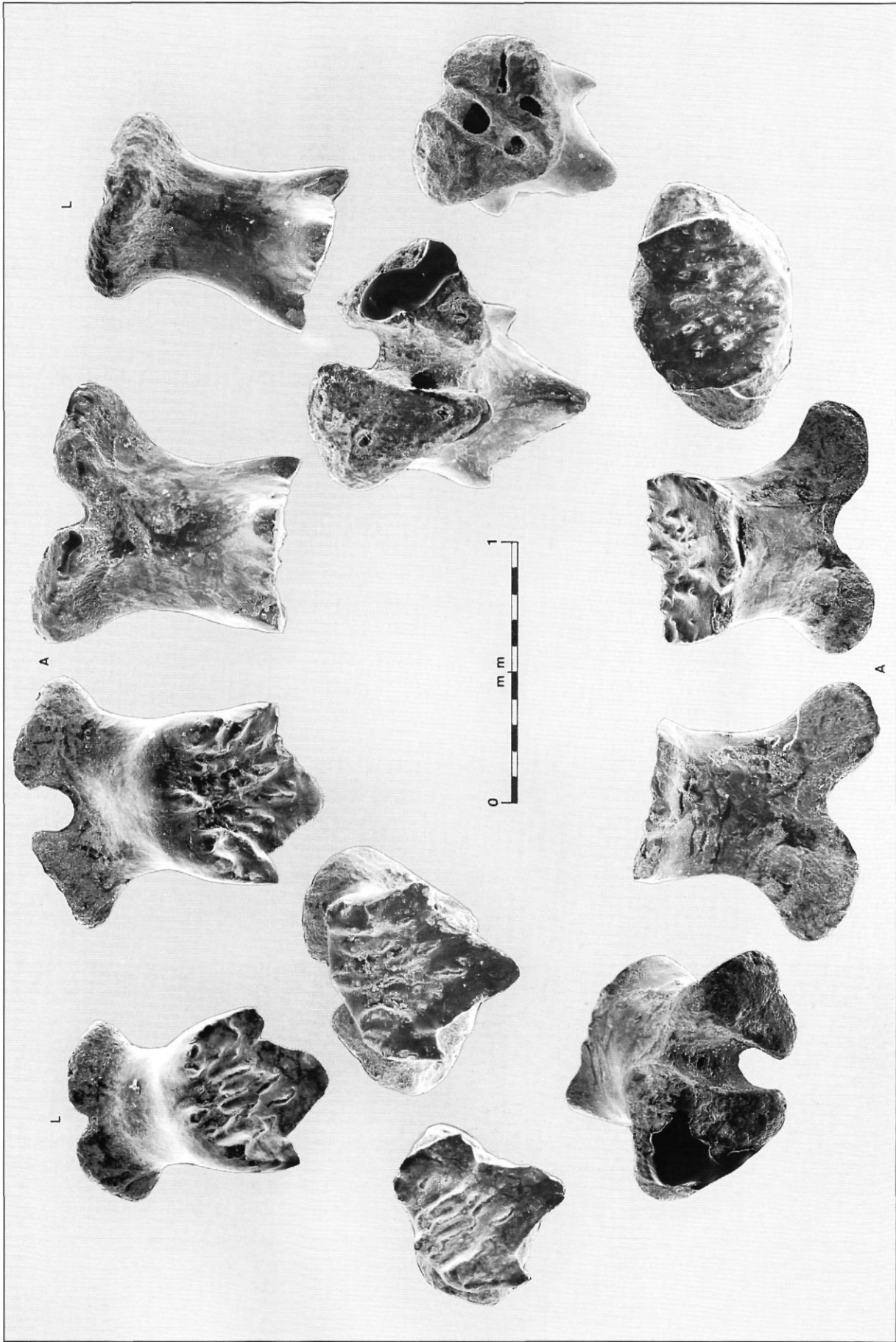


Plate 24. - *Mobula mobular* (BONNATERRE, 1788). Male 124 cm d.w., Sicily Channel, Italia. Two upper and one lower teeth.

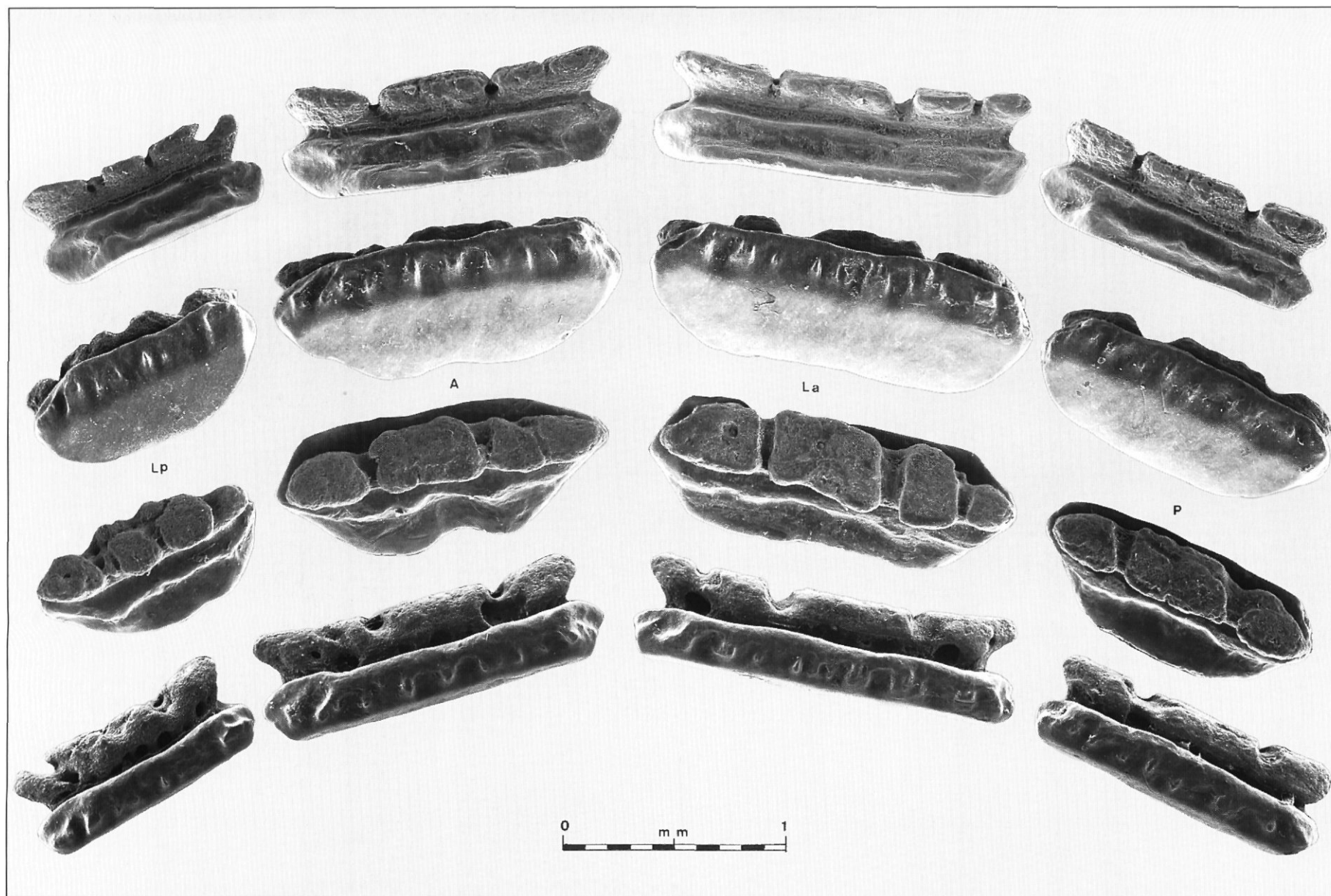


Plate 25. – *Ceratobatis robertsii* BOULENGER, 1837. Holotype, female 77 cm d.w., off Jamaica. Upper teeth (only extant).

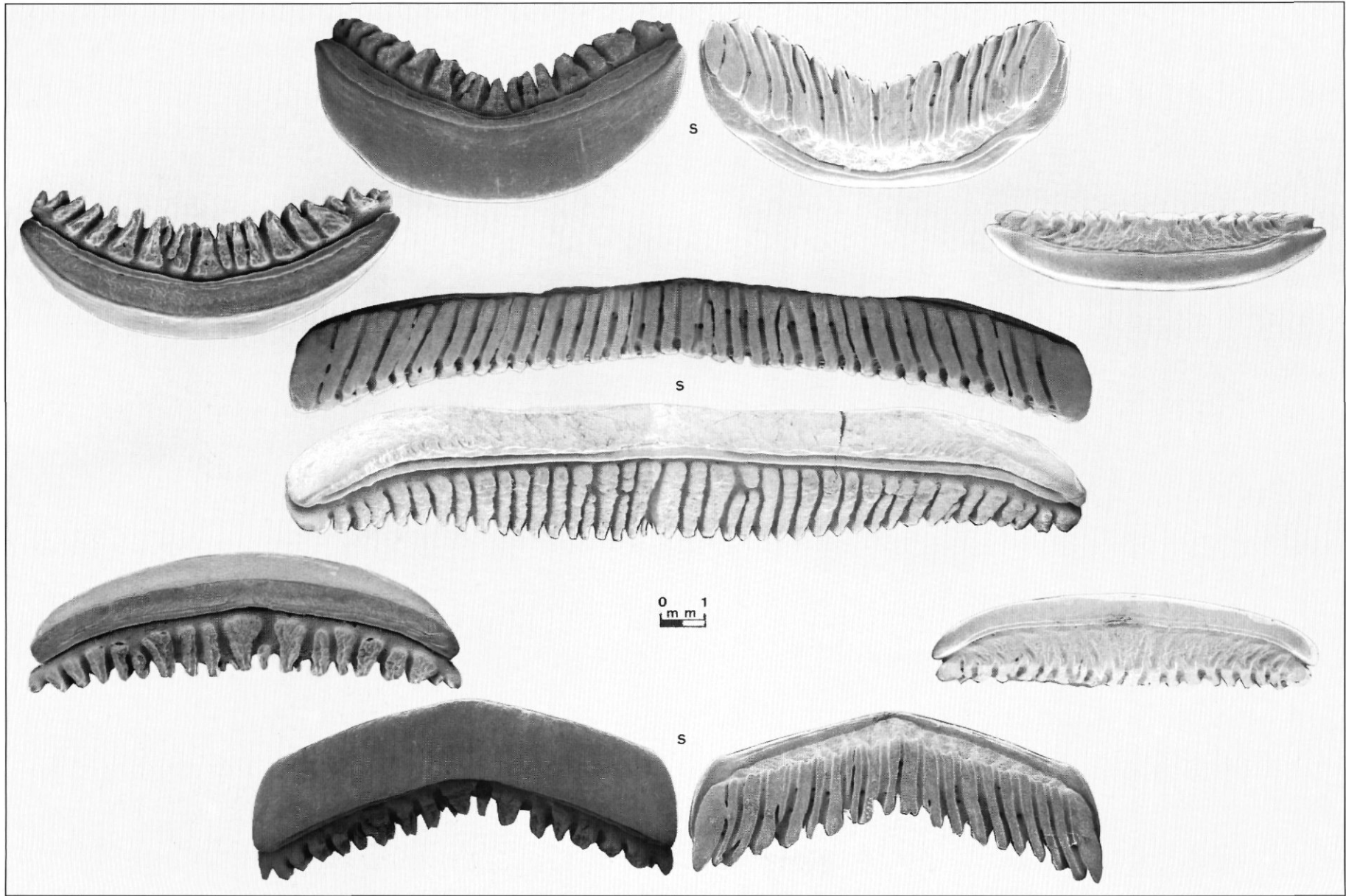


Plate 26. – *Aetobatus narinari* (EUPHRASEN, 1790). Male 42 cm d.w., upper and lower teeth. Male 72 cm d.w., upper tooth. Off Carriaco, Granada, Spain.

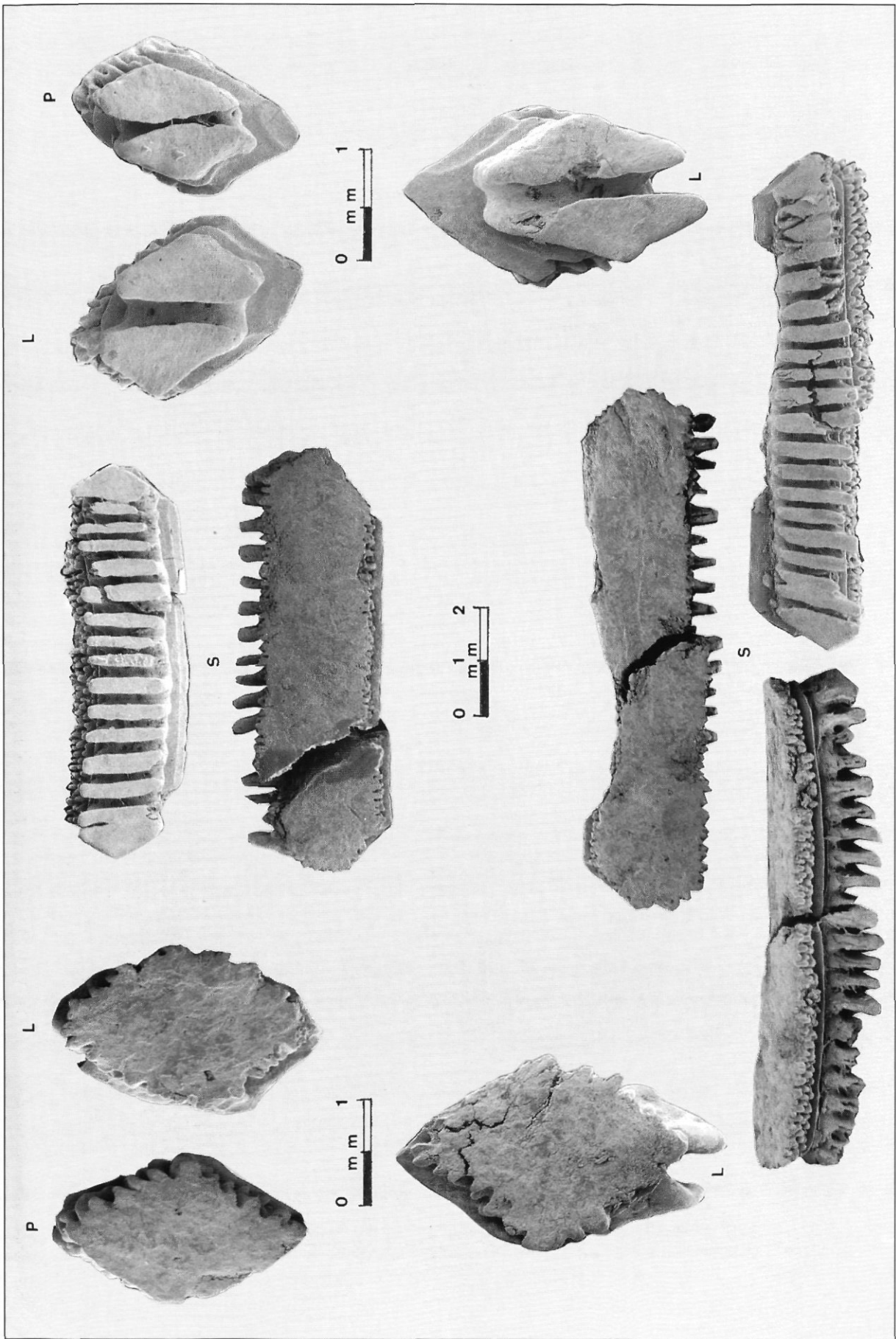


Plate 27. - *Aetomyia maculatus* (GRAY, 1834). Female 33.5 cm d.w., off Karwar, Kanataka, India. Upper and lower teeth.

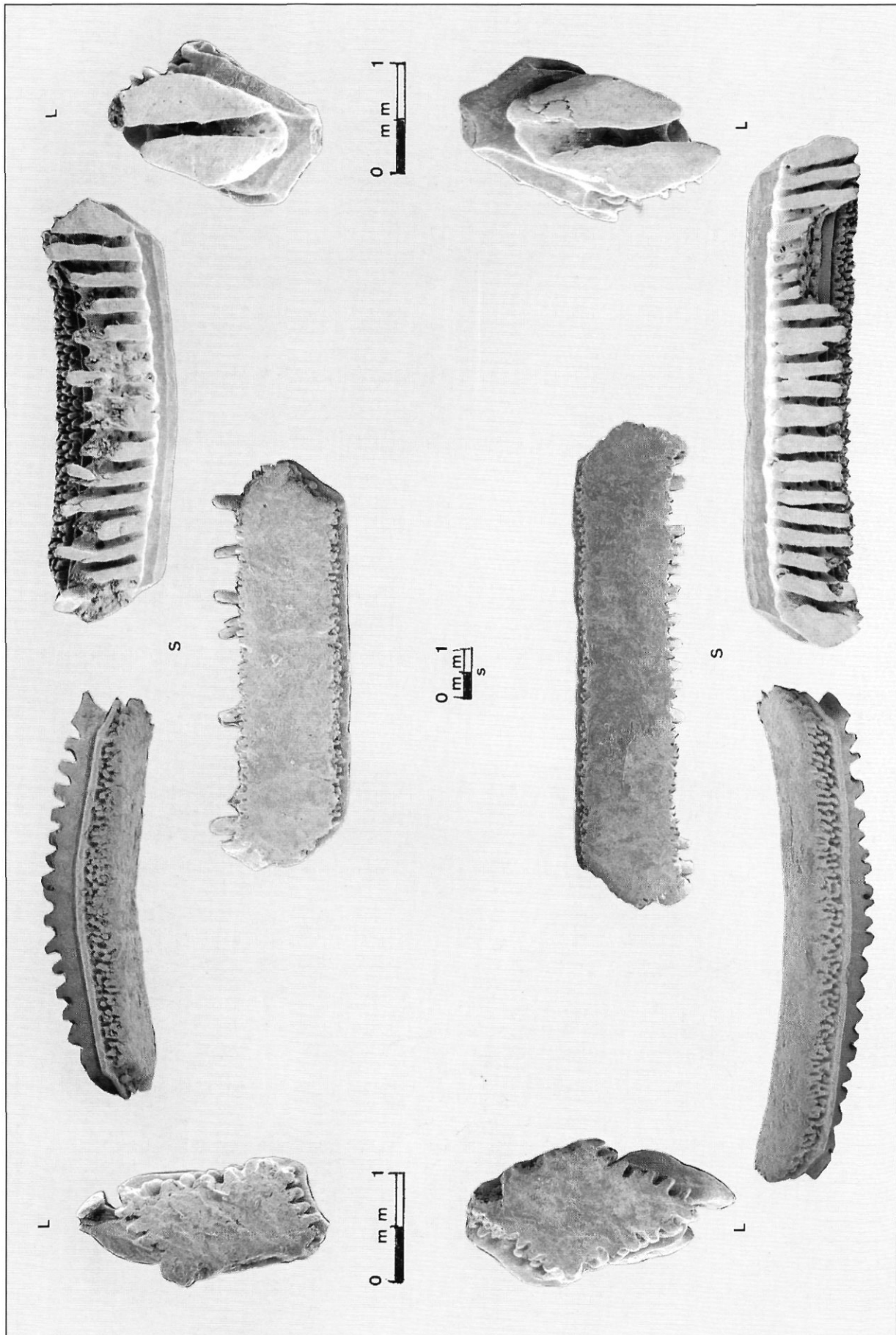


Plate 28. — *Aetomylaetus maculatus* (GRAY, 1834). Male 35.5 cm d.w., off Karwar, Kanataka, India. Upper and lower teeth.

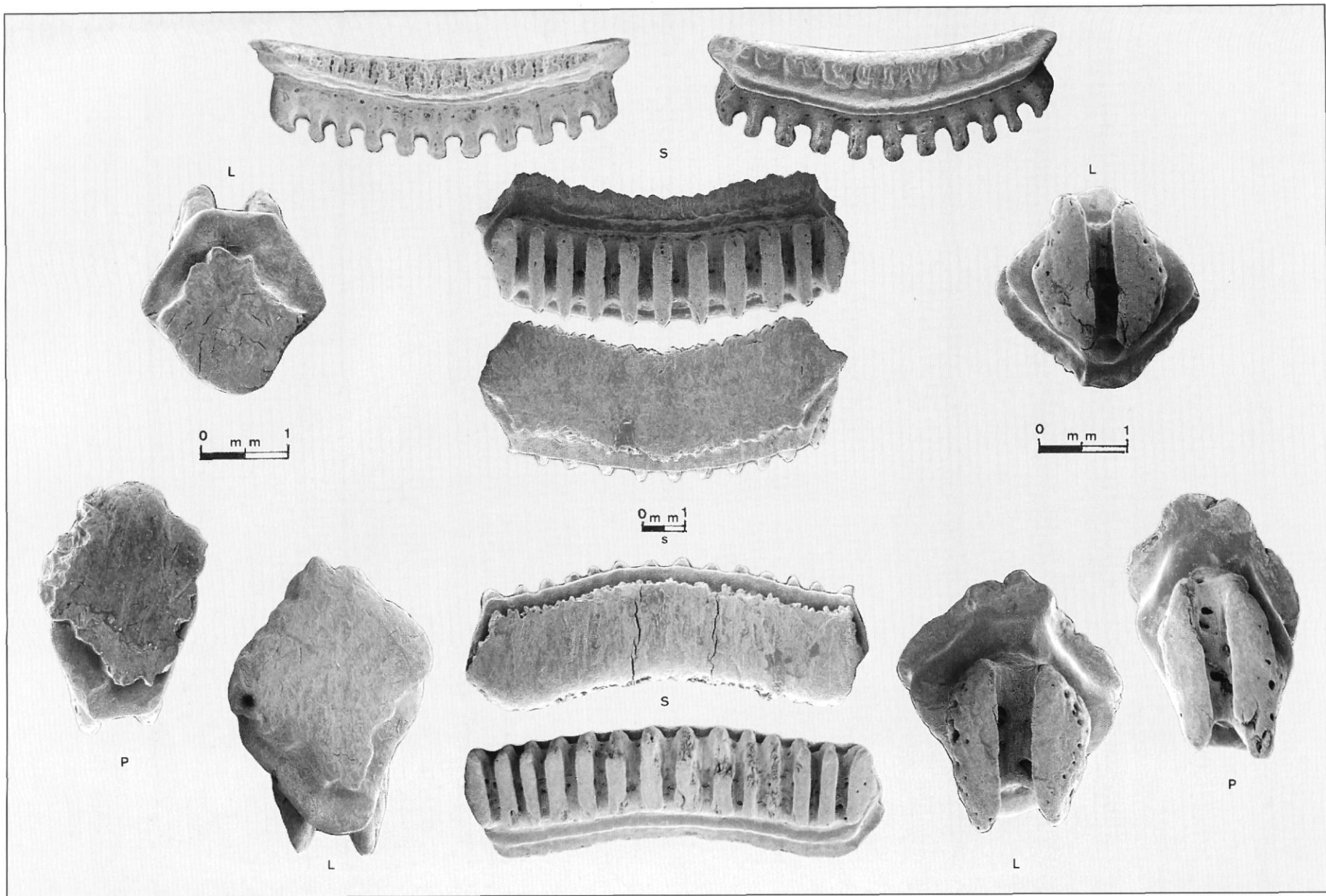


Plate 29. – *Myliobatis aquila* CUVIER, 1816. Female 44 cm d.w., Gulf of Gascogne, France. Upper and lower teeth.

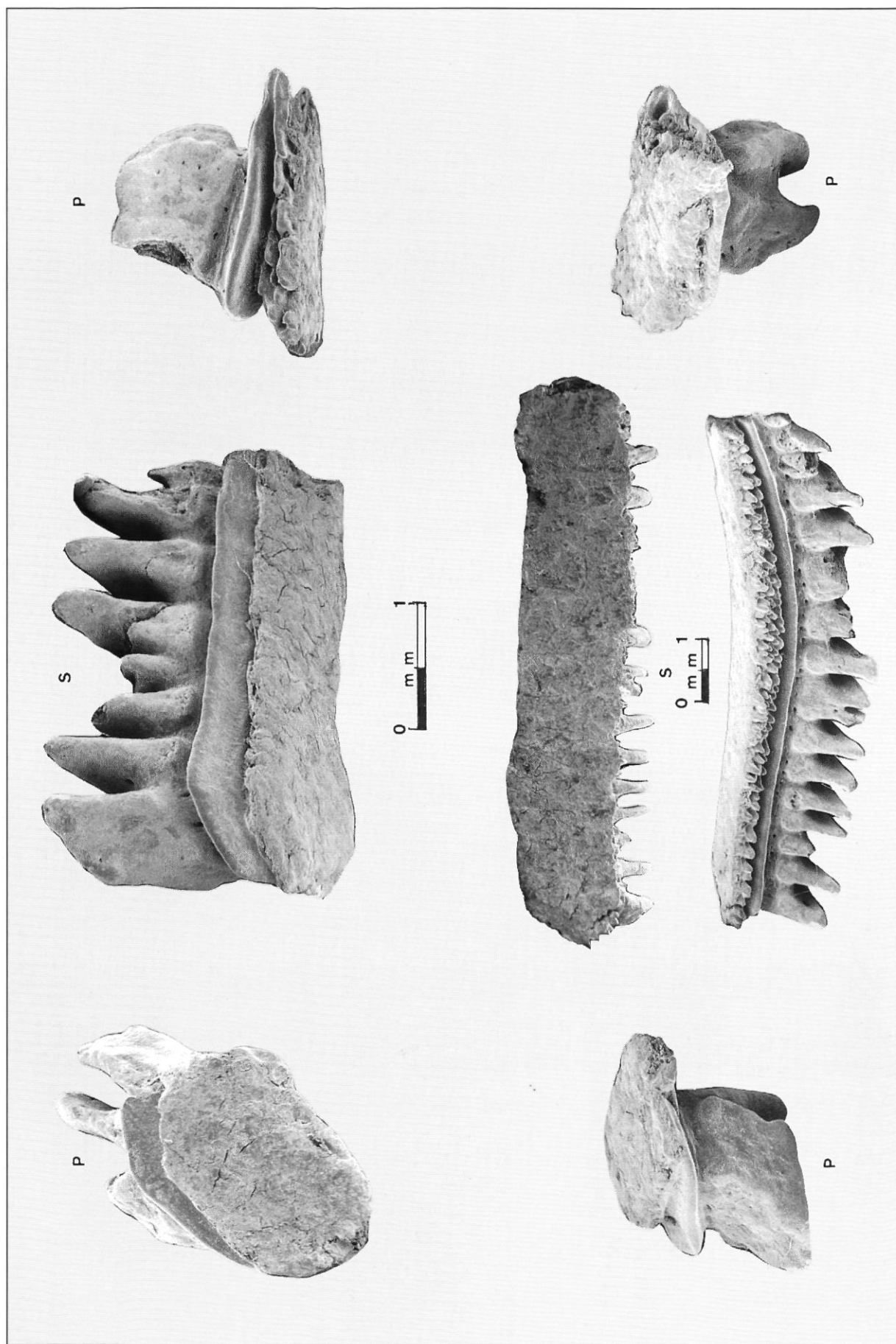


Plate 30. — *Pteromyliacrus bovinus* (GEOFFROY SAINT HILAIRE, 1817). Male 47 cm d.w., Gulf of Guinea. Upper and lower teeth. Lower scale bar refers only to lower symphyseal tooth.

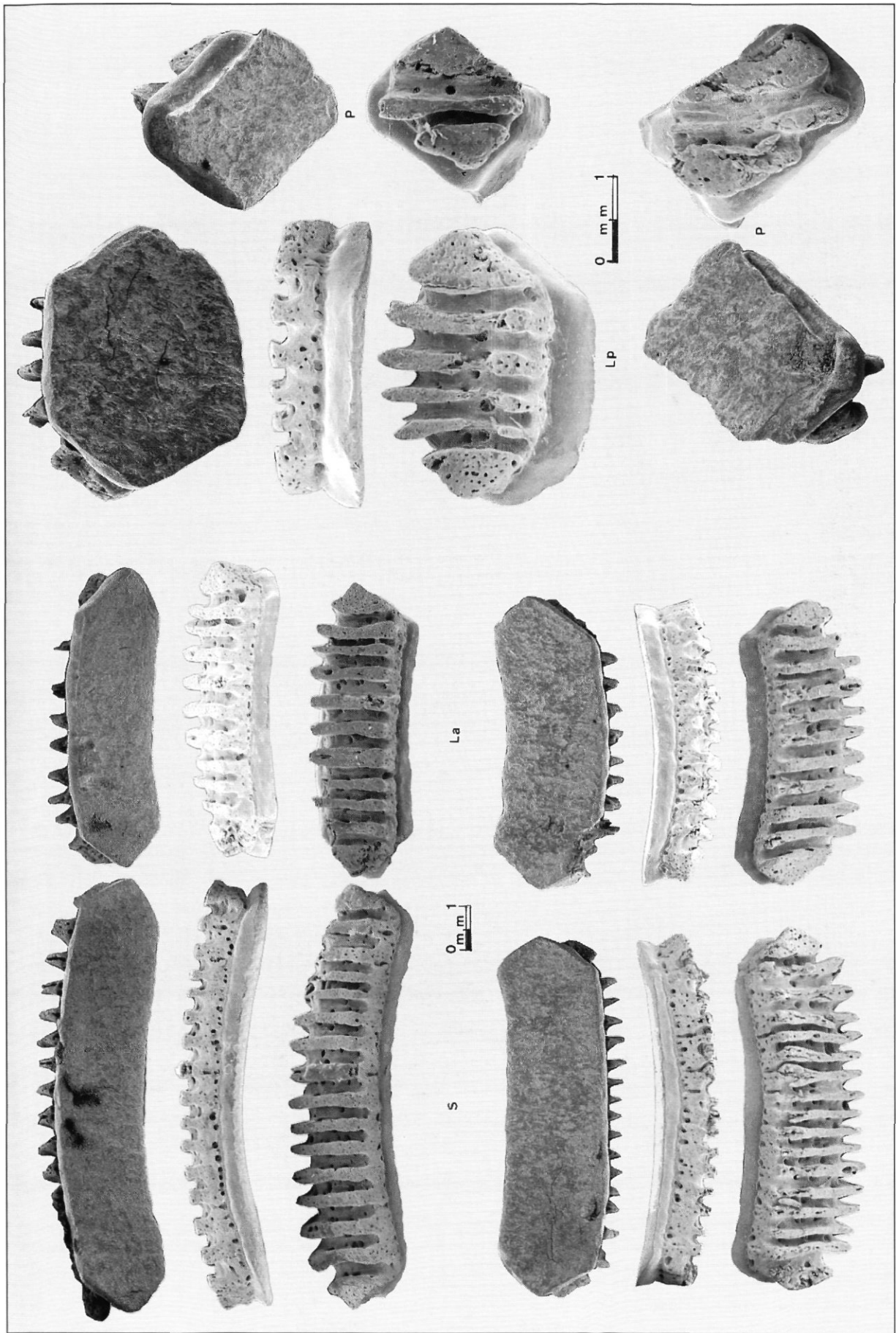


Plate 31. — *Rhinoptera marginata* (GEOFFROY SAINT HILAIRE, 1817). Female 42 cm d.w., off Laurent, Senegal. Upper and lower teeth.

Part B.

Addendum to 4a: Genus *Pteroplatytrygon*

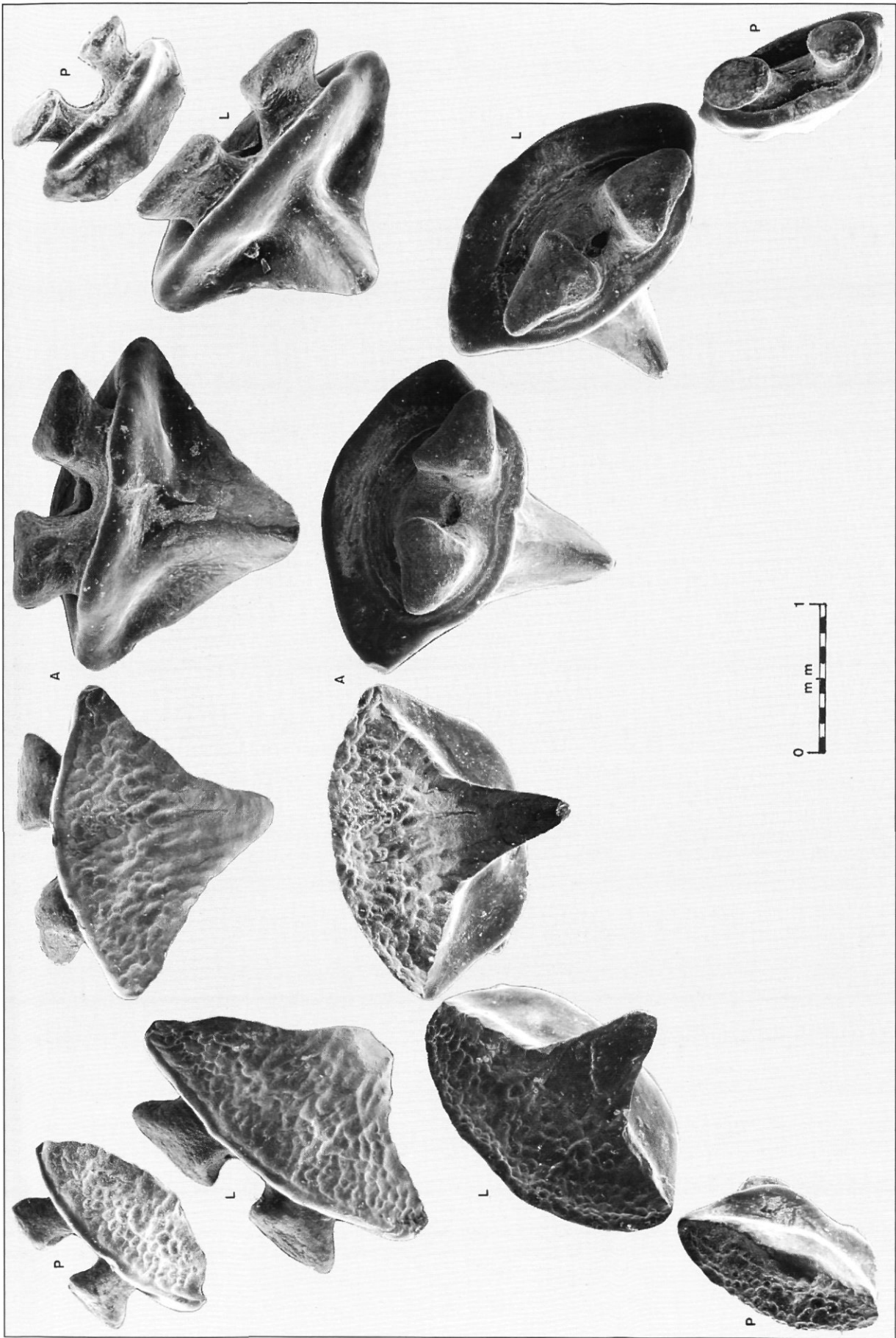


Plate 32. — *Pteroplatytrigon violacea* (BONAPARTE, 1832). Male 44.5 cm d.w., Channel of Sicilia, Italy. Upper teeth.

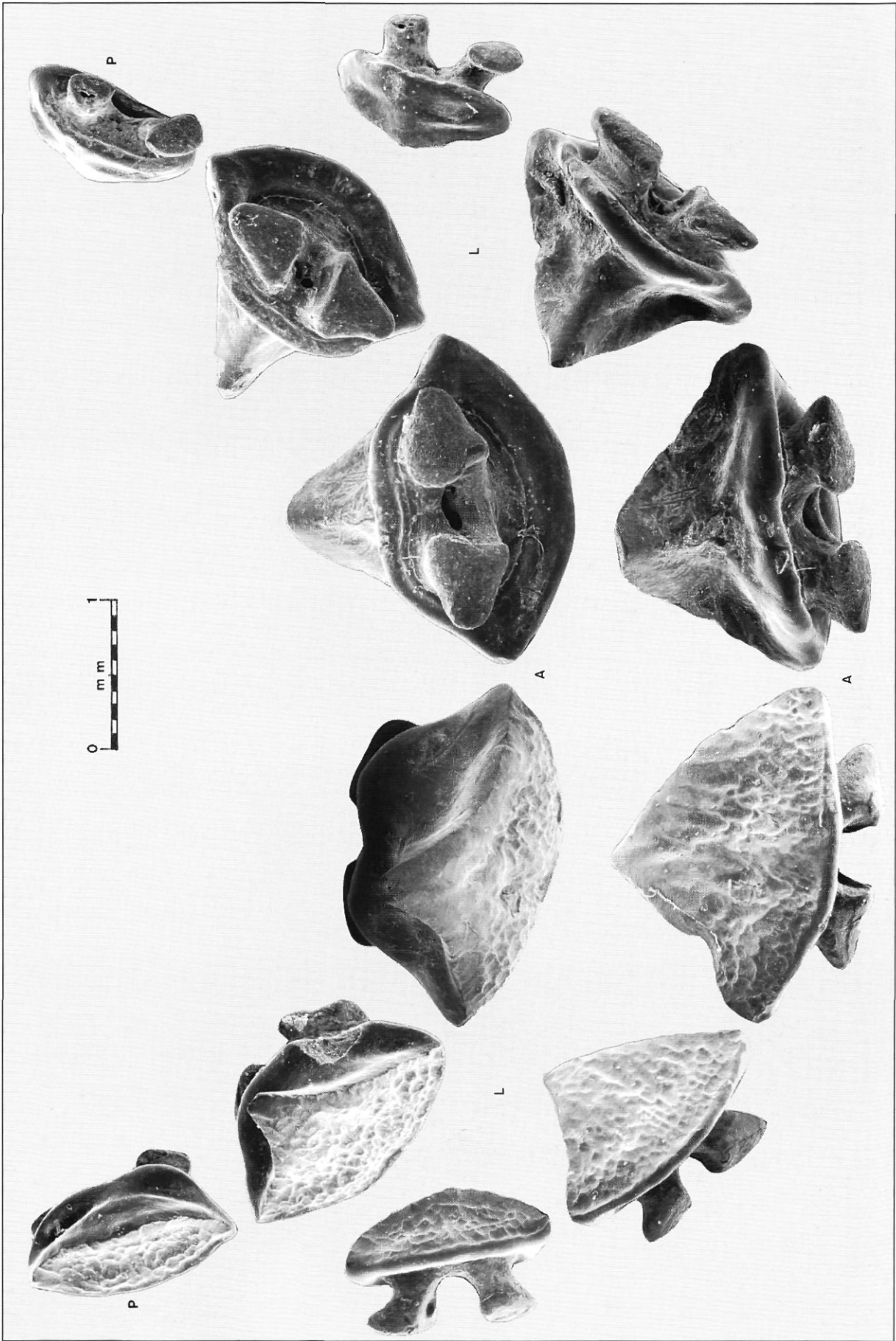


Plate 33. — *Pteroplatyrygon violacea* (BONAPARTE, 1832). Male 44.5 cm d.w., Channel of Sicilia, Italy. Lower teeth.

