Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supra-specific taxa of Chondrichthyan fishes Editor: M. STEHMANN

Part B: Batomorphii No. 2: Order Rajiformes - Suborder: Pristoidei - Family: Pristidae - Genera: *Anoxypristis* and *Pristis* No. 3: Suborder Rajoidei -Superfamily Rhinobatoidea - Families: Rhinidae - Genera: *Rhina* and *Rhynchobatus* and Rhinobatidae - Genera: *Aptychotrema, Platyrhina, Platyrhinoidis, Rhinobatos, Trygonorrhina, Zanobatus* and *Zapteryx.* by J. HERMAN, M. HOVESTADT-EULER, D.C. HOVESTADT and M. STEHMANN

Abstract

The tooth and rostral spine morphology of representatives öf the pristid genera Anoxypristis and Pristis, of the rhinid genera Rhina and Rhynchobatus and of the rhinobatid genera: Aptychotrema, Platyrhina, Platyrhinoidis, Rhinobatos, Trygonorrhina, Zanobatus and Zapteryx is described and illustrated by SEM photographs. A differential diagnosis is given to distinguish the genera by tooth morphology.

Key-words: Elasmobranchii - Batomorphii - Pristoidei - Rajoidei - Rhinobatoidea - Odontology - Systematics.

Résumé

La morphologie dentaire, et éventuellement celle des épines rostrales, des onze genres que comprennent les pristidés: *Anoxypristis* et *Pristis*, les rhinidés: *Rhina* et *Rhynchobatus* et les rhinobatidés: *Aptychotrema*, *Platyrhina*, *Platyrhinoidis*, *Rhinobatos*, *Trygonorrhina*, *Zanobatus* et *Zapteryx* est décrite et illustrée (clichés MEB et macrophotographiques). Une diagnose différentielle permettant de distinguer ces genres sur base de leur morphologie dentaire est proposée.

Mots-clés: Elasmobranchii - Batomorphii - Pristoidei - Rajoidei - Rhinobatoidea - Odontologie - Systématique.

Kurzfassung

Die Zahnmorphologie und Morphologie der Rostralstacheln von Vertretern der Pristidengattungen Anoxypristis und Pristis, der Rhinidengattungen Rhina und Rhynchobatus und der Rhinobatidengattungen: Aptychotrema, Platyrhina, Platyrhinoidis, Rhinobatos, Trygonorrhina, Zanobatus and Zapteryx wird beschrieben und mit REM-Photos illustriert. Eine Differentialdiagnose erlaubt die Unterscheidung der verschiedenen Gattungen nach ihrer Zahnmorphologie.

Schlüsselwörter: Elasmobranchii - Batomorphii - Pristoidei - Rajoidei - Rhinobatoidea - Odontologie - Systematik.

Part B: Batomorphii No.2 - Order: Rajiformes -Suborder: Pristoidei - Family: Pristidae

Introduction

After the first classification of the Pristidae by LATHAM (1794), several revised concepts followed. FOWLER, (1941) subdivided *Pristis* into the two subgenera *Pristis* and *Pristiopsis* based on presence or absence of a marked lower caudal lobe; BIGELOW & SCHROEDER (1953) likewise subdivided the family into species groups, **a**: with distinct lower caudal lobe and **b**: without marked lower caudal lobe but did not draw nomenclatorial consequences; COMPAGNO (1973) recognized the two genera *Anoxypristis* and *Pristis*, followed by NELSON (1994), with six species in total. We follow the classification of the latter author as the most recent one.

The tooth and rostral spine morphology of both genera is described and illustrated by SEM photographs. Because their morphology is not tooth-like the term rostral spines is used here instead of rostral teeth.

Material

The jaws of the following 7 specimens of the 2 genera and the rostra 26 specimens were examined for this issue:

Pristis pectinata

Coll.HOVESTADT uncatalogued:	Ŷ	780 mm TL
Coll.HERMAN uncatalogued:	Ŷ	3750 mm TL
Coll.HERMAN uncatalogued:	δ	3750 mm TL

Anoxypristis cuspidata

MNHN uncatalogued	♀ 700 mm TL
MNHN uncatalogued	ර් 620 mm TL
IRSNB R489ß	♀ 800 mm TL
IRSNB R489Y	් 670 mm TL

Description of the odontological characters

As sexual heterodonty was never reported for any species of both genera, the best preserved set of teeth was selected for studying irrespective of sex.

The large rostral spines are also studied and will be described and illustrated.

Genus: Anoxypristis WHITE & MOY-THOMAS, 1941

This genus is monotypic with Anoxypristis cuspidata.

Anoxypristis cuspidata (LATHAM, 1794) (Pl: 1, 2, 7 to 9 and 11)

Pristis cuspidatus LATHAM 1794, An essay of the various species of sawfish. Transactions of the Linnean Society London. 2: 279. pl.26 fig.3.

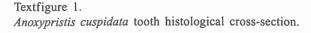
HETERODONTY

The dentition is gradient monognathic heterodont, in that lateral teeth become broader toward the commissure. Sexual or ontogenetic heterodonty is not to be expected on oral teeth, although juveniles were examined only, but males present broader rostral spines than females.

VASCULARIZATION

The teeth have an anaulacorhizid root, characterized by a relatively broad, low pulp cavity. A mesial and distal lateral inner, as well as an outer foramen connect the pulp cavity with the outside. Vascular tubes of the circumpulpar dentine radiate into crown. Osteodentine was not found. (See textfigure 1)





FEMALES AND MALES

The teeth have a flattened crown, which is divided by a weakly arched transverse keel into an inner and outer face. Both, outer and inner faces are strongly convex and have smooth surfaces. The inner face presents a small, prominent uvula.

The weakly arched basal part of the outer face more or less overhangs the crown-root junction.

The low root generally presents two outer foramina, and also a distal and mesial foramen at each side of the uvula. The root base is flat and lacks any trace of a median groove.

ROSTRAL SPINES

The rostral spines of this species consist of a crown, covered with an enameloid layer and a root-like base, in which the enameloid layer of which is extremely thin or even absent in juveniles. The straight, extremely elongated crown is flattening toward the apex and thus forming cutting edges at front and rear where as the base is ovalshaped. Both front and rear cutting edges are smooth in adults, but the rear one has a harpoon - like constriction about half way its length in juveniles.

The basal face shows a V-shaped median groove, which is front- rear directed. A large basal foramen in absent, but numerous minute foramina are present as external openings of parallel vascular canals in the root, and these canals merge at half of their length in a way like osteodentine.

Genus: Pristis LINCK, 1790

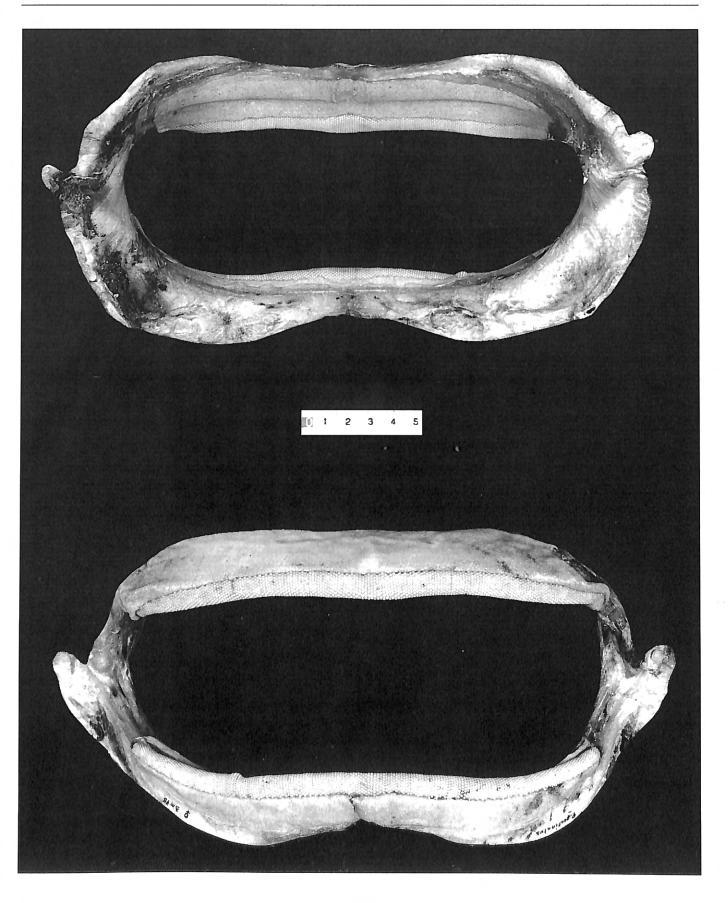
With the exception of *Pristis cuspidata* the genus *Pristis* comprises after BIGELOW & SCHROEDER (1953) the following species: *P. clavata, P. leichhardti, P. pectinata, P. perotteti, P. pristis* (type species) and *P. zijsron.* Teeth of the type species were not available for examination, and therefore teeth of *Pristis pectinata* were used instead.

Pristis pectinata LATHAM, 1794 (Plates: 3 to 8, 10 and 11; Textplates: 1 and 2)

Pristis pectinatus LATHAM 1794. An essay of the various species of sawfish. Transactions of the Linnean Society London. 2: 278. pl.26 fig.2

HETERODONTY

The dentition is gradient monognathic heterodont in that lateral teeth become slightly broader toward the commissure. Sexual heterodonty is not shown in oral teeth, but males possess broader rostral spines than females. Ontogenetic heterodonty is presented by a less developed uvula in juveniles.



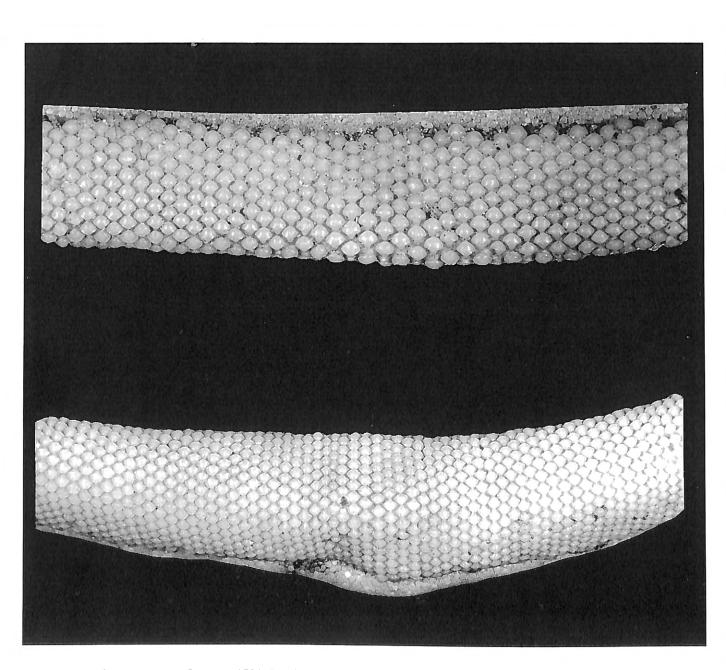
Textplate 1. – Pristis pectinata LATHAM, 1794. Inner and outer views of the jaws of a female 375 cm t.l., Gorea, Senegal. Photos Luc Zwijsen.

VASCULARIZATION

The teeth show a holaulacorhizid root type with a relatively small pulp cavity, from which two or three vascular strings enter the crown. Tubes of the circumpulpar dentine radiate into crown and root. Osteodentine was not found. The vascularization system enters the pulp cavity through a large foramen in the center of the median groove and a distal and mesial foramen at each side of the uvula. (See textfigure 2)



Textfigure 2. Pristis pectinata tooth histological cross-section.



Textplate 2. – Pristis pectinata LATHAM, 1794. Details of upper and lower central parts of the dentition the same female 375 cm t.l., Gorea, Senegal. Photos Luc Zwijsen.

MALES AND FEMALES

The teeth have a flattened crown, which is divided into an inner and an outer face by a strongly arched transverse keel. Both, outer and inner faces are strongly convex and have smooth surfaces. The inner face presents a prominent uvula, which is relatively narrow and strongly protruded inward.

The weakly arched outer crown base more or less overhangs the crown-root junction.

The low root presents a well developed central median groove on the basal face, that includes a large foramen. It divides the root into two root lobes, which are strongly protruded inward. These relatively narrow protrusions support the uvula. Outer foramina are absent. The inner face shows a large foramen at each side of the uvula just above the origin of the protrusions.

ROSTRAL SPINES

The rostral spines are covered with an enameloid layer. The straight, extremely elongated crown is flattening toward the apex and thus forming a smooth cutting front edge but a groove from the base to apex along the rear edge. The rostral spines of juveniles are less flattened and lack the rear groove.

The basal face is flat, more or less quadrangular and lacks a median groove. A large basal foramen in absent, but numerous minute foramina are the openings of parallel vascular canals in the basal part, which canals merge at half of their length in a way like osteodentine.

DIFFERENTIAL DIAGNOSIS

Although *Anoxypristis* and *Pristis* share some general tooth morphological characteristics, like the presence of an uvula and a low crown, they basically have a different tooth morphology. *Pristis* representatives show a prominent and well developed uvula, supported by the inward protruded holaulacorhizid root, and a strongly arched median keel on the crown. *Anoxypristis cuspidata*, in contrast, has a poorly developed uvula, with a mild protrusion of the anaulacorhizid root.

Rostral spines of *Anoxypristis* possess a root-like, poorly enameloid-covered base, with a V-shaped median groove. Rostral spines of *Pristis* are very different, in that they are fully covered with enameloid, lack a basal median groove and the rear edge is a groove instead of a cutting edge.

Conclusions

The significant morphological differences in both oral teeth and rostral spines of *Anoxypristis* and *Pristis* indicate possible separated phylogenetic lineages within Pristoidei.

Acknowledgements

We would like to thank Dr.J.P.Gosse, Institut Royal des Sciences naturelles de Belgique, Brussels and Mr.B.Seret, Musée National d'Histoire Naturelle, Paris for permission to take tooth samples and to examine specimens at their disposal.

Bibliography

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COMPAGNO, L.J.V. - 1973. Interrelationships of living elasmobranchs. In: GREENWOOD, P.H. et al. (Eds). Interrelationships of fishes. *Zoological Journal of the Linnean Society*, 53 (Supplement No.1): pp.15-61.

FOWLER, H.W. - 1941a. The fishes of the groups Elasmobranchii, Holocephali, Isospondyli, and Ostariophysi obtained by United States Bureau of Fisheries Steamer 'Albatross' in 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. *Bulletin United States National Museum* (100) 13: pp.1-879.

LATHAM, J. - 1794. An essay of the various species of sawfish. *Transactions of the Linnean Society of London*, 2 (25): pp. 273-282.

NELSON, J.S. - 1994. Fishes of the World. John Wiley & Sons: XVII + 600. (3rd ed.)

SERET, B. - 1990. Pristidae. In: C. LEVEQUE, D. PAUGY et G.G. TEUGELS (Eds), Faune des poissons d'eaux douces et saumâtres de l'Afrique de l'Ouest - XXVIII(1): 60-72.

Part B: Batomorphii No.3 - Order: Rajiformes -Suborder: Rajoidei - Superfamily: Rhinobatoidea -Families: Rhinidae and Rhinobatidae.

Introduction

In their monographic review of the entire Elasmobranchii, MÜLLER & HENLE (1841) assigned the genera Rhina and Rhynchobatus into the Rhinidae and the genera Rhinobatos, Trygonorrhina and Platyrhina to the Rhinobatidae. The genus Rhinobatos was subdivided by these authors into the subgenera Rhinobatos and Syrrhina. NORMAN (1926) lumped nine genera in one family Rhinobatidae, subdividing the genus Rhinobatos (with its valid original spelling and authorship as by LINCK, 1790) into the subgenera Rhinobatos and Leiobatus, which was followed by FOWLER (1941). BIGELOW & SCHROEDER (1953) included two families into the Rhinobatoidea, namely Rhynchobatidae with the genera Rhina and Rhynchobatus and Rhinobatidae with the genera Aptychotrema, Platyrhina, Platyrhinoidis, Rhinobatos, Trygonorrhina, Zanobatus and Zapteryx. Other authors assigned Platyrhinoidis, Zanobatus and Platyrhina to a separate family Platyrhinidae. COMPAGNO (1973) recognized 4 families within the suborder Rhinobatoidei, namely Rhinidae with the genus Rhina, Rhynchobatidae with the genus Rhynchobatus, Rhinobatidae with the genera Aptychotrema, Rhinobatos, Trygonorrhina and Zapteryx and Platyrhinidae with the genera Platyrhina, Platyrhinoidis and Zanobatus. NELSON (1994) divided the Superfamily Rhinobatoidea into two families, namely Rhinidae with the genera Rhina and Rhynchobatus and Rhinobatidae with the genera Aptychotrema, Platyrhina, Platyrhinoidis, Rhinobatos, Trygonorrhina, Zanobatus and Zapteryx. The classification of the latter author has been adopted here as the most recent one.

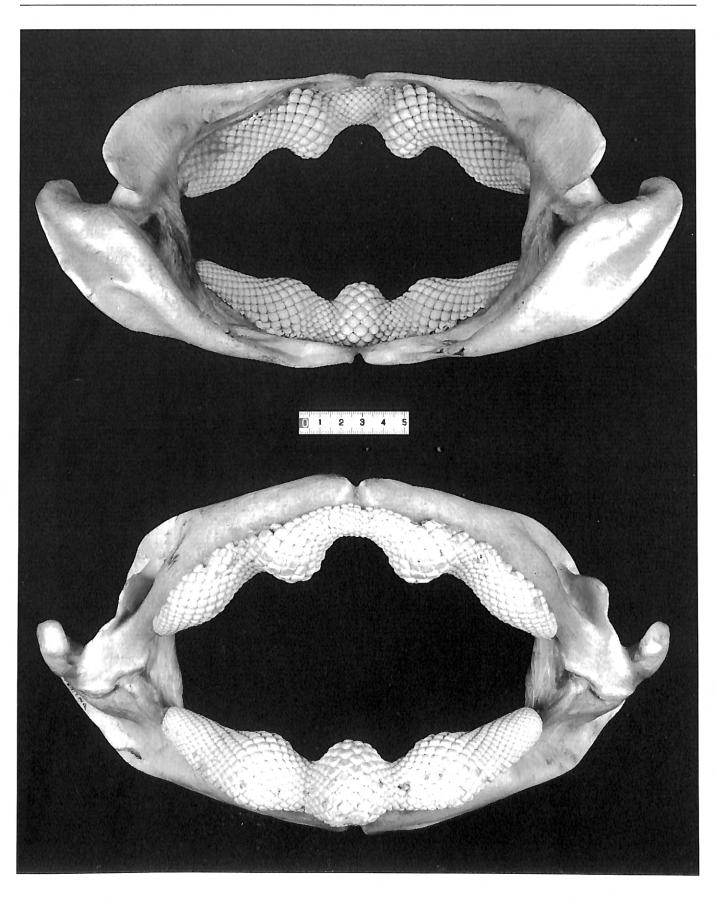
The number of about 15 nominal species mentioned by NELSON (1994) was not accompanied by a listing of the species. The information on nominal species is rather old and needs revision according to modern criteria. Therefore, a listing will not be given of the nominal species comprising the genera described below. Type species have been used for investigations and descriptions as far as specimens were available. Exceptions are mentioned in the text.

Material

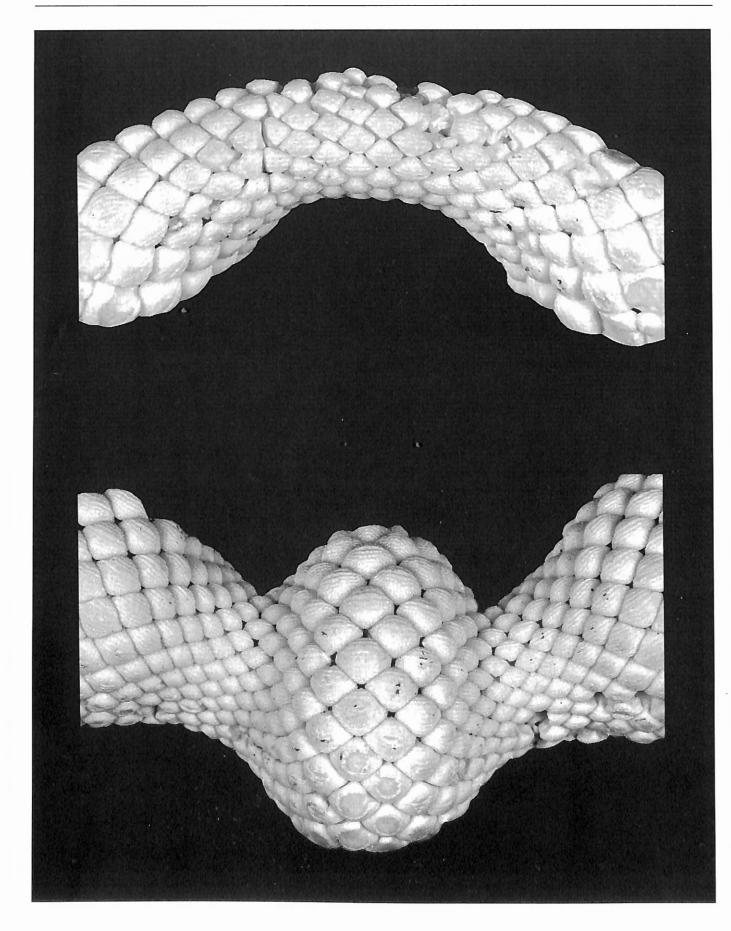
The following 42 specimens of 13 species were examined for this issue:

Aptychotrema bougainvillei Coll.IRSNB 1299:	రే 910 mm TL.
Platyrhina sinensis BMNH uncatalogued: BMNH uncatalogued:	♀ 450 mm TL. ♂ 450 mm TL.

<i>Platyrhinoidis triseriata</i> Coll.IRSNB 6960:	♀ 445 mm TL.
Rhina ancylostoma Coll.HERMAN uncatalogued: Coll.IRSNB (Ex collection COUPATH	ර් 520 mm TL. EZ)
Rhinobatos albomaculatus Coll.HERMAN uncatalogued:	් 520 mm TL.
Rhinobatos cemiculus Coll.Herman uncatalogued: Coll.Herman uncatalogued: Coll.Herman uncatalogued:	ి 2400 mm TL. రి 2920 mm TL. ♀ 1795 mm TL.
Rhinobatos irvinei Coll.HERMAN uncatalogued:	ad.ð ? mm TL
Rhinobatos rhinobatos Coll.HOVESTADT M&D81W0056: Coll.HOVESTADT M&D81W0055: Coll.HERMAN uncatalogued: Coll.HERMAN uncatalo	 ♀ 800 mm TL ♂ 640 mm TL ♀ 730 mm TL ♀ 405 mm TL ♀ 405 mm TL ♀ 405 mm TL ♀ 805 mm TL ♀ 810 mm TL ♀ 848 mm TL ♀ 645 mm TL ♀ 645 mm TL ♀ 848 mm TL ♂ 380 mm TL ♂ 725 mm TL ♂ 595 mm TL ♂ 670 mm TL
Coll.IRSNB 491: <i>Rhynchobatus lübberti</i> Coll.HERMAN uncatalogued:	no data ♀ 1310 mm TL
Coll.HERMAN uncatalogued: Trygonorrhina fasciata Coll.ISRNB 1249	ి 1595 mm TL రి 200 mm TL
Zanobatus schoenleinii Coll.HOVESTADT M&D92Z0528: Coll.HOVESTADT M&D92Z0529: Coll.HERMAN uncatalogued: Coll.HERMAN uncatalogued: Coll.HERMAN uncatalogued: Coll.HERMAN uncatalogued:	 200 mm TL 2 157 mm TL 2 123 mm TL 2 185 mm TL 2 590 mm TL 3 620 mm TL 3 455 mm TL
Zapteryx brevirostris Coll.BMNH:	♀ 420 mm TL



Textplate 3. – *Rhina ancyclostoma* BLOCH & SCHNEIDER, 1801. Inner and outer views of the jaws of an adult specimen circa 250 cm t.l.,Indian Ocean. *Photos Luc Zwijsen.*



Textplate 4. – Rhina ancyclostoma BLOCH & SCHNEIDER, 1801. Details of upper and lower central parts of the dentition of the same specimen, circa 250 cm t.l.,Indian Ocean. Photos Luc Zwijsen.

Description of the odontological characters

Family: Rhinidae

The family comprises the two genera Rhina and Rhynchobatus.

Genus: Rhina BLOCH & SCHEIDER, 1801

Rhina ancylostoma BLOCH & SCHEIDER, 1801 (Plates: 12 to 14; Textplates: 3 and 4)

Rhina ancylostomus BLOCH & SCHEIDER, 1801. Blochii Systema Ichthyologiae iconibus ex illustratum. Post obitum auctoris opus inchoatum absolvit, correxit, interpolavit J.G. Schneider, Saxo. Berolini: p.352, pl.72.

HETERODONTY

The jaws of this species underwent extraordinary development, in that they became undulated. This has resulted in a large lower symphysial protrusion and a less developed lateral one of each lower jaw half. The upper jaw halves have therefore, an indentation at the corresponding positions allowing exact interlocking of both jaws. Heterodonty is distinctive, in that lower jaw teeth are broad on top of the symphysial and lateral protrusions but narrower down their sides and in the intermediate depressions, as well as toward the commissure. The opposite phenomenon is presented in the upper jaw, which shows narrow teeth at the symphysial and both lateral depressions but wider teeth in the intermediate protrusions and toward the commissure. Sexual heterodonty is absent (information supplied by Dr. H. Cappetta), but ontogenetic heterodonty is given by a lower transverse keel, the absence of an ornamentation of the outer part of the crown and secondary hemiaulacorhizy of the tooth roots in juveniles.

VASCULARIZATION

The tooth roots show holaulacorhizy in adults and secondary hemiaulacorhizy in juveniles. In both cases the teeth have a large pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. A large foramen is present in the median groove in adults, whereas juveniles show one large central and one or two scattered smaller outer foramina, as well as a central and a smaller mesial and distal inner foramen, that all connect the pulp cavity with the outside. Osteodentine was not found.

(See textfigure 3)

FEMALES AND MALES

The crown has a high, strongly arched transverse keel, which is slightly arched inward in occlusal view this keel



Textfigure 3. Rhina ancyclostoma tooth histological cross-section.

divides the crown into a convex outer part, the outer edge of which is bluntly angled in the center, and an inner part with likewise angled inner edge. The latter part has a smooth surface and shows traces of trilobation by slight undulation of the edges. The outer part is smooth in teeth of juveniles, but exhibits a fine, well developed reticulated ornamentation in adults.

The root is relatively high, most of it situated on the inner half of the crown base in basal view. Its outer part is angled in basal view, whereas the inner part shows well developed trilobation. A large foramen is present more or less in the center of a deep median groove. A mesial and distal foramen are present at each side of the protuberation of the central lobe, along the crownroot junction. Root coating is absent.

Genus: Rhynchobatus MÜLLER & HENLE, 1837

The type species is *Rhynchobatus djiddensis*. To illustrate the interspecifically different kind of ornamentation, teeth of Rhynchobatus lübberti are illustrated additionally (Plates: 17 and 18).

> Rhynchobatus djiddensis FORSKAL, 1775 (Plates: 15 and 16; Textplates: 5 and 6)

Rhynchobatus djiddensis FORSKAL, 1775. Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium, quae in itirene orientali observavit: pp.164.

HETERODONTY

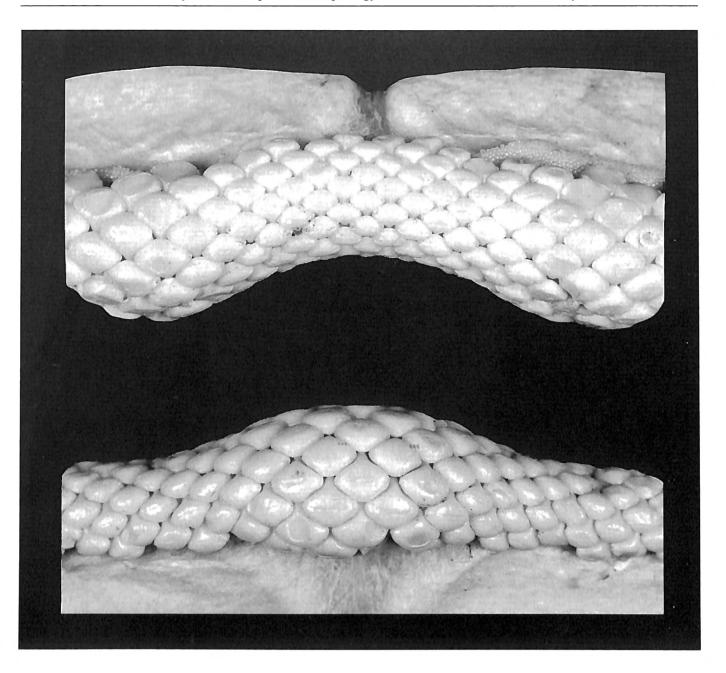
The jaws are undulation similar to Rhina ancylostoma described above, with a corresponding, but less distinctive kind of heterodonty. Sexual and ontogenetic heterodonty are absent.

VASCULARIZATION

The teeth show holaulacorhizy with a large pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. A large foramen is present in the median groove, as well as a smaller mesial and



Textplate 5. – Rhynchobatus djiddensis (FORSSKAL, 1775). Inner and outer views of the jaws of an adult specimen, Indian Ocean. Photos Luc Zwijsen.



Textplate 6. – Rhynchobatus djiddensis (FORSSKAL, 1775). Details of upper and lower central parts of the dentition of the same specimen Photos Luc Zwijsen.

distal foramen, which all connect the pulp cavity with the outside. Some osteodentine was found below the pulp cavity, in the root area. (See textfigure 4)



Textfigure 4. *Rhynchobatus djiddensis* tooth histological cross-section.

FEMALES AND MALES

The crown has a weakly arched transverse keel dividing the crown into a convex outer part, of which the outer edge is arched, and an inner part with an irregularly shaped, well developed uvula. The outer part exhibits a shallow, coarse reticulated ornamentation. The inner part has a smooth surface and shows shallow mesial and distal depressions.

The root is relatively high and largely situated on the inner half of the crown base in basal view. Its outer part is angled in basal view, whereas the inner part shows well developed trilobation. A large foramen is present more or less in the center of a deep median groove. A mesial and distal foramen are present at each side of the protuberated central lobe, along the crown-root junction. Root coating is absent.

Family: Rhinobatidae

This family comprises the genera *Aptychotrema*, *Platyrhina*, *Platyrhinoidis*, *Rhinobatos*, *Trygonorrhina*, *Zanobatus* and *Zapteryx*. To illustrate the interspecifically different tooth morphology for the genus *Rhinobatos*, *R.cemiculus* is illustrated additionally.

Genus: Aptychotrema NORMAN, 1926

Aptychotrema bougainvillei (VALENCIENNES, 1841) (Plates: 19 and 20)

Rhinobatus (Syrrhina) bougainvillei VALENCIENNES, 1841. in: MÜLLER & HENLE 1841. Systematische Beschreibung der Plagiostomen: 117.

Note: LAST & STEVENS (1994:285-288) recognize three species of *Aptychotrema* in Australian waters, namely an undescribed *A.* sp.A, *A. rostrata* (SHAW & NODDER, 1794) and *A. vincentiana* (HAAKE, 1885). They noted under *A. rostrata* as synonyms *A. banksii* and *A. turberculatus* and said *A. bougainvillei* was 'doubtfully distinct' from *A. rostrata*.

HETERODONTY

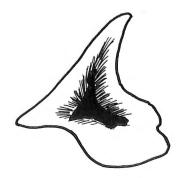
The dentition is gradient monognathic heterodont. Sexual or ontogenetic heterodonty could not be clarified because of lacking female and juvenile specimens.

VASCULARIZATION

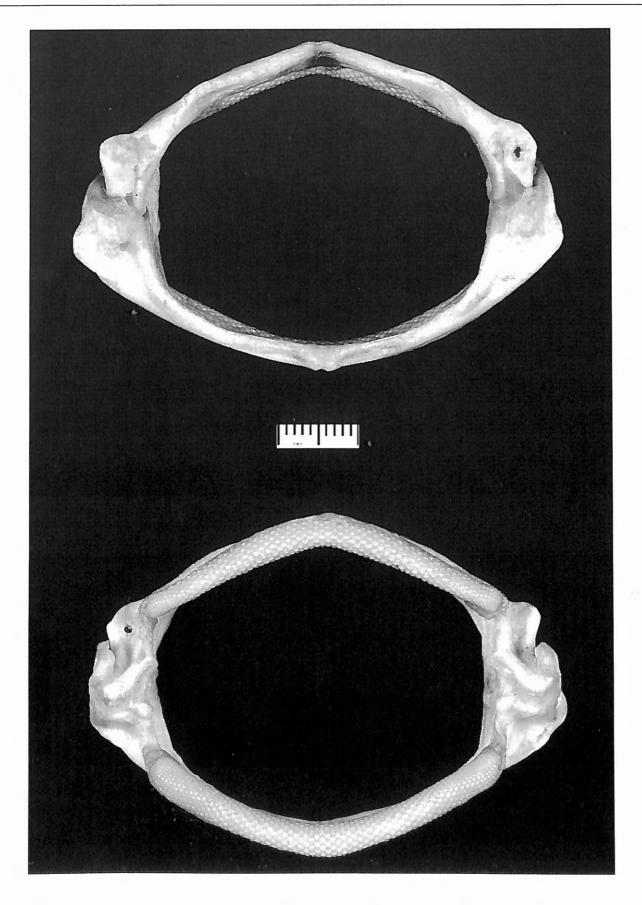
The teeth show holaulacorhizy, with an extremely large pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. One large central foramen in the median groove and a smaller mesial and distal one connect the pulp cavity with the outside. Osteodentine was not found. (See textfigure 5)

MALES

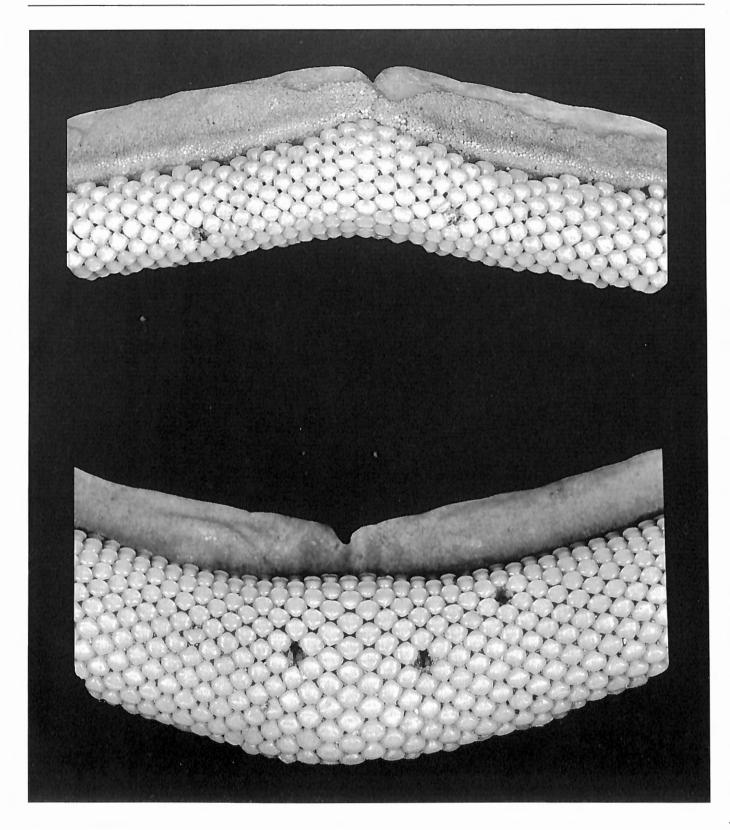
The crown exhibits a relatively elongated, inward directed principal cusp. It has concavely arched cutting edges in anterior teeth but diminishes in height rapidly on lateral teeth to become finally a transverse keel on posterior teeth. In occlusal view the convex outer part exhibits a strongly arched outer edge and a trilobed inner part, with irregularly shaped, well developed mesial, distal and central uvulas. An outer ornamentation is absent. The inner part



Textfigure 5. Aptychotrema bougainvillei tooth histological cross-section.



Textplate 7. – Rhinobatos rhinobatos (LINNAEUS, 1758). Inner and outer views of the jaws of a female 81 cm t.l., Djounia, Lebanon. Photos Luc Zwijsen.



Textplate 8. – Rhinobatos cemiculus E. GEOFFROY DE SAINT HILAIRE, 1817. Details of upper and lower central parts of the dentition of a male 292 cm t.l., Abidjan, Ivory Coast. Photos Luc Zwijsen.

shows coarse basal costules, which more distinct in anterior teeth, on all three lobes.

The root is relatively low and largely situated on the inner half of the crown base in basal view. Its outer part is bluntly angled in basal view, whereas the inner part shows well developed trilobation. A pair of large foramen is present more or less in the center of a deep median groove. Mesial and distal foramina, as well as root coating are absent.

Genus: Platyrhina MÜLLER & HENLE, 1838

Platyrhina sinensis (BLOCH & SCHNEIDER, 1801) (Plates: 23 to 25)

Raja sinensis BLOCH & SCHNEIDER,1801. Blochii systema Ichthyologiciae iconibus ex illustratum. Post obitum auctoris opus inchoatum absolvit, correxit, interpolavit J.G. SCHNEIDER: Saxo Beroffini: 34, 157

HETERODONTY

The dentition is gradient monognathic heterodont. Sexual heterodonty is given by a relatively high, elongated principal cusp on teeth of males, versus lower cusps in females. Although a juvenile individual was not available for examination, ontogenetic heterodonty is to be expected because of usually female-like characters of teeth of juveniles.

VASCULARIZATION

The teeth show holaulacorhizy, with a small pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. One large central foramen in the median groove and a smaller mesial and distal foramen connect the pulp cavity with the outside. Osteodentine was not found. (See textfigure 6)

FEMALES

The crown has a low, weakly arched transverse keel, which is straight in occlusal view It divides the crown into a slightly convex outer part, of which the outer edge of which is weakly arched outward, and a trilobed inner



Textfigure 6. *Platyrhina sinensis* tooth histological cross-section.

part, with well developed mesial, distal and central uvulas. Inner and outer faces are a smooth.

The root is relatively low and largely situated on the inner half of the crown base in basal view. Its outer part is weakly arched in basal view, whereas the inner part shows well developed trilobation, with the central lobe extremely protruding inward. A large foramen is present more or less in the center of a deep median groove. A small mesial and distal foramen is present at each side of the protuberation of the central lobe, along the crownroot junction. Root coating is absent.

MALES

The crown exhibits a relatively elongated, inward directed principal cusp with concavely arched cutting edges. In occlusal view the slightly convex outer part exhibits a weakly arched outer edge and a trilobed inner part, with well developed mesial, distal and central uvulas. The central uvula is longer than the mesial and distal ones. Inner and outer ornamentation is absent.

The root is relatively high and largely situated on the inner half of the crown base in basal view. Its outer part is bluntly angled in basal view, whereas the inner part shows well developed trilobation. A large foramen is present more or less in the center of a deep median groove. The edges of the median groove tend to merge, giving the median groove a tube-like appearance. A large mesial and distal foramen is present at each side of the protuberated central root lobe. Root coating is absent.

Genus: Platyrhinoidis GARMAN, 1881

This genus is monotypic with only P. triseriata.

Platyrhinoidis triseriata (JORDAN & GILBERT, 1880) (Plates: 21 and 22)

Platyrhina triseriata JORDAN & GILBERT, 1880. Description of a new ray (Platyrhina triseriata) from the coast of California. Proceedings of the United States National Museum, 3: 36.

HETERODONTY

The dentition is gradient monognathic heterodont. Neither sexual nor ontogenetic heterodonty could be clarified because of lacking male and juvenile specimens.

VASCULARIZATION

The teeth show holaulacorhizy, with a small pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. One large central foramen in the median groove and a smaller mesial and distal foramen connect the pulp cavity with the outside. Osteodentine was not found. (See textfigure 7)



Textfigure 7. *Platyrhinoïdis triseriata* tooth histological cross-section.

Textfigure 8. *Rhinobatos rhinobatos* tooth histological cross-section.

FEMALES

The crown bears a strongly arched transverse keel, which divides the crown into a convex outer part, the outer edge of which is arched, and an inner part with a well developed central and less developed mesial and distal uvulas. Inner and outer ornamentation are absent.

The root is relatively high and largely situated on the inner half of the crown base in basal view. Its outer part is angled in basal view, whereas the inner part shows trilobation. A large foramen is present more or less in the center of a deep, but relatively narrow median groove. A small mesial and distal foramen is present at each side of the protuberated central lobe, along the crown-root junction. Root coating is absent.

Genus: Rhinobatos LINCK, 1790

Rhinobatos rhinobatos (LINNAEUS, 1758) (Plates 27 and 28)

Raja rhinobatos LINNAEUS, 1758. Systema naturae, ed. X: 232.

To offer an indication of interspecific variation of the tooth morphology with this genus *R. cemiculus* is illustrated additionally (Plate 26).

HETERODONTY

FEMALES

The dentition is gradient monognathic heterodont. Sexual heterodonty is shown by a low cusp on anterior and lateral teeth of males, versus a slightly arched transverse keel in females. Male juveniles show ontogenetic heterodonty by having a transverse keel instead of the low cusp of adult males.

VASCULARIZATION

The teeth show holaulacorhizy, with a small pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. One large central foramen in the median groove and a smaller mesial and distal foramen connect the pulp cavity with the outside. Osteodentine was not found. (See textfigure 8) The crown has a low, weakly arched transverse keel, which is straight in occlusal view. It divides the crown into a slightly convex outer part, the outer edge of which is weakly arched outward, and a trilobed inner part with a poorly developed mesial and distal, but a well developed central uvula. Inner and outer ornamentation is absent. The root is relatively low and largely situated on the inner half of the crown base in basal view. Its outer part is weakly arched in basal view, whereas the inner part shows well developed trilobation with the central lobe stronger protruding inward. A large foramen is located more or less in the center of a deep median groove. A small mesial and distal foramen is present at each side of the protuberated central lobe, along the crown-root junction. Root coating is absent.

MALES

The crown bears a low cusp with concavely arched cutting edges on anterior and lateral teeth. In occlusal view, the slightly convex outer part exhibits a strongly arched outer edge and a trilobed inner part, with a poorly developed mesial and distal but a well developed central uvula. Inner and outer ornamentation is absent.

The root is relatively high and largely situated on the inner half of the crown base in basal view. Its outer part is bluntly angled in basal view, whereas the inner part shows well developed trilobation. A large foramen is present more or less in the center of a deep median groove. A small mesial and distal foramen is present at each side of the protuberated central root lobe. Root coating is absent.

Genus: Trygonorrhina Müller & Henle, 1838

Trygonorrhina fasciata Müller & Henle, 1841 (Plates: 29 and 30)

Trygonorrhina fasciata MÜLLER & HENLE, 1841 Systematische Beschreibungen der Plagiostomen: 124.

HETERODONTY

The dentition is gradient monognathic heterodont. Neither sexual nor ontogenetic heterodonty could be determined clarifies because of lacking male and juvenile specimens.

VASCULARIZATION

The teeth show holaulacorhizy, with an extremely large pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. One large central foramen in the median groove and a smaller mesial and distal foramen connect the pulp cavity with the outside. Osteodentine was not found. (See textfigure 9)



Textfigure 9.

Trygonorrhina fasciata tooth histological cross-section.

FEMALES

The crown bears a rounded, hardly perceptible, weakly arched transverse keel. It divides the crown into a convex outer part, the outer edge of which is weakly arched outward, and a trilobed inner part with a poorly developed mesial and distal, but a well developed, more or less triangularly shaped central uvulas. The outer face is smooth. Coarse costulation is present at the edges of the central uvula, slightly affecting also the mesial and distal uvulas. The root is relatively low and largely situated on the inner half of the crown base in basal view. Its outer part is weakly arched in basal view, whereas the inner part hardly shows trilobation. A large foramen is present more or less in the center of a deep median groove. Mesial and distal foramina are absent. Traces of root coating are perceptible near the crown-root junction.

Genus: Zanobatus GARMAN, 1913

Zanobatus schoenleinii (MÜLLER & HENLE, 1841) (Plates: 33 to 35)

Platyrhina schoenleinii MÜLLER & HENLE, 1841 Systematische Beschreibung der Plagiostomen: 125

HETERODONTY

The dentition is gradient monognathic heterodont. Sexual heterodonty is poorly developed with a small central cusp, sometimes flanked by two poorly developed cusplets on the crown in adult males, instead of a transverse keel in females. Ontogenetic heterodonty is documented by the absence of this particular cusp on teeth of male juveniles.

VASCULARIZATION

The teeth show holaulacorhizy, with a small pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. One large central foramen in the median groove connects the pulp cavity with the outside.



Textfigure 10. Zanobatus schoenleinii tooth histological cross-section.

FEMALES

The crown has a low, weakly arched transverse keel, which is straight in occlusal view, dividing the crown into a slightly convex outer and an inner part, the edges of which are weakly arched but not trilobated. Inner and outer ornamentation is absent. The root is relatively low. A foramen is present more or less in the center of a deep, short median groove. Mesial and distal foramina are absent. Root coating is absent.

MALES

The crown has a well developed cusp, with concavely arched cutting edges, sometimes flanked by two cusplets. The crown exhibits a slightly convex outer and an inner part, the latter with more or less triangular but not trilobated edge. Inner and outer ornamentation is absent. The root is relatively low. A foramen is present more or less in the center of a deep, short median groove. Mesial and distal foramina are absent. Root coating is absent.

Genus: Zapteryx JORDAN & GILBERT, 1880

Teeth of the type species *Zapteryx exasperata* were not available for examination. For the description and illustration were teeth of the only other species *Zapteryx brevirostris* used instead.

Zapteryx brevirostris (MÜLLER & HENLE, 1841) (Plates: 31 and 32)

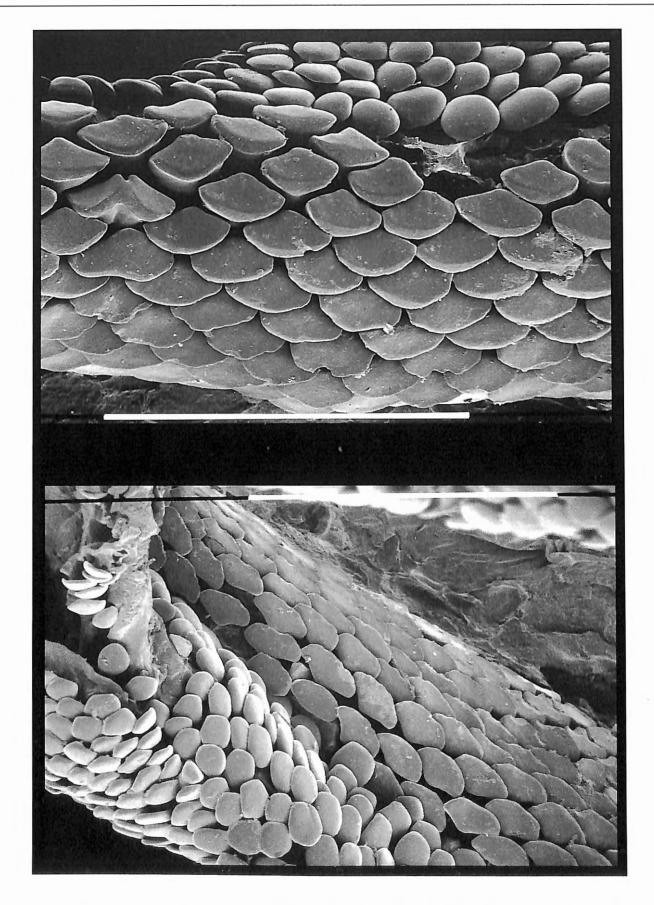
Rhinobatus (Syrrhina) brevirostris MÜLLER & HENLE, 1841 Systematische Beschreibung der Plagiostomen: 114.

HETERODONTY

The dentition is gradient monognathic heterodont. Neither sexual nor ontogenetic heterodonty could be clarified because of lacking male and juvenile specimens.

VASCULARIZATION

The teeth show holaulacorhizy, with a small pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. One large central foramen in the median groove and a smaller mesial and distal



Textplate 9. – Zanobatus schoenleinii SEM photos of the upper central and of the lower right commissural parts of the jaws of a female 18.5 cm t.l., Saly, Senegal. Scale bar represents 1 mm.

foramen connect the pulp cavity with the outside. Osteodentine was not found. (See textfigure 11)



Textfigure 11.

Zapteryx brevirostris tooth histological cross-section.

FEMALES

The crown bears a low, weakly arched transverse keel, which is straight in occlusal view and divides the crown into a slightly convex outer part, of which the outer edge is weakly arched, and a trilobed inner part. The mesial and distal uvulas are poorly developed. The irregularly shaped central one is better developed. Inner and outer faces are smooth. The root is relatively low, not particularly protuberated inward. A foramen is present more or less in the center of a deep, short median groove. Mesial and distal foramina are absent. Root coating is presented along the crown-root junction.

DIFFERENTIAL DIAGNOSIS

Except for Zanobatus and Zapteryx all rhinobatid species have a trilobed root. Teeth of Zanobatus, however, lack a true uvula, which character distinguishes this genus from Zapteryx.

Rhina and *Rhynchobatus* only possess a true reticulated ornamentation, which on teeth of the latter is less developed. The tooth crown of *Rhina* is generally more irregularly shaped than of *Rhynchobatus*.

Both mesial and distal uvulas of *Rhinobatos, Trygonorrhina* and *Platyrhinoidis* are poorly developed in contrast to those of *Aptychotrema* and *Platyrhina*, in which they are well developed and separated by a notch from the central one. The central uvula of *Trygonorrhina* is triangularly shaped and bears coarse costules, whereas those of *Rhinobatos* and *Platyrhinoidis* are smooth, with a more or less rounded edge. The central uvula of *Rhinobatos* is relatively narrower and longer than that of *Platyrhinoidis*.

The teeth of *Aptychotrema* and *Platyrhina* can be distinguished by the much higher root and a much more protuberated central root lobe in species of the latter genus. The teeth of *Pristis* are compared here, because of their generally similar morphology. *Pristis* teeth, however, are distinguishable by their extremely long, well developed central uvula and the absence of true distal and mesial uvulas from those of the rhinobatid and rhinid species.

CONCLUSIONS

Rhinobatoidean tooth morphology is known from fossilized teeth of the Lower Jurassic, but the specific tooth characteristics of rhinobatid species are recognized in the Lower Cretaceous by teeth of the genus *Rhinobatos*. Teeth of *Platyrhina* and *Zapteryx* appear first in the Palaeocene, and an almost complete articulated skeleton of *Platyrhina* is known from the Eocene.

Although in general the tooth morphology of the different taxa appears similar, particular differences offer an important tool for distinguishing between the taxa of Rhinobatoidea.

Tooth morphology supports dividing the Rhinobatoidea into three suprageneric groups:

1 Rhina and Rhynchobatus

- 2 Aptychotrema, Platyrhina, Platyrhinoidis, Rhinobatos and Trygonorrhina.
- 3 Zanobatus and Zapteryx

Due to the stable tooth morphology, there is no evidence for a possible ongoing explosive development, as it was observed in Rajidae (HERMAN, HOVESTADT-EULER, HOVESTADT & STEHMANN, 1996). The large number of living nominal species of the genus *Rhinobatos* (ca.40), with very minor differences in their tooth morphology and the extremely low number of fossil records during the whole tertiary period (2 species) gives reason to doubt the validity of all these nominal species.

TYPE OF WASCULARIZATION

The tooth vascularization system of all taxa concerned was also examined, described and illustrated. All vascularization types showed more or less the same principle: a small pulp cavity situated in the root center, which is connected to apertures that are mostly found in the center of a median groove in case of a holaulacorhizid types of root, or on the inner and/or outer faces of the root in case of secondary hemiaulacorhizy (HOVESTADT & HOVESTADT, 1993) and a mesial and distal one flanking the central uvula. One or two additional inner and/or outer foramina may be present at irregular positions but sometimes just above the median groove, which are connected to the pulp cavity too. The pulp cavity is, even in the root area, always surrounded by orthodentine, and the vascular capillary tubes of the orthodentine radiate from the pulp cavity into root and crown.

Previous issues of this series have provided odontological keys for identification of the different genera and subgenera of an order or family. Such a key cannot be given for the Rhinobatoidea because both sexes were not equally available for examination.

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

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.

Transversal Outer/inner direction of a row.

CONCERNING THE TOOTH

An-,Hemi-,Hol- and Polyaulacorhizid

Concerning their vascularization, E.Casier(1947) recognized and described 4 phylogetically 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.

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-holaulacorhizy

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 orthodentine layer.

Osteodont

Histotype of vascularization, by which a tooth is supplied without any pulp cavity by scattered tiny cavities and canals penetrating the osteodentine 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 osteo-dentine.

Pulp cavity

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

Root

Non-enamelated 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 enameloid).

Root stem

Root part between the crown base and root lobe section. Secondary anaulacorhizy

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

Secondary hemiaulacorhizy

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 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.

Transversal

Mesio-distally directed.

Transverse keel

Transverse ridge dividing the crown into inner and outer face.

Uvula

Lobate extension of the inner crown base.

Composition of the plates

As far as possible plates of isolated teeth of one juvenile (male or female) and of adult males and females 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

- \mathbf{a} = anterior position
- $\mathbf{l} =$ lateral position
- \mathbf{p} = posterior position
- $\mathbf{c} = \text{commissural position}$

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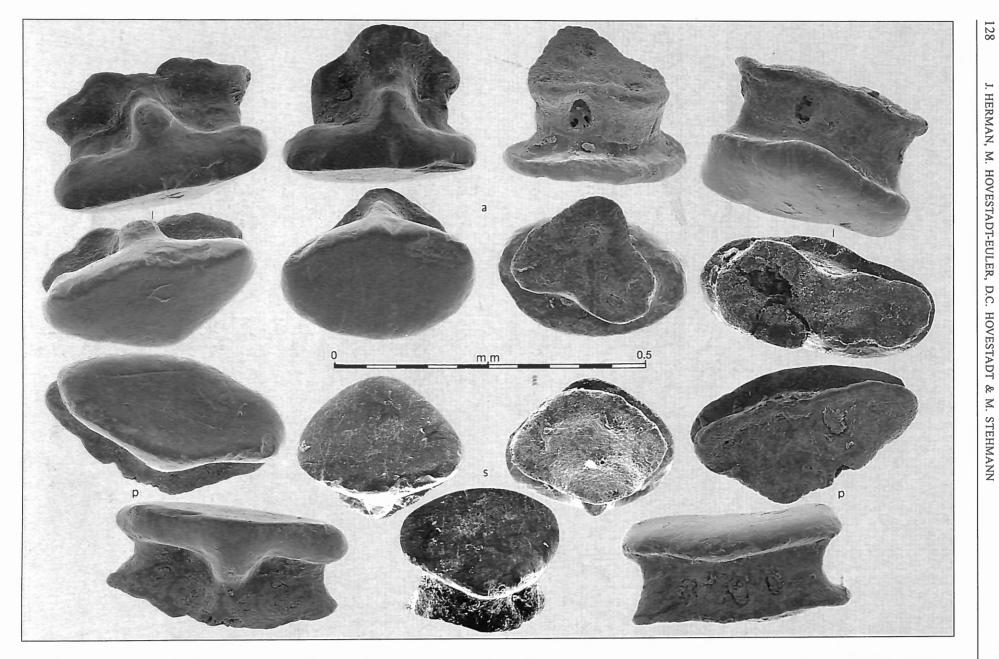
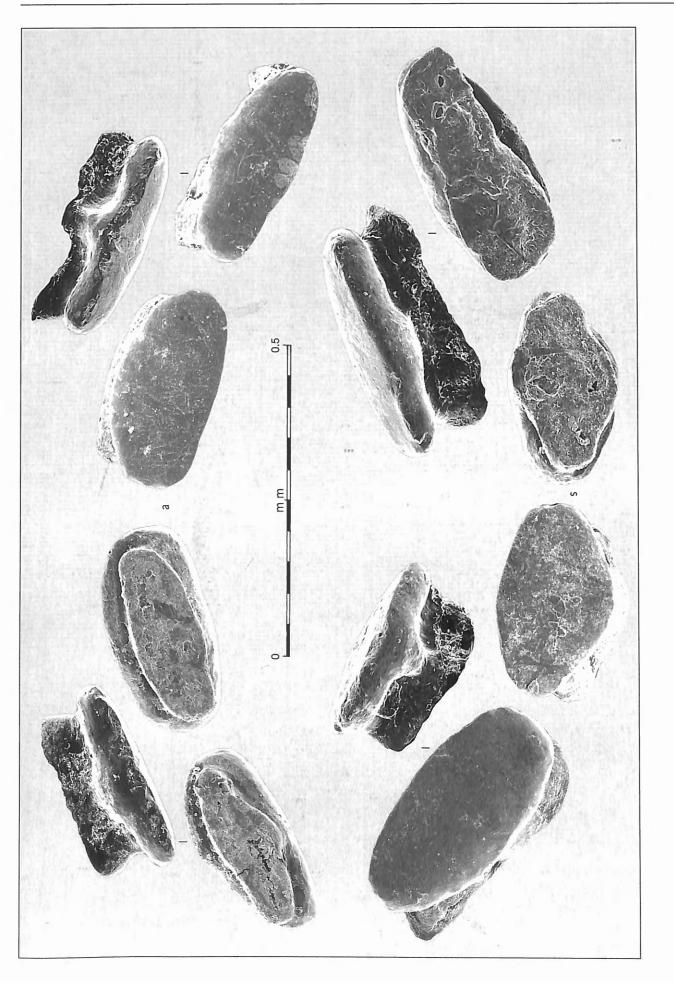
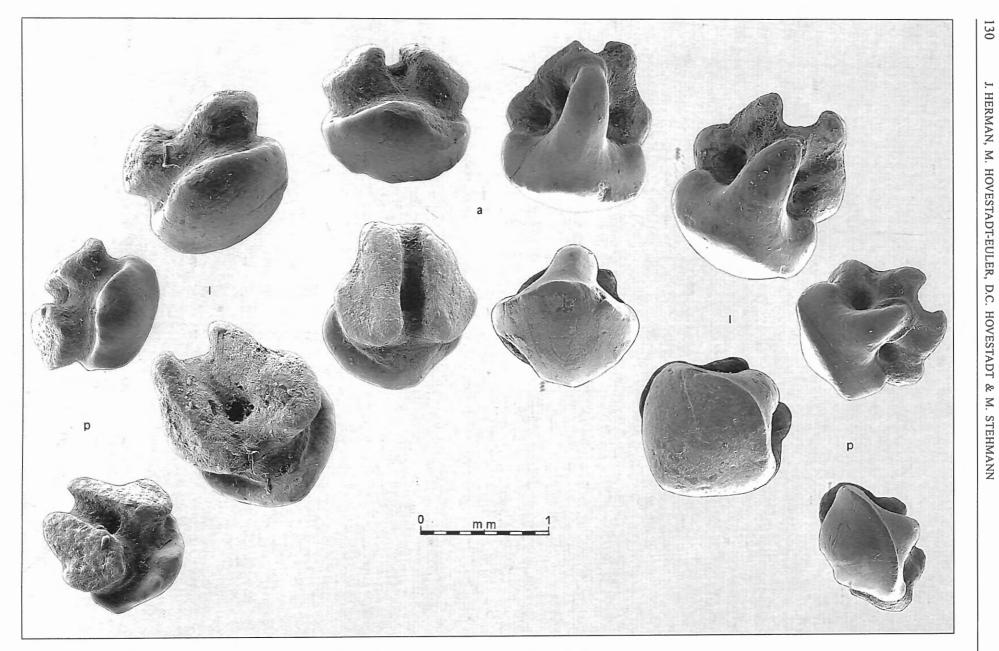
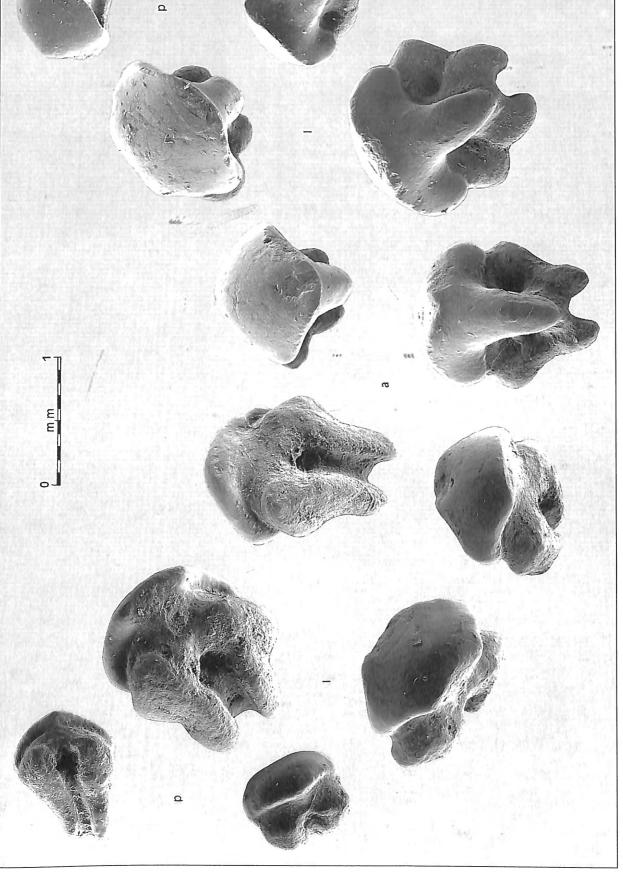


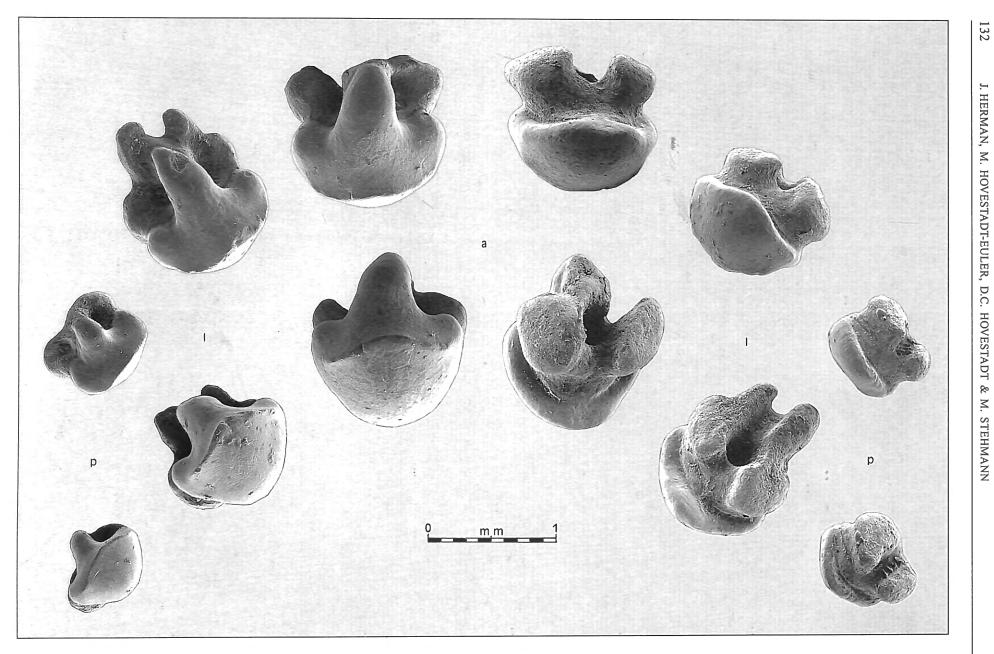
Plate 1. - Anoxypristis cuspidata (LATHAM, 1794). Female 70 cm t.l., Indian Ocean (MNHN). Upper and lower teeth.

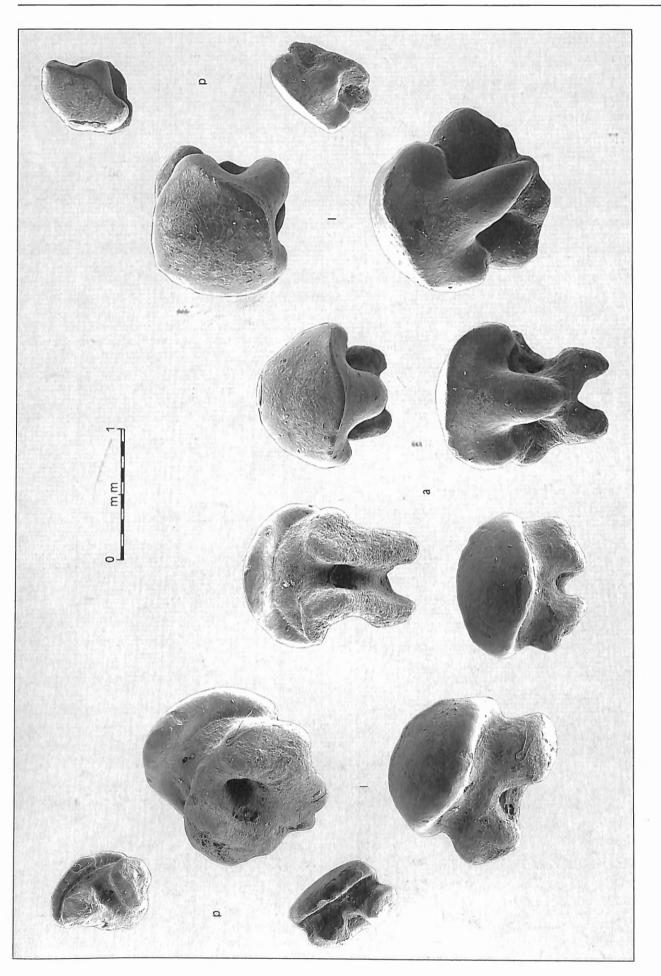












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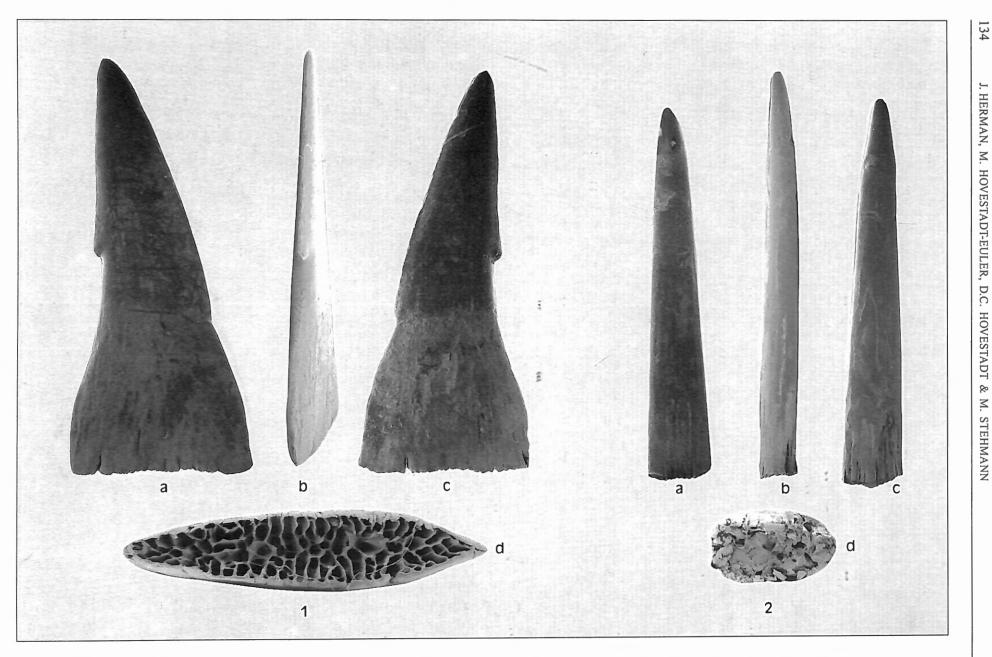


Plate 7. – 1. Anoxypristis cuspidata (LATHAM, 1794). Dorsal (a), posterior (b), ventral (c) and basilar (d) views of a rostral spine of a female 79 cm t.l.; b. Pristis pectinata LATHAM, 1794. Same views of a rostral spines of a female 80 cm t.l. The dorsal and ventral views are ten times enlarged.

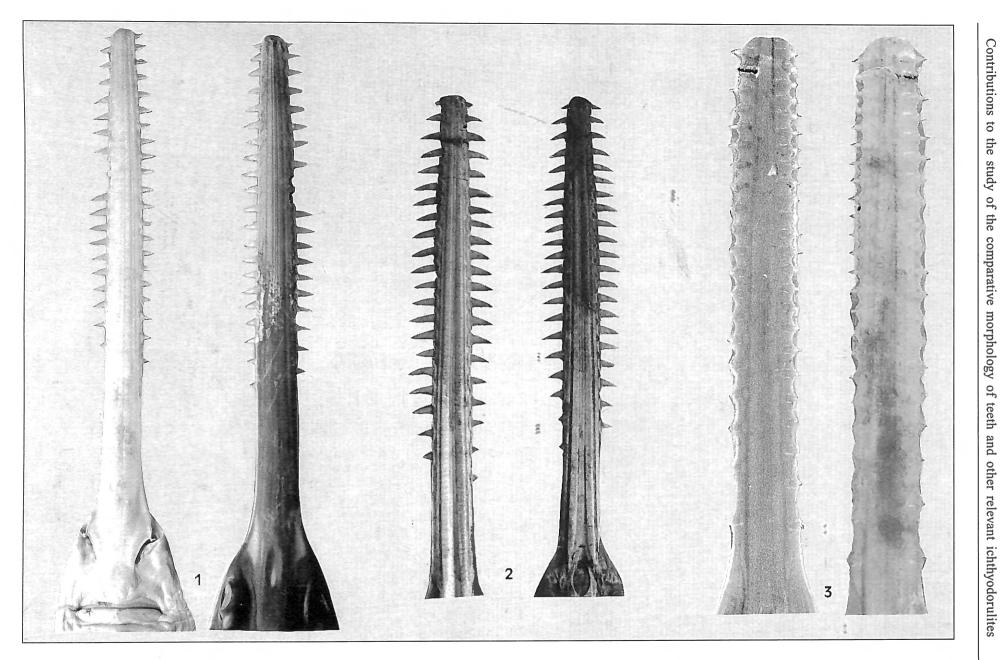


Plate 8. – 1. Anoxypristis cuspidata (LATHAM, 1794), ventral and dorsal views of the rostrum of a female 80 cm t.l.; 2. same views of the rostrum of a male of the same species 67 cm t.l.; 3. Pristis pectinata, same views of the rostrum of a female 79 cm t.l. The lenght of all the rostra is circa fifty procent reduced. Photos 1 & 2: Eric Vanderhoeft, 3: Inga Goethals.

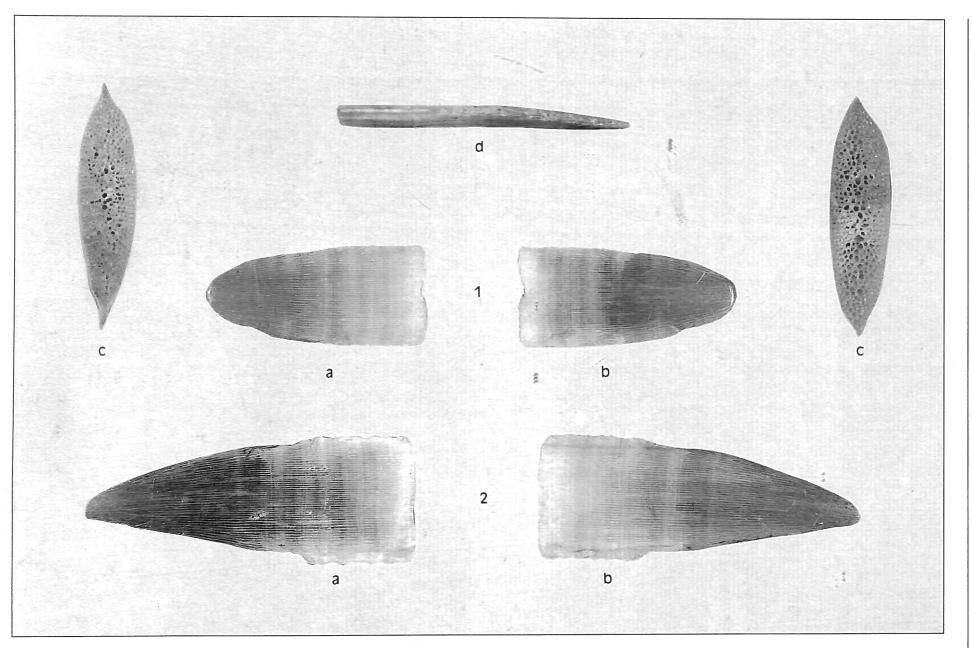


Plate 9. - Anoxypristis cuspidata (LATHAM, 1794): dorsal (a), ventral (b), basilar (c) and one back profile (d) views of the third (1) and eleventh (2) left rostral spines of an adult female, Indian Ocean. The dorsal and ventral views are twice enlarged. Photos Inga Goethals.

J. HERMAN, M. HOVESTADT-EULER, D.C. HOVESTADT & M. STEHMANN

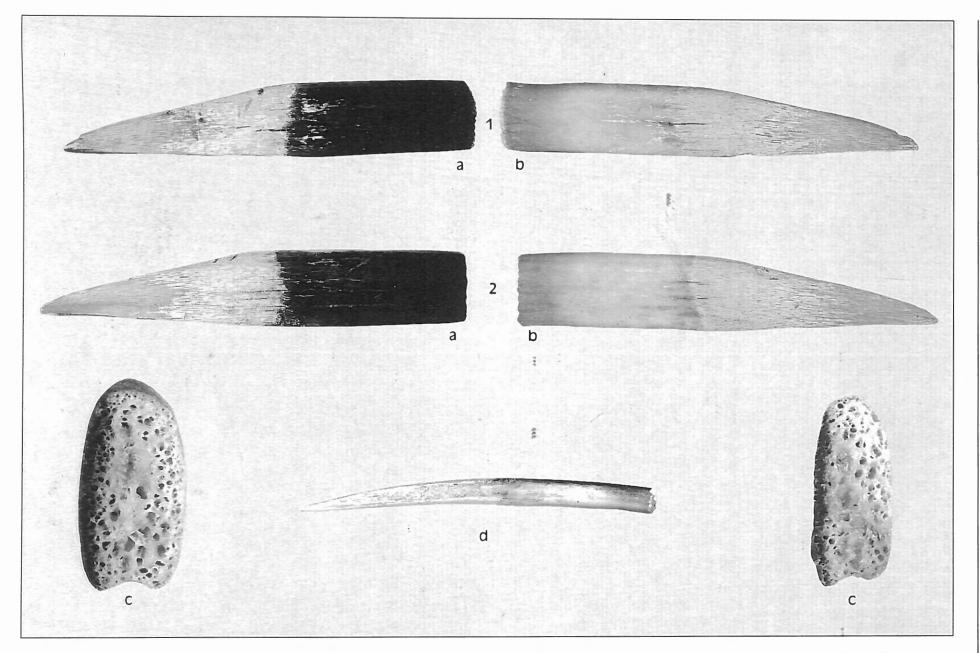


Plate 10. – Pristis pectinata LATHAM, 1794: dorsal (a), ventral (b), basilar (c) and one back profile (d) views of the third and twelft left rostral spines of an adult female, Indian Ocean. The dorsal and ventral views are twice enlarged. Photos Inga Goethals.

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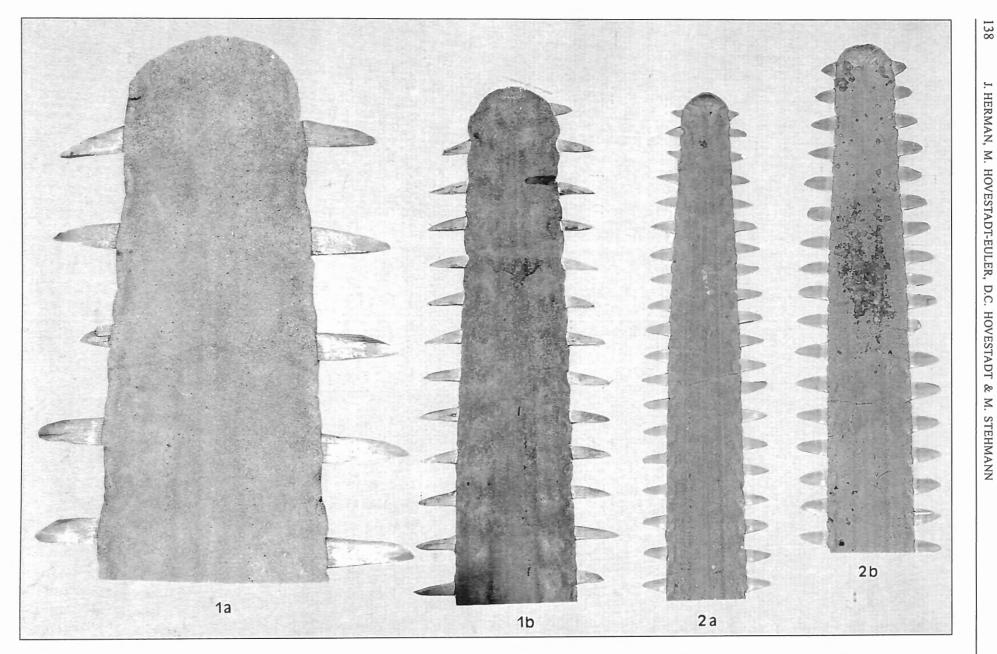
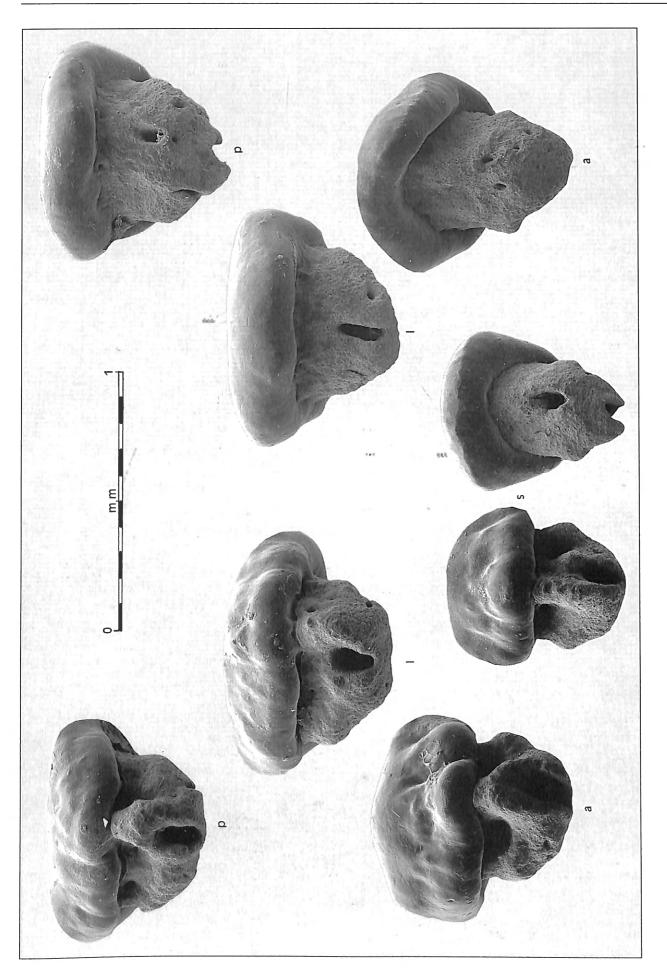
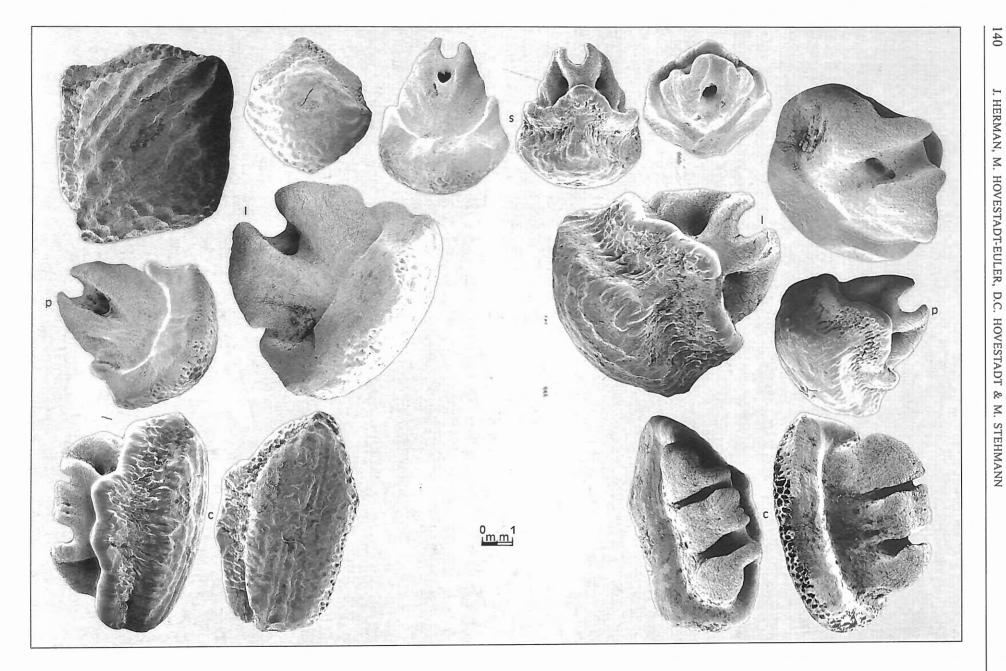


Plate 11. - 1. Pristis pectinata LATHAM, 1794 and 2. Anoxypristis cuspidata (LATHAM, 1794): dorsal views of both male and female adult rostra; largest are those of the males. Indian Ocean, no data. The lenght of the rostra is circa fifty procent reduced. Photos Inga Goethals.





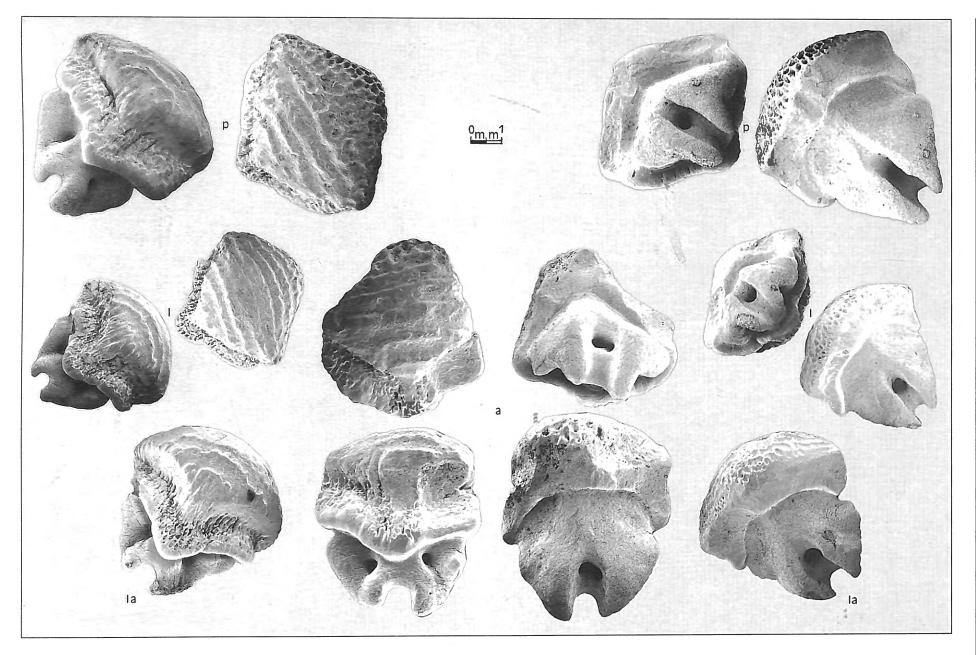
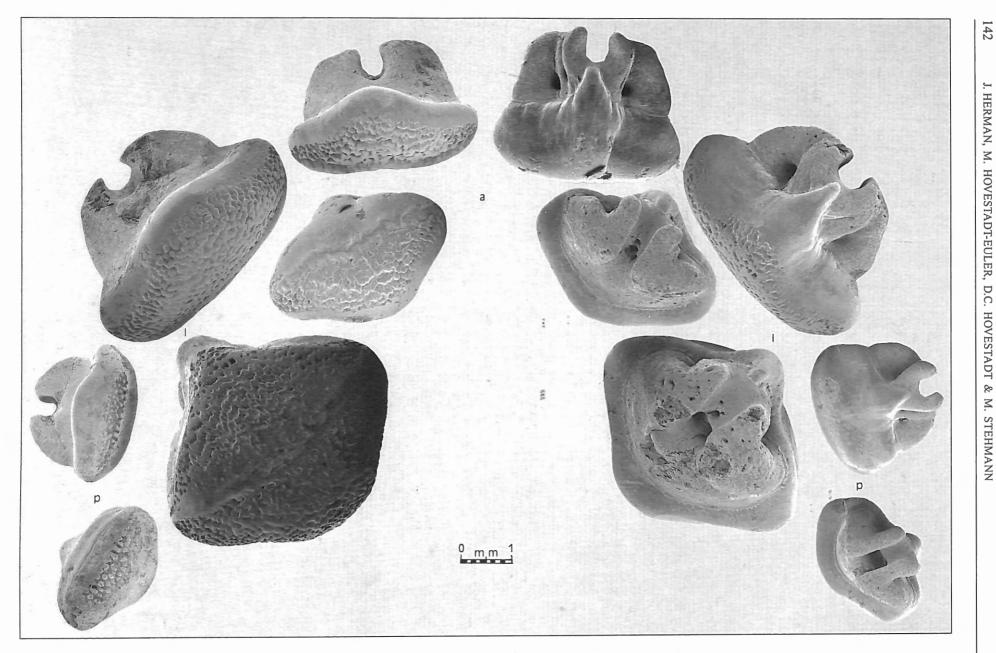
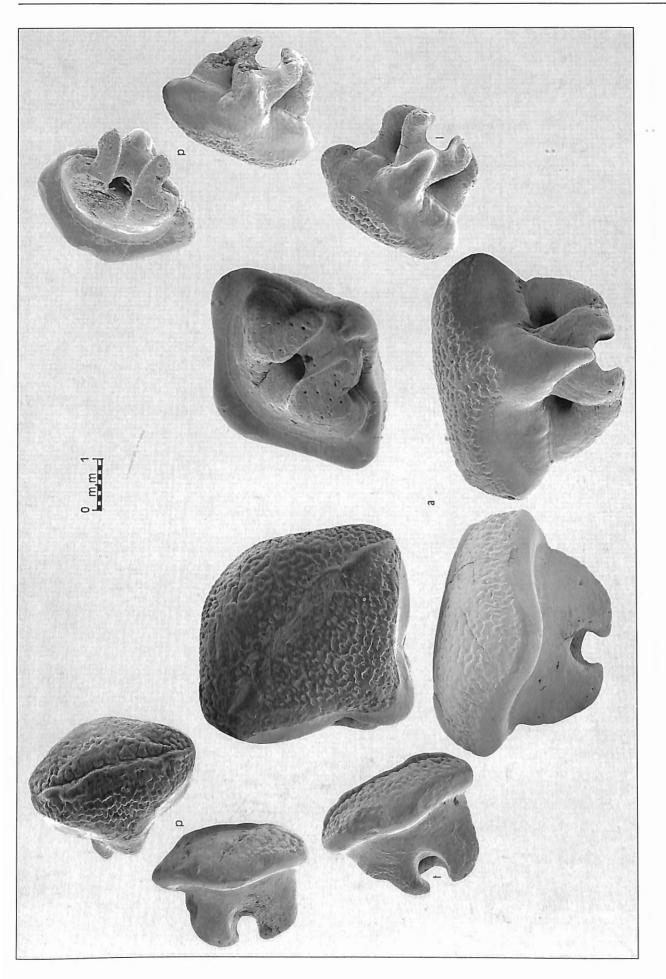
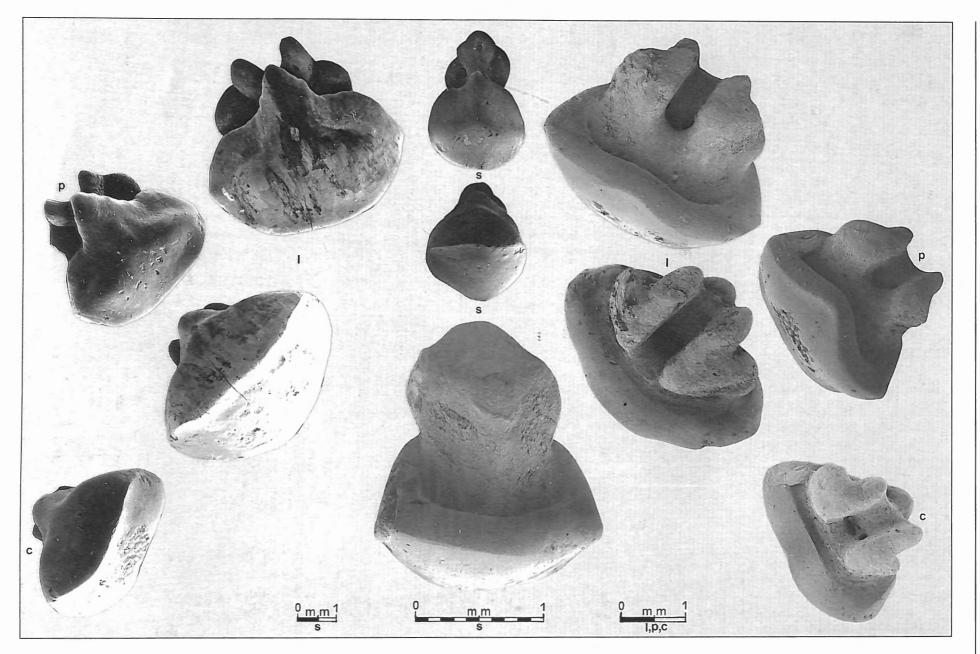


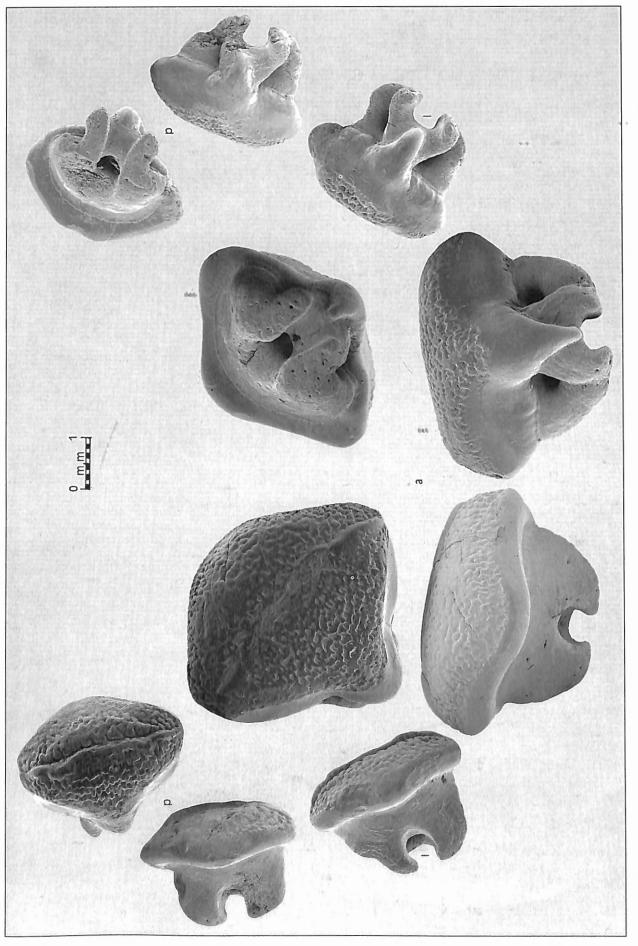
Plate 14. - Rhina ancyclostoma BLOCH & SCHNEIDER, 1801. Adult specimen circa 250 cm t.l., Indian Ocean. Lower teeth, the commissural one is twice enlarged.

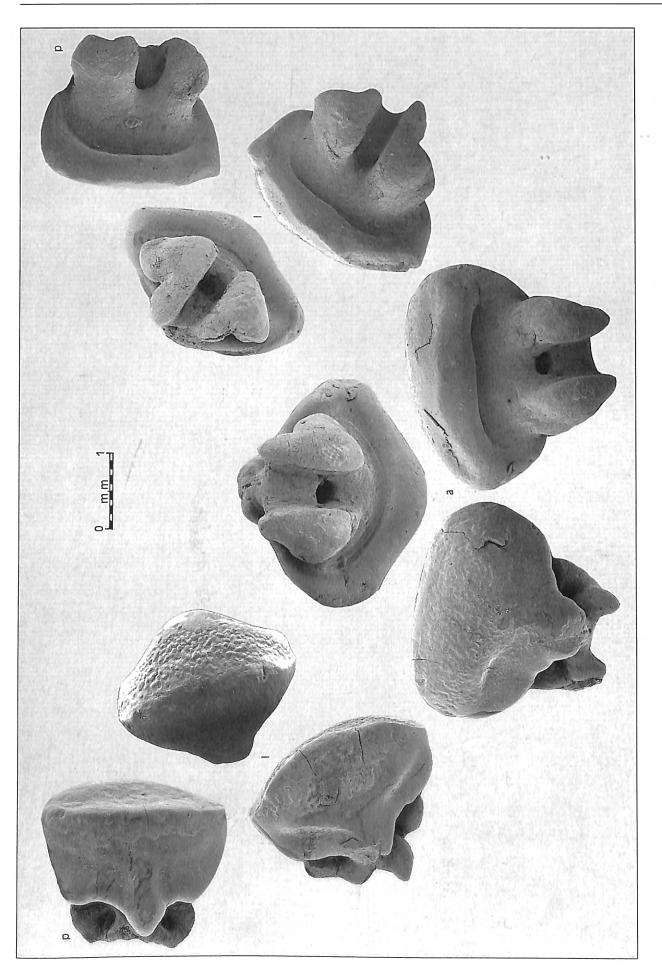
141











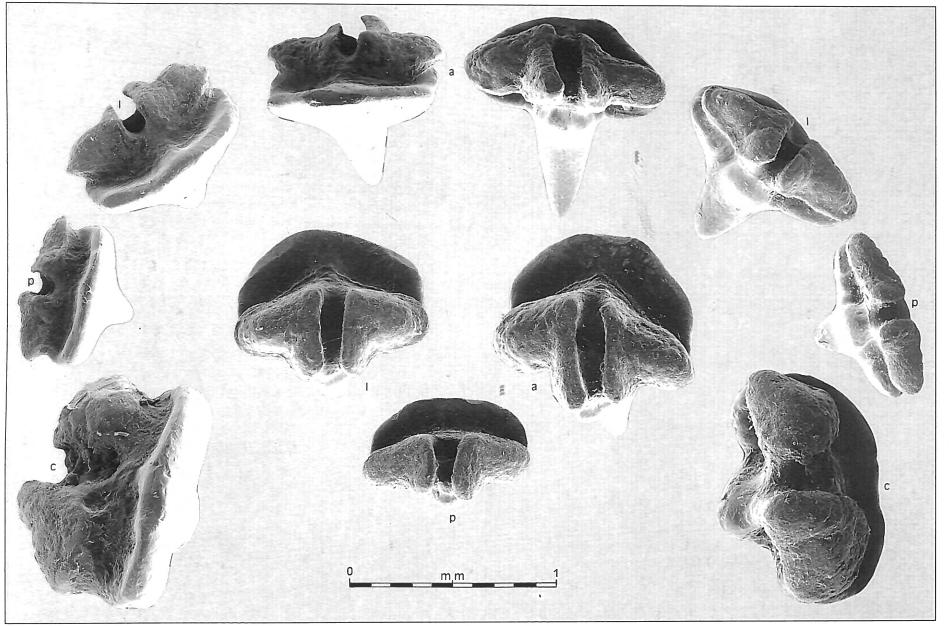
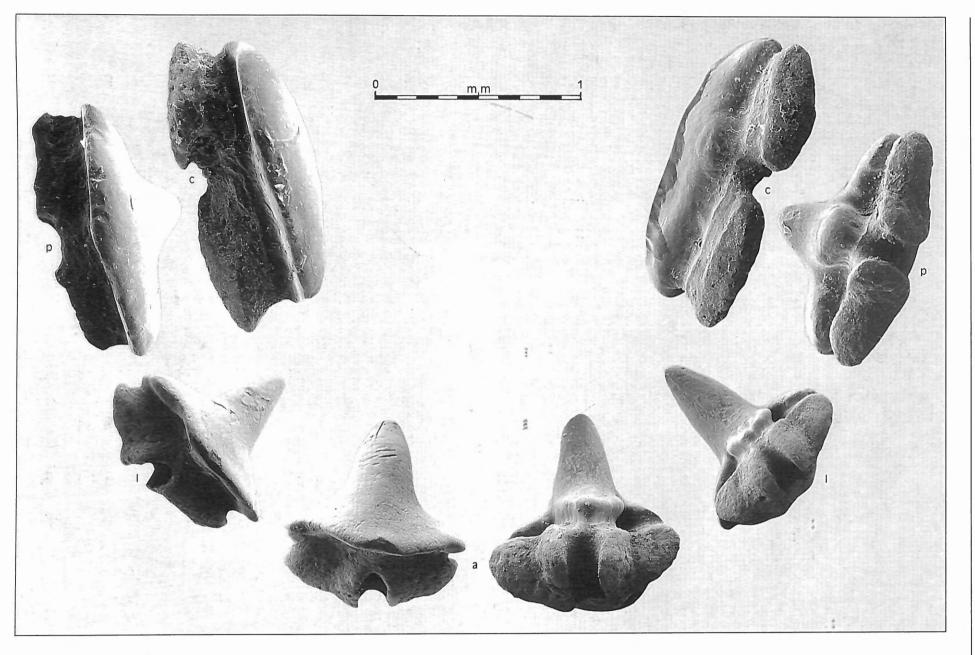
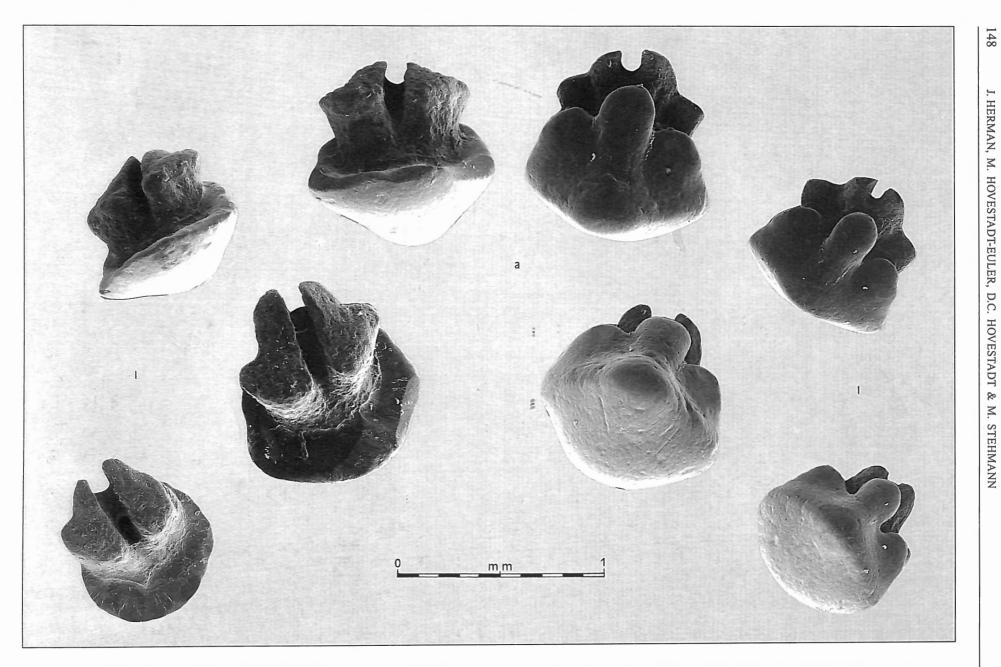
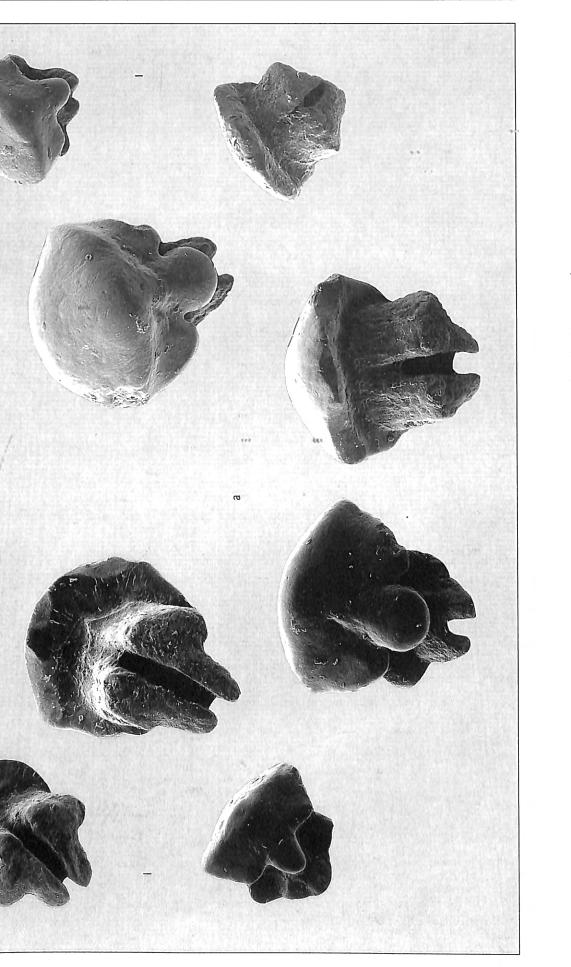


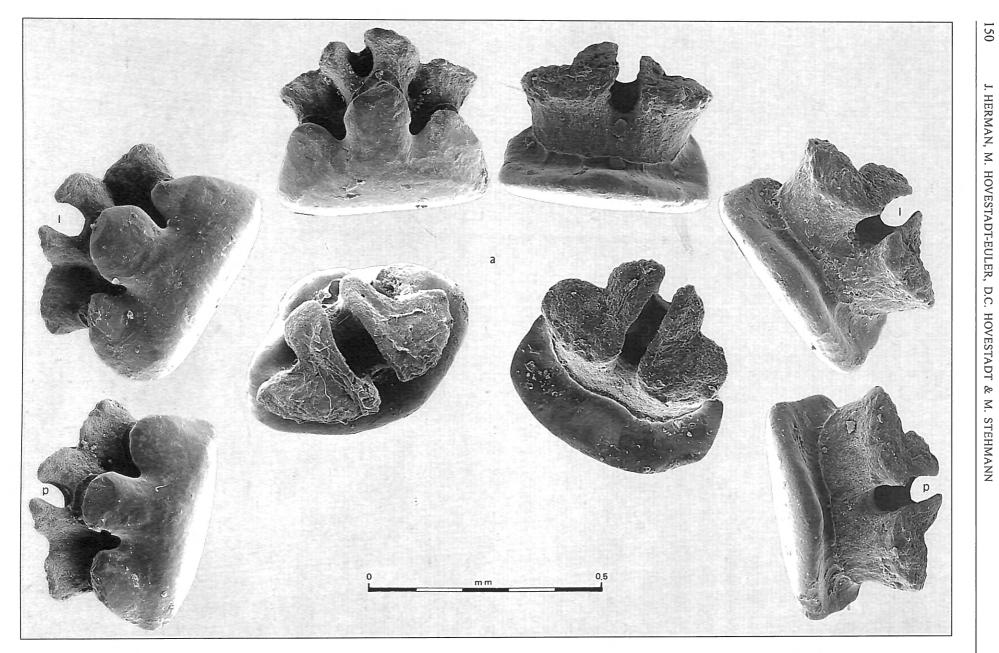
Plate 19. - Aptychotrema bougainvillei MULLER & HENLE, 1801. Male 91 cm t.l., Port Jackson, Australia. Upper teeth, the commissural one is twice and a half enlarged.







m,m



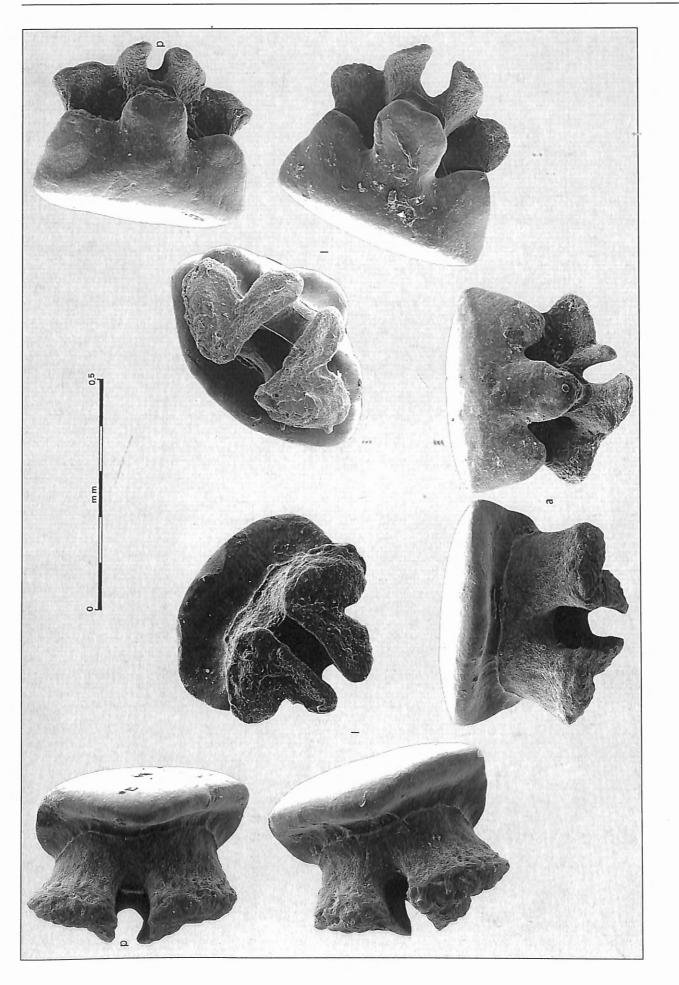
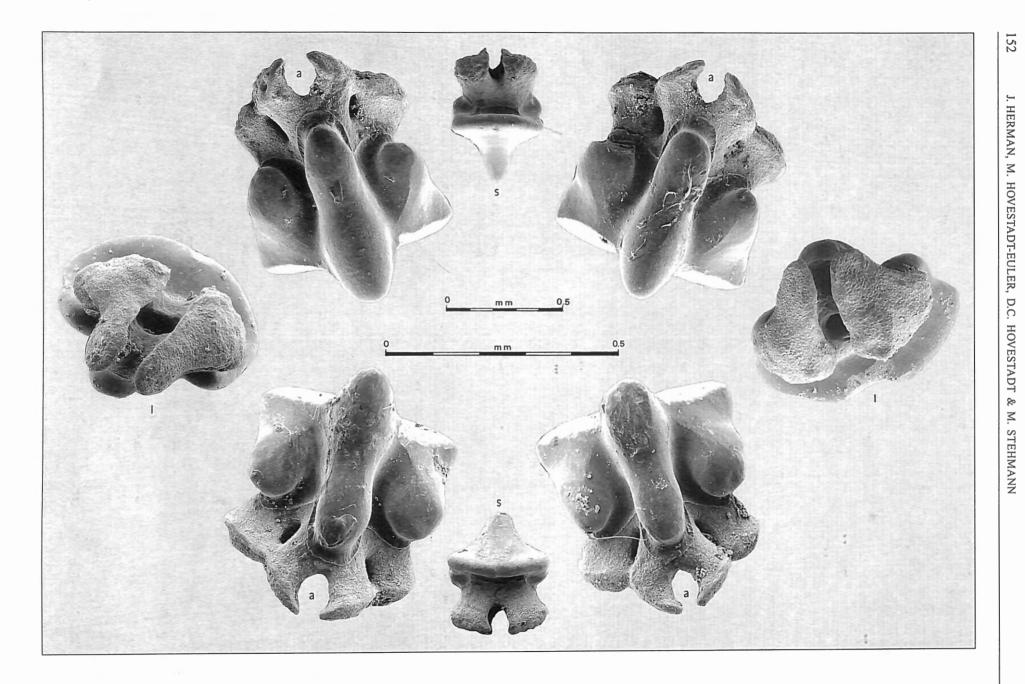


Plate 24. - Platyrhina sinensis (BLOCH & SCHNEIDER, 1801). Female 45 cm t.l., Japan Sea. Lower teeth.



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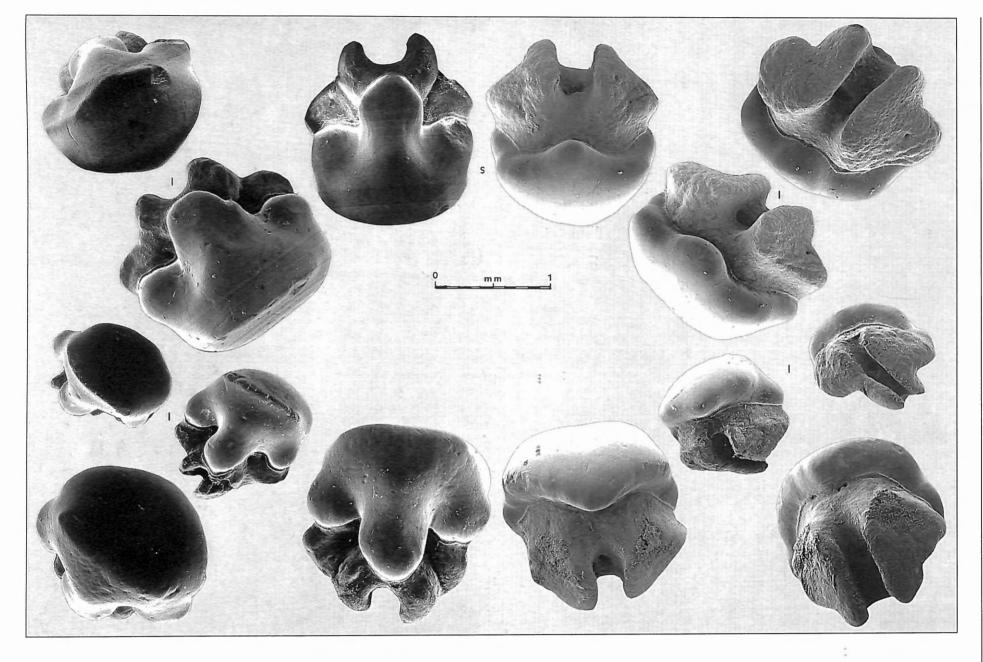
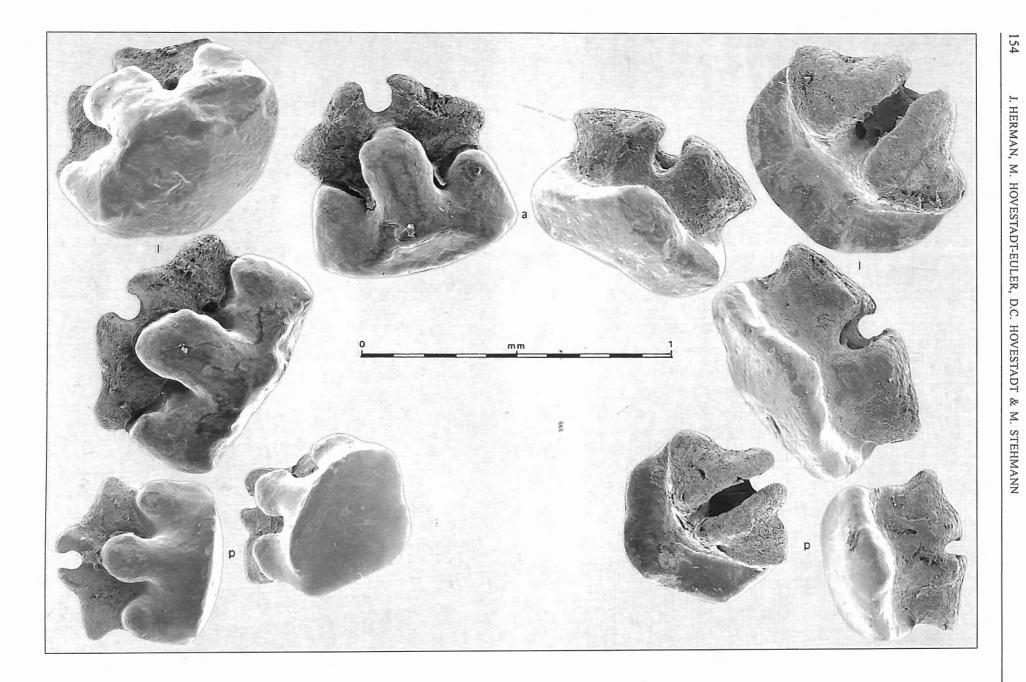
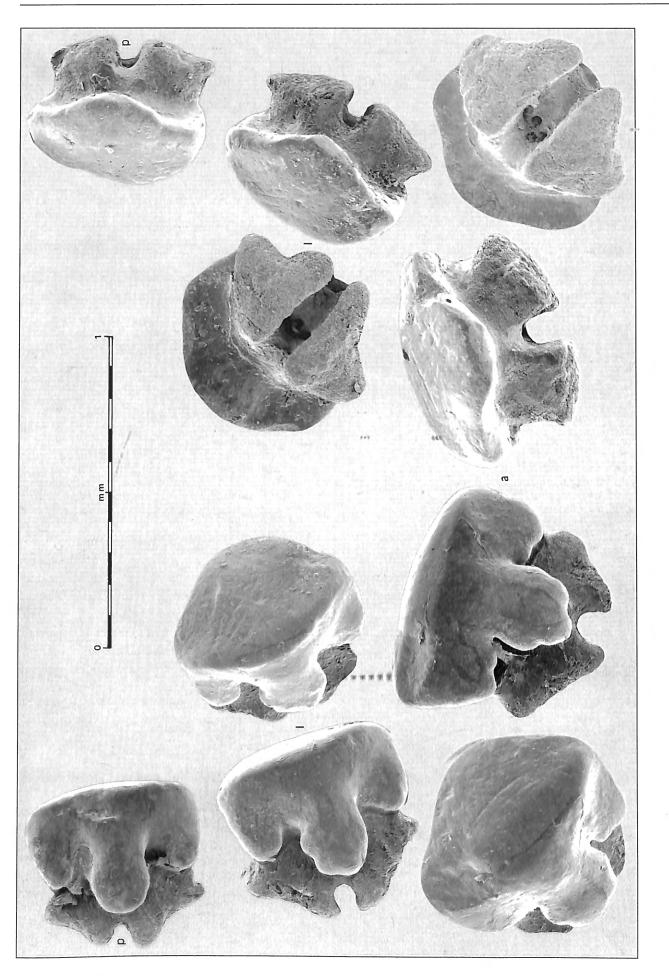
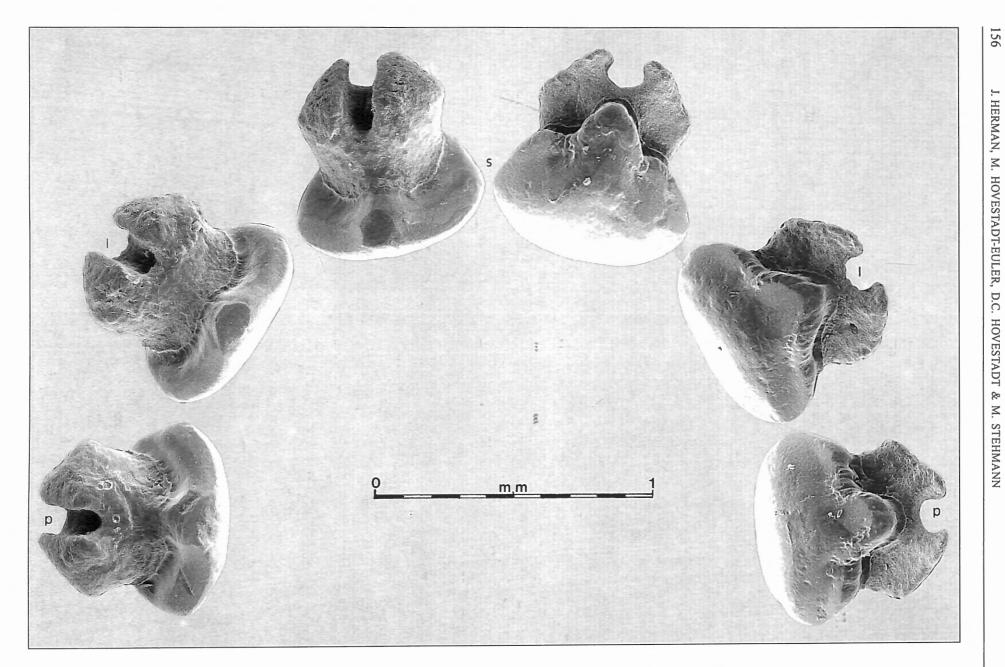


Plate 26. - Rhinobatos cemiculus E. GEOFFROY DE SAINT HILAIRE, 1817. Male 292 cm t.l., Abidjan, Ivory Coast. Upper and lower teeth.







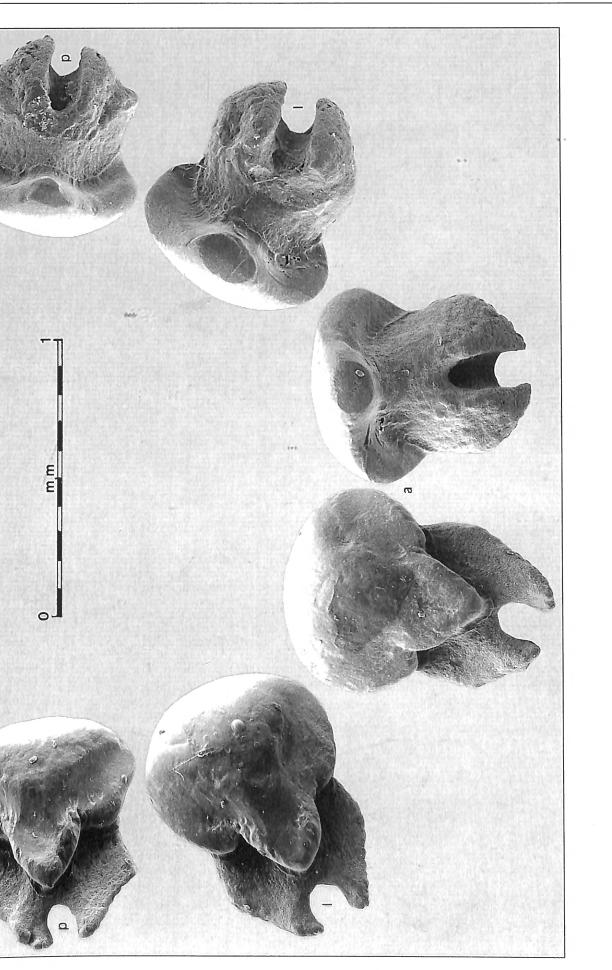
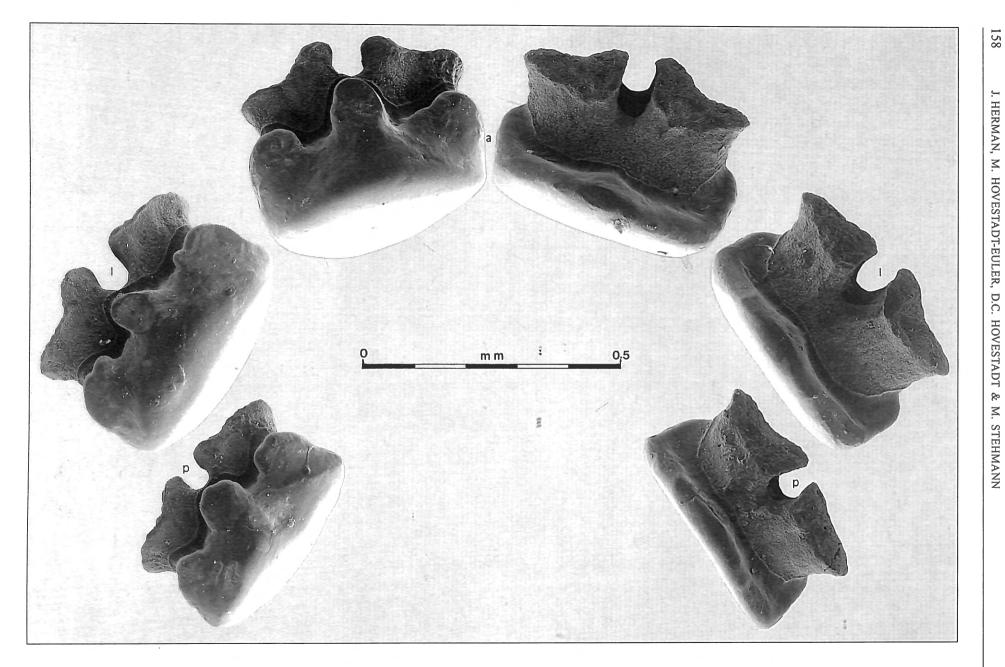
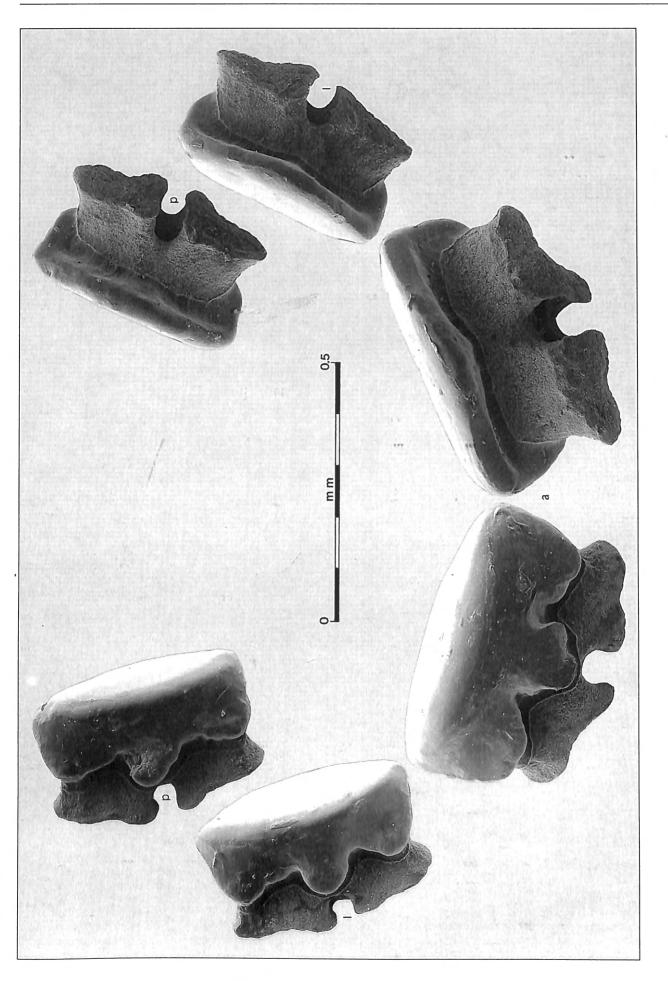
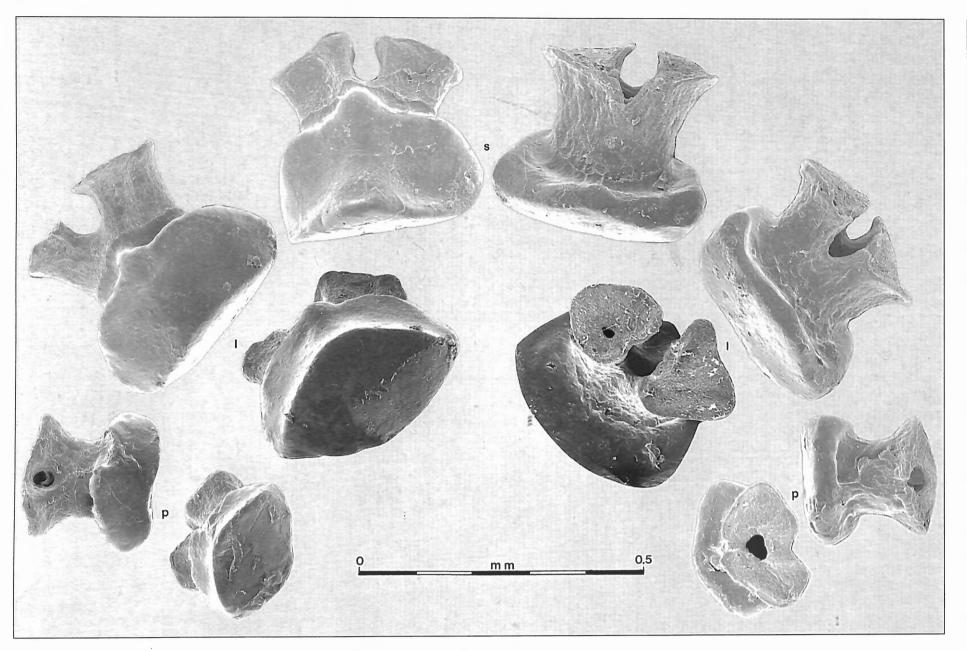


Plate 30. - Trygonorrhina fasciata MULLER & HENLE, 1841. Female 72 cm t.l., Port Jackson, Australia. Lower teeth.







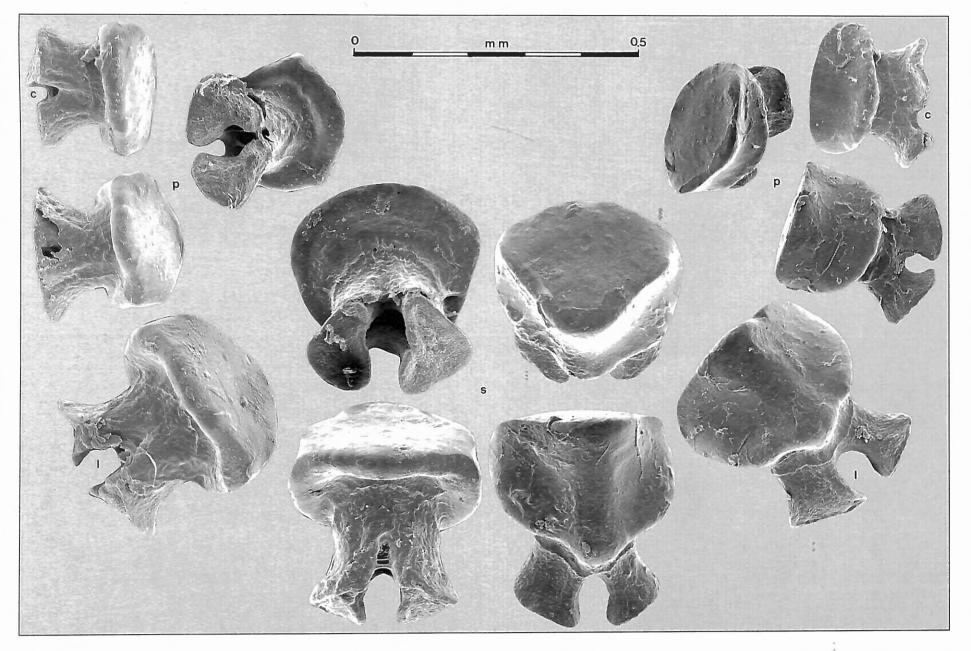


Plate 34. – Zanobatus schoenleinii (MULLER & HENLE, 1841). Female 43 cm t.l., Saly Beach, Senegal. Lower teeth.

