

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

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Part A : Selachii. No. 3 : Order : Squaliformes Families : Echinorhinidae, Oxynotidae and Squalidae

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Abstract

The teeth of nearly all supraspecific taxa of squaliformes are described and illustrated by SEM photos. The tooth morphology allows a direct assignment to all these taxa and some proposals of taxonomic adjustments.

The results support opinions of other authors, that Echinorhinidae represent a separate order, Oxynotidae coincide odontologically with Squalidae; Squalid genera could be grouped into 8 subfamilies, 4 of which could not be defined hitherto; *Centroselachus* GARMAN, 1913 is confirmed and should be revalidated; significant odontological differences do not exist between *Cirrhigaleus* and *Squalus*, *Lepidorhinus* and *Centrophorus*, *Scymnodon* and *Scymnodalatis*, likewise *Squaliolus* and *Heteroscymnoides* and *Euprotomicrus* on the other hand; 2 subgenera appear to be justified for the 3 species of *Somniosus*: *Somniosus* (*Somniosus*) and *Somniosus* (*Rhinoscymnus*).

An odontological key is given for all these supraspecific taxa.

Key-words : Elasmobranchii - Selachii - Squaliformes - Echinorhinidae - Squalidae - Odontology.

Résumé

Les dents de la plupart des taxons supraspécifiques des squaliformes sont décrites et figurées (clichés MEB). La morphologie dentaire permet une identification générique ou subgénérique ainsi que la formulation d'un certain nombre de propositions de réajustements taxonomiques. Dans l'ensemble, ces résultats concordent avec l'opinion d'autres chercheurs.

Ainsi, les Echinorhinidae représenteraient un ordre distinct; les Oxynotidae ne se distinguent odontologiquement pas des Squalidae. Les divers genres de Squalidae pourraient être regroupés en 8 sous-familles, dont 4 non encore définies.

Centroselachus GARMAN, 1913 est revalidable. Il n'existe aucune différence odontologique significative entre *Cirrhigaleus* et *Squalus*, *Lepidorhinus* et *Centrophorus*, *Scymnodalatis* et *Scymnodon*, pas plus qu'entre *Squaliolus*, *Heteroscymnoides* et *Euprotomicrus*.

Les 3 espèces de *Somniosus* peuvent être réparties au sein de 2 sous-genres : *Somniosus* (*Somniosus*) et *Somniosus* (*Rhinoscymnus*).

Une clé odontologique est proposée pour la distinction de tous ces taxons.

Mots-clés : Elasmobranchii - Selachii - Squaliformes - Echinorhinidae - Oxynotidae - Squalidae - Odontologie.

Kurzfassung

Die Kieferzähne fast aller squaliformen supraspezifischen Taxa werden beschrieben und mit REMPhotos illustriert.

Erlaubt eine direkte generische Zuordnung und einige taxonomische Anpassungsvorschläge. Die Ergebnisse stützen Auffassungen früherer Autoren, dass die Echinorhinidae eine eigene Ordnung darstellen; die Oxynotidae odontologisch mit den Squalidae übereinstimmen; die Squalidae-Gattungen in 8 Unterfamilien gruppiert werden könnten, von denen 4 bisher nicht definierbar waren; *Centroselachus* GARMAN, 1913 findet sich bestätigt und sollte wieder errichtet werden; odontologisch finden sich keine signifikanten Unterschiede zwischen *Cirrhigaleus* und *Squalus*, *Lepidorhinus* und *Centrophorus*, *Scymnodon* und *Scymnodalatis*, ebensowenig *Squaliolus* sowie *Heteroscymnoides* einerseits und *Euprotomicrus* andererseits; den 3 *Somniosus*-Arten waren 2 Untergattungen zuzuordnen: *Somniosus* (*Somniosus*) und *Somniosus* (*Rhinoscymnus*). Ein morphologischer Schlüssel zur generischen Bestimmung wird gegeben.

Schlüsselwörter : Elasmobranchii - Selachii - Squaliformes - Echinorhinidae - Oxynotidae - Squalidae - Odontologie.

Introduction

Major revisions of shark systematics and squaloids in particular were published by Bigelow & Schroeder (1957), Bass, d'Aubrey and Kistnasamy (1976) and Compagno (1973, 1977 and 1984).

The teeth of Squaliformes were the subject of a study to compare fossil teeth by Ledoux (1970, 1972), who described and figured several genera, as well as Casier (1961).

Also Welton (1973) described and figured several genera in an unpublished thesis.

In this fascicle, will be described and illustrated the teeth of all living squaliform families and genera belonging to this order, with the exception of *Mollisquama parini* DOLGANOV, 1984, which was not available for examination.

Also *Zameus squamulosus*, a genus which is in discussion (Taniuchi & Garrick, 1986), was not available for examination.

The ordering of genera and species is according to the grouping of taxa based on the present result.

The nomenclature of taxa is according to Compagno (1984). The original literature reference of each specific taxon will be given in the descriptive part, respectively and not be repeated in the bibliography.

Systematics and materials

ORDER : SQUALIFORMES,
sensu COMPAGNO (1984)

This order comprises the families Echinorhinidae, Oxynotidae and Squalidae, which will be described and illustrated in detail below.

With the addition of *Mollisquama parini* DOLGANOV, 1984, that was not yet included, these families comprise the following genera :

Family : ECHINORHINIDAE GILL, 1872

Genus : *Echinorhinus* BLAINVILLE, 1816

type species : *Echinorhinus brucus*

Family : OXYNOTIDAE

Genus : *Oxynotus* RAFINESQUE, 1810

type species : *Oxynotus centrina*

Family : SQUALIDAE BLAINVILLE, 1816

Genus : *Aculeola* DE BUEN, 1959

type species : *Aculeola nigra*

Genus : *Centrophorus* MÜLLER & HENLE, 1837

type species : *Centrophorus granulosus*

Genus : *Centroscyllium* MÜLLER & HENLE, 1841

type species : *Centroscyllium fabricii*

Genus : *Centroscymnus* BOCAGE & CAPELLO, 1864

type species : *Centroscymnus coelolepis*

Genus : *Cirrhigaleus* TANAKA, 1912

type species : *Cirrhigaleus barbifer*

Genus : *Dalatias* RAFINESQUE, 1810

type species : *Dalatias licha*

Genus : *Deania* JORDAN & SNYDER, 1902

type species : *Deania calcea*

Genus : *Etmopterus* RAFINESQUE, 1810

type species : *Etmopterus spinax*

Genus : *Euprotomicroides* HULLEY & PENRITH, 1966

type species : *Euprotomicroides zantedeschia*

Genus : *Euprotomicrus* GILL, 1864

type species : *Euprotomicrus bispinatus*

Genus : *Heteroscymnoides* FOWLER, 1934

type species : *Heteroscymnoides marleyi*

Genus : *Isistius* GILL, 1864

type species : *Isistius brasiliensis*

Genus : *Mollisquama* DOLGANOV, 1984

type species : *Mollisquama parini*

Genus : *Scymnodalatias* GARRICK, 1956

type species : *Scymnodalatias sherwoodi*

Genus : *Scymnodon* BOCAGE & CAPELLO, 1864

type species : *Scymnodon ringens*

Genus : *Somniosus* LESUEUR, 1818

type species : *Somniosus microcephalus*

Genus : *Squaliolus* SMITH & RADCLIFFE, 1912

type species : *Squaliolus laticaudus*

Genus : *Squalus* LINNAEUS, 1758

type species : *Squalus acanthias*

The following 904 specimens belonging to 48 species were examined :

<i>Aculeola nigra</i>	3 males	1 female
<i>Centrophorus acus</i>	1 male	
<i>Centrophorus granulosus</i>	18 males	28 females
<i>Centrophorus lusitanicus</i>		2 females
<i>Centrophorus uyato</i>	3 males	1 female
<i>Centrophorus squamosus</i>	15 males	47 females
<i>Centroscyllium fabricii</i>	4 males	51 females
<i>Centroscyllium granulosum</i>	18 males	24 females
<i>Centroscyllium nigrum</i>	3 males	3 females
<i>Centroscyllium ritteri</i>	1 male	
<i>Centroscymnus coelolepis</i>	47 males	47 females
<i>Centroscymnus crepidater</i>	25 males	48 females
<i>Centroscymnus owstoni</i>		1 female
<i>Cirrhigaleus barbifer</i>		1 female
<i>Dalatias licha</i>	22 males	40 females
<i>Deania calcea</i>	48 males	45 females
<i>Deania histricosa</i>	1 male	1 female
<i>Deania profundorum</i>	2 males	6 females
<i>Echinorhinus brucus</i>	2 males	3 females
<i>Echinorhinus cookei</i>	2 males	1 female
<i>Etmopterus bullisi</i>	1 male	2 females
<i>Etmopterus hillianus</i>	6 males	12 females
<i>Etmopterus lucifer</i>	2 males	2 females
<i>Etmopterus polli</i>	1 male	2 females
<i>Etmopterus princeps</i>	5 males	4 females
<i>Etmopterus pusillus</i>	2 males	3 females
<i>Etmopterus schultzi</i>	3 males	1 female
<i>Etmopterus spinax</i>	45 males	61 females
<i>Etmopterus virens</i>		2 females
<i>Euprotomicroides zantedeschia</i>	1 male	1 female
<i>Euprotomicrus bispinatus</i>	1 male	2 females
<i>Heteroscymnoides marleyi</i>		1 female
<i>Isistius brasiliensis</i>	1 male	3 females
<i>Oxynotus brunniensis</i>	1 male	
<i>Oxynotus caribbaeus</i>	1 male	
<i>Oxynotus centrina</i>	13 males	16 females
<i>Oxynotus paradoxus</i>	4 males	2 females
<i>Scymnodalatias albicauda</i>		1 female
<i>Scymnodon obscurus</i>	2 males	2 females
<i>Scymnodon ringens</i>	18 males	30 females
<i>Somniosus microcephalus</i>	7 males	18 females
<i>Somniosus pacificus</i>	1 male	2 females
<i>Somniosus rostratus</i>	1 male	4 females
<i>Squaliolus laticaudus</i>	1 male	4 females
<i>Squalus acanthias</i>	36 males	45 females
<i>Squalus asper</i>		1 female
<i>Squalus blainvillei</i>	4 males	18 females
<i>Squalus cubensis</i>	1 male	

There is a remarkable morphological difference in tooth arrangement between Echinorhinidae, Oxynotidae and Squalidae. The lower tooth files are very compressed in Oxynotidae and Squalidae (with the exception of the genera *Centroscyllium* and *Aculeola*), resulting in interlocking of the teeth. This interlocking is demonstrated by positioning the outer mesial part of

each tooth behind the inner distal part of the previous tooth. This phenomenon is even present in both upper and lower jaws in some genera of the Squalidae. These teeth have therefore a particular depression on outer mesial and inner distal part of the root. Interlocking is neither existing in upper, nor lower teeth of Echinorhinidae.

Several degrees of dignathic heterodonty are shown within the genera of the order SQUALIFORMES. This is demonstrated by slightly smaller upper teeth (particularly in juvenile specimens) in *Echinorhinus*, *Centroscyllum*, *Aculeola*, *Squalus* and *Cirrhigaleus*; smaller, longitudinally more compressed upper teeth in *Deania* and *Centrophorus*; smaller, longitudinally, still stronger compressed upper teeth in *Oxynotus* and *Somniosus*; much smaller, longitudinally very strongly compressed upper teeth in *Centroscymnus*, *Dalatias*, *Isistius*, *Etmopterus*, *Scymnodon*, *Euprotomicrus*, *Squaliolus*, *Heteroscymnoides* and *Euprotomicroides*. Several of the genera have either symphyseal, or parasymphyseal, or pseudosymphyseal teeth in upper and or lower jaws. The lower jaw teeth are considered as particularly important for this phenomenon, because they are not affected by nostrils and eyes. A lower symphyseal tooth is present in *Oxynotus*, *Dalatias*, *Isistius*, *Euprotomicroides* and *Echinorhinus* (in *Echinorhinus* it may only be the relict of a true symphyseal tooth row). Parasymphyseal teeth were observed in *Etmopterus*, *Aculeola*, *Centroscyllum*, *Squalus*, *Centrophorus*, *Deania*, *Somniosus* and *Centroscymnus*. Pseudosymphyseal teeth were observed in species of the genera *Squalus* ($\pm 5\%$) and *Centroscymnus* ($\pm 40\%$). This phenomenon appears to be of no further use and is presented as additional information only.

The tooth counts are also very remarkable within the genera of the SQUALIFORMES. We noted the following counts in upper and lower jaw halves :

	upper	lower
<i>Aculeola nigra</i>	30	30
<i>Centroscyllum fabricii</i>	32/51	33/52
<i>Centroscymnus coelolepis</i>	24/33	17/18
<i>Centroscymnus crepidater</i>	16/26	14/18
<i>Centrophorus granulosus</i>	18/19	14/16
<i>Centrophorus squamosus</i>	15/19	13/32
<i>Dalatias licha</i>	16/19	8/9
<i>Deania calcea</i>	11/17	12/16
<i>Echinorhinus brucus</i>	10/14	9/13
<i>Etmopterus spinax</i>	11/16	13/20
<i>Euprotomicrus bispinatus</i>	9/11	10/11
<i>Euprotomicroides zantedeschia</i>	14/15	17
<i>Heteroscymnoides marleyi</i>	6/7	11/12
<i>Isistius brasiliensis</i>	15/17	12/15
<i>Isistius plutodus</i>	10/14	8/9
<i>Oxynotus centrina</i>	5/6	4
<i>Scymnodalatias albicauda</i>	25*	15
<i>Scymnodalatias sherwoodi</i>	16*	16

(GARRICK, 1956)

<i>Scymnodon ringens</i>	24/25	14/15
<i>Somniosus microcephalus</i>	20/24	24/29
<i>Somniosus rostratus</i>	30	16/18
<i>Squaliolus laticaudus</i>	10/11	9
<i>Squalus acanthias</i>	11/15	11/12

* = or more

Remarkable is the extremely large number of tooth rows in *Centroscyllum fabricii* and the extreme reduction of tooth rows in *Oxynotus*, *Squaliolus*, *Heteroscymnoides* and *Euprotomicrus*.

In a remark, COMPAGNO (1984 : 28, 29) suggested to group the genera of the families Squalidae and Oxynotidae into one family with the following subfamilies :

Family : SQUALIDAE

Subfamily : *Etmopterinae*

Genus : *Etmopterus*

Genus : *Aculeola*

Genus : *Centroscyllum*

Subfamily : *Squalinae*

Genus : *Squalus*

Genus : *Cirrhigaleus*

Genus : *Centrophorus*

Genus : *Deania*

Subfamily : *Dalatiinae*

Genus : *Dalatias*

Genus : *Heteroscymnoides*

Genus : *Euprotomicroides*

Genus : *Euprotomicrus*

Genus : *Isistius*

Genus : *Squaliolus*

Subfamily : *Somniosinae*

Genus : *Somniosus*

Genus : *Centroscymnus*

Genus : *Scymnodalatias*

Genus : *Scymnodon*

Genus : *Oxynotus*

Although no further arguments nor comments were presented for this grouping, odontology now also allows grouping into subfamilies. In general, this grouping is similar to that of COMPAGNO (1984) but differs in some particular cases.

Tooth morphology offers important phylogenetic information based on types of root vascularisation. In the first issue of this series (1987), however, the authors have declared their intention not to draw nomenclatorially valid conclusions from their odontological results, respectively. Being aware of dealing with one complex of characters only, they will only present this according odontological conclusions and leave it to following revising authors to incorporate also odontological points of view for a full systematic review with possible taxonomic and nomenclatorial changes.

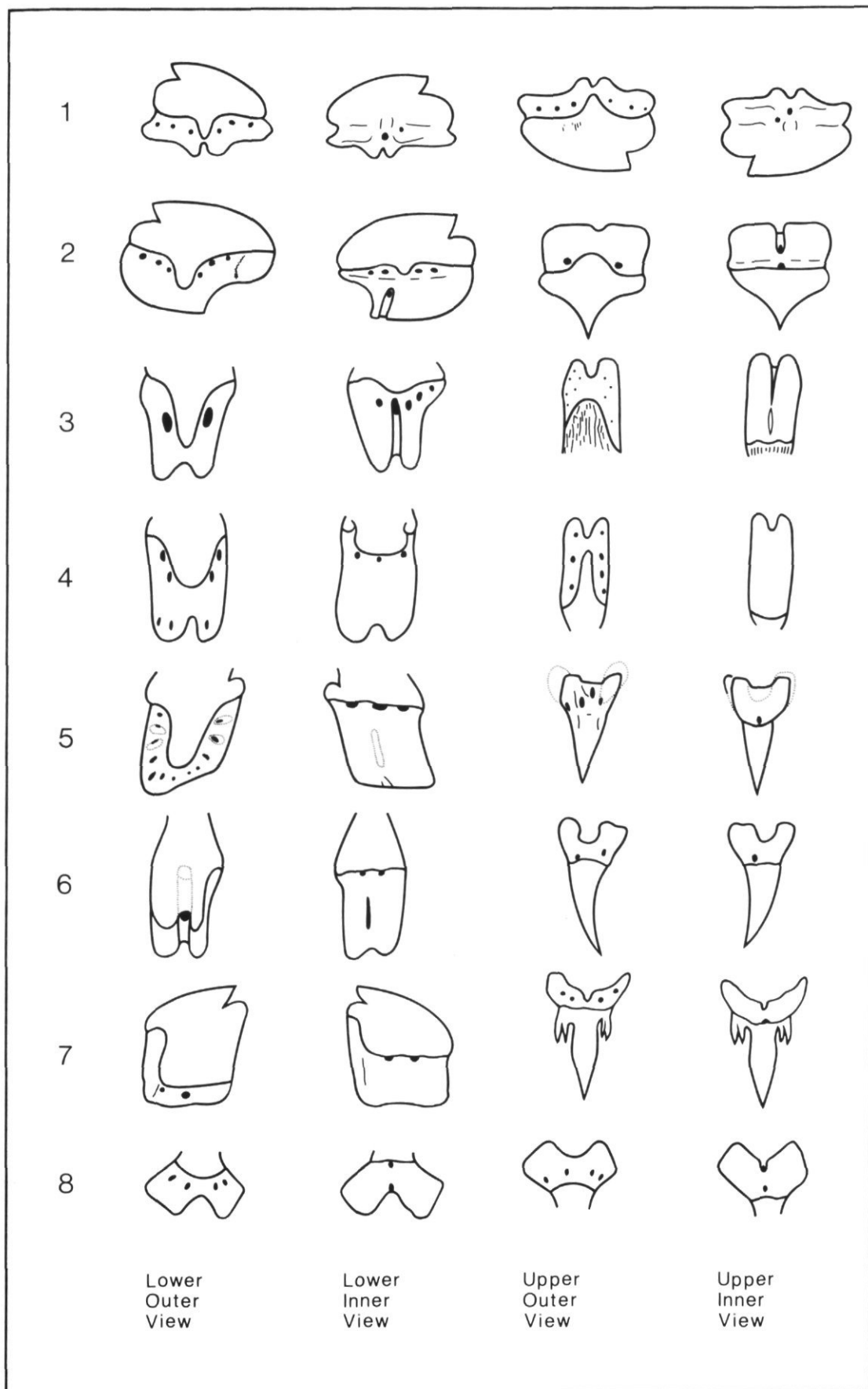


Fig. 1. Main tooth types of the Squaliformes.

Descriptions of the odontological morphotypes

Echinorhinus brucus BONNATERRE, 1788
Pl. 1, T. pl. 1.

Squalus brucus BONNATERRE, 1788, Tabl. encyclop. méthod. trois règ. Nat., Ichthyol., Paris : 11.

The species shows a very weak dignathic heterodonty in having parasymphysial teeth with poorly developed mesial cusplets in the lower jaw. Also the gradient monognathic heterodonty is weak. The ontogenetic heterodonty is very strong by monocuspid teeth in juveniles and multicuspoid teeth in adults. The dimensions of the teeth are hemicentimetric to subcentimetric in range.

The inner part shows a slightly convex crown surface, forming a weak angle with inner root surface. The outer part shows a less convex crown surface with an indented crown-root junction.

The crown is multicuspoid with a principal cusp strongly inclined toward the commissure. One to three mesial cusplets arise from the arched mesial cutting edge of the principal cusp on the anterior and lateral teeth, all directed strongly toward the symphysis. The mesial cusplets diminish to remain as a serration only on posterior teeth. The parasymphysial lower teeth have one small, poorly developed mesial cusplet. Only one distal cusplet is present on almost all teeth, that is directed toward the commissure, disappearing in the crown base in posterior teeth. On the anterior teeth a poorly developed second distal cusplet can be present. There is no trace of any outer, or inner crown ornamentation.

The root is anaulacorhizid, rectangular with sometimes rounded mesial and distal ends. On the outer face well developed vertical protuberances are present near the crown-root junction. An outer mesial and distal depression is present. Numerous foramina are scattered over the whole width of the depressed crown-root junction. The inner face of the root shows one two three median apertures near the crown-root junction, from which poorly developed vertical grooves run to the root base. The surface of the inner face is pierced with randomly scattered, vertically elongated foramina.

Family : Oxynotidae GILL, 1872

This family is monotypic with *Oxynotus* RAFINESQUE, 1810 ; type species *Oxynotus centrina*.

Genus : *Oxynotus* RAFINESQUE, 1810

The genus *Oxynotus* comprises four species : *Oxynotus paradoxus* FRADE, 1929, *Oxynotus caribbaeus* CERVIGNON, 1961, *Oxynotus bruniensis* (OGILBY, 1893) and *Oxynotus centrina* (LINNAEUS, 1758).

Oxynotus centrina (LINNAEUS, 1758)
Pl. 2, T. pl. 2

Squalus centrina LINNAEUS, 1758, Syst. Nat., éd. 10, 1 : 233.

This species shows a strong dignathic heterodonty and a weak gradient monognathic heterodonty. The root is always anaulacorhizid.

The dimensions of the lower teeth are subcentimetric, those of the upper teeth plurimillimetric.

Upper jaw.

The teeth are compressed, having a more or less vertically elongated crown and root.

The crown is twice as high as the crown base width. The symphysial tooth has a symmetrically triangular crown. The lateral teeth show a crown becoming increasingly asymmetrical, less high, and broader based toward the commissure. Both mesial and distal cutting edges are smooth.

The inner face is strongly convex. There is no trace of an uvula. The outer face of the crown is weakly convex, and a convex and broad apron extends nearly to the root base. The apron is not overhanging the root but forms one part with it. A true outer or inner ornamentation is absent.

The root is elongated and has a more or less rectangular appearance. From the crown-root junction downward, the root is narrowing and the basal edges are slightly rounded. The inner face is flat, showing a median aperture near the crown-root junction ; sometimes a poorly developed median vertical groove is present, which is more distinct on the lateral and posterior teeth. A deep medio-basal sulcus is always present.

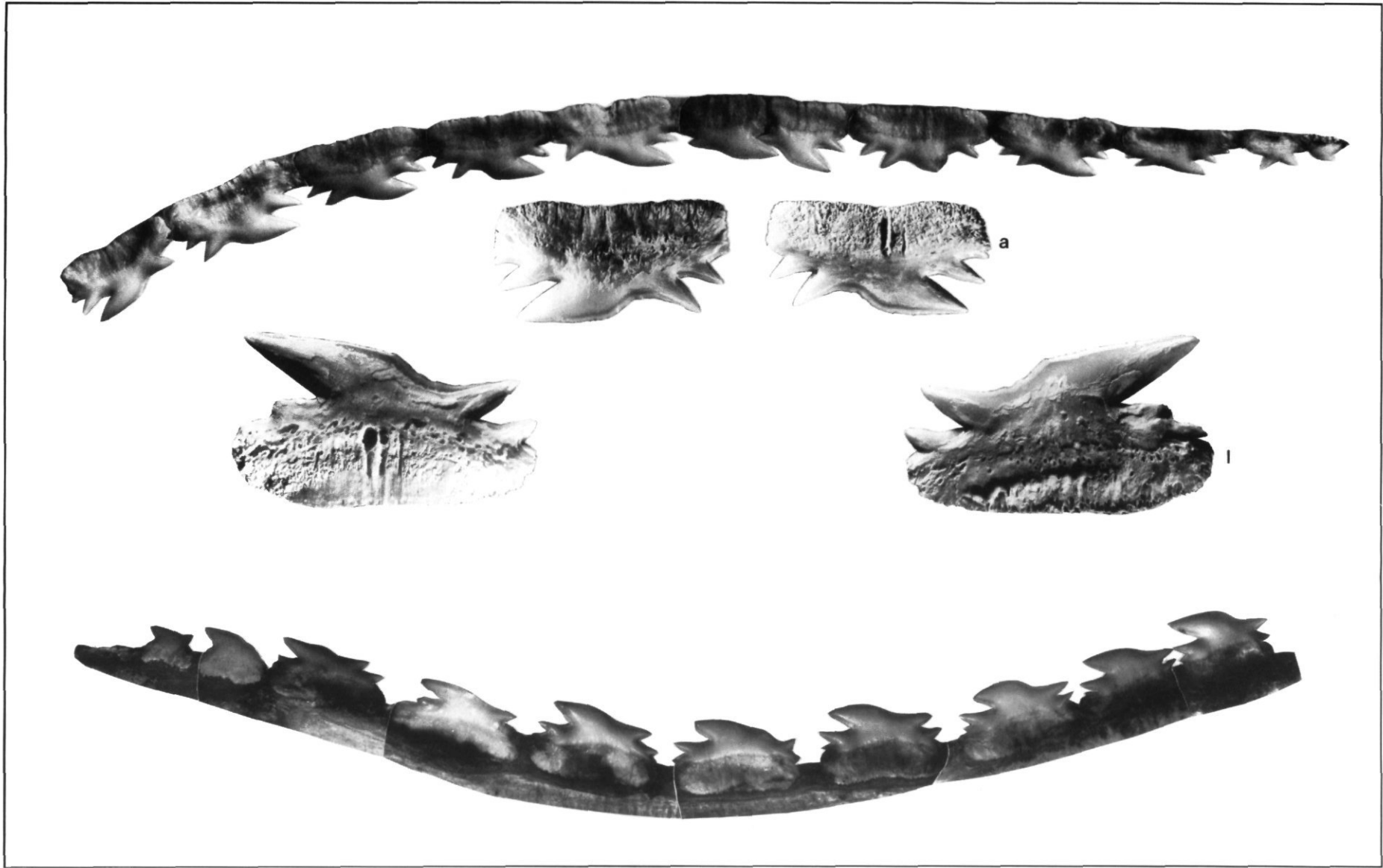
The outer face shows on both sides of the apron three to four main foramina. At the basal edge, several randomly scattered foramina are present.

Lower jaw.

The teeth are strongly compressed and interlocked. The triangular crown is as high as the crown base width. The crown is high and symmetrically triangular in the symphysial tooth but becomes increasingly asymmetrical and less high in lateral teeth. It consists of a bluntly rounded, cusplet-like knob at each basal edge, continued upward as strong serration, which becomes reduced in upper crown half and finally disappears totally toward the apex. A true ornamentation is absent.

The slightly convex inner crown face shows a broad, flat uvula, that is rectangular on the symphysial tooth and becomes more oblique on teeth toward the commissure.

On the inner face there is a large aperture at each side of the uvula and one large median aperture below the basal depression. A short, broad, medio-basal sulcus is present. The inner surface is flat, and sometimes one or



Text plate 1. *Echinorhinus brucus* (BONNATERRE, 1788). Female 228 cm. t.l., Senegal.
Upper and lower tooth set : x 1.5. Isolated teeth are macrophotographics of Mr. K. Jansen, Oudenbosch, the Netherlands. Upper tooth : x 3,
lower teeth x 4.

two foramina appear above the sulcus. A weak inner distal depression is due to interlocking of the lower teeth.

The outer face shows a large aperture at each side of the apron. Near the junction of the apron and root, some vertical protuberances are present.

Two to four foramina surround the sulcus, and several scattered foramina are on the outer basal edge of the root. A weak outer mesial depression is also due to interlocking.

Family : Squalidae BLAINVILLE, 1816

This family comprises eighteen genera as listed in the introduction.

Genus : *Squalus* LINNAEUS, 1758

After COMPAGNO, 1984, this genus comprises eight species : *Squalus asper* MERRETT, 1973, *Squalus blainvillei* (RISSO, 1826), *Squalus japonicus* ISHIKAWA, 1908, *Squalus megalops* (MACLEAY, 1881), *Squalus melanurus* FOURMANOIR & RIVATON, 1979, *Squalus mitsukurii* JORDAN & SNYDER, 1903, *Squalus rancureli* FOURMANOIR & RIVATON, 1979 and type species *Squalus acanthias* LINNAEUS, 1758.

Squalus acanthias LINNAEUS, 1758
Pl. 3, T. pl. 3.

Squalus acanthias LINNAEUS, 1758, Syst. Nat., éd. 10, 1: 233.

This species shows a very weak dignathic heterodonty in having slightly shorter upper teeth. A gradient monognathic heterodonty is rather strong in antero-lateral teeth becoming broader toward the commissure. Sexual heterodonty is indicated by a sigmoidal mesial cutting edge in males, contrasting an arched mesial cutting edge in females.

Both upper and lower teeth are interlocked, presenting a weak inner distal but a strong outer mesial depression. The dimensions of the teeth are hemicentimetrical in range.

The crown has a distally strongly inclined principal cusp, which is mesio-basally rounded. Its long mesial cutting edge is arched or sigmoidal, while its short distal cutting edge joins a low distal blade in a notch. Weak serrations are sometimes present on the cutting edges of the principal cusp. Except for some short basal costules, a true inner or outer ornamentation is absent. On the inner face, the principal cusp is weakly convex. A well developed, short central-basal uvula is present. On the outer face, both principal cusp and distal blade are weakly convex, showing a well developed central-basal apron, that strongly overhangs the root, and extends to the base of the root. This apron is narrow and more or less rectangular with a rounded basal edge.

The crown base overhangs the crown-root junction. The inner crown-root junction is depressed.

The anaulacorhizid root is strongly compressed.

The inner face of the root is low and strongly convex longitudinally, more or less supporting the uvula. Several foramina are present along the crown-root junction. There is a large central-basal aperture present, that affects also the root base. The root base is thickened centrally throughout its length. The outer face is about twice as high as the inner face. Two or three apertures with several foramina are present on both sides of the apron.

Genus : *Cirrhigaleus* TANAKA, 1912

This genus is monotypic with the type species *Cirrhigaleus barbifer*.

Cirrhigaleus barbifer TANAKA, 1912
Pl. 4.

Cirrhigaleus barbifer TANAKA, 1912, Fig. Descr. Fish. Japan, 9 : 151.

This species shows a very weak dignathic heterodonty in having slightly shorter upper teeth. A gradient monognathic heterodonty is rather obvious in antero-lateral teeth, which becomes broader toward the commissure. Sexual heterodonty could not be examined, because only teeth of a female were available.

Both, upper and lower teeth are interlocked, presenting a weak inner distal, and a strong outer mesial depression.

The dimensions of the teeth are hemicentimetrical in range.

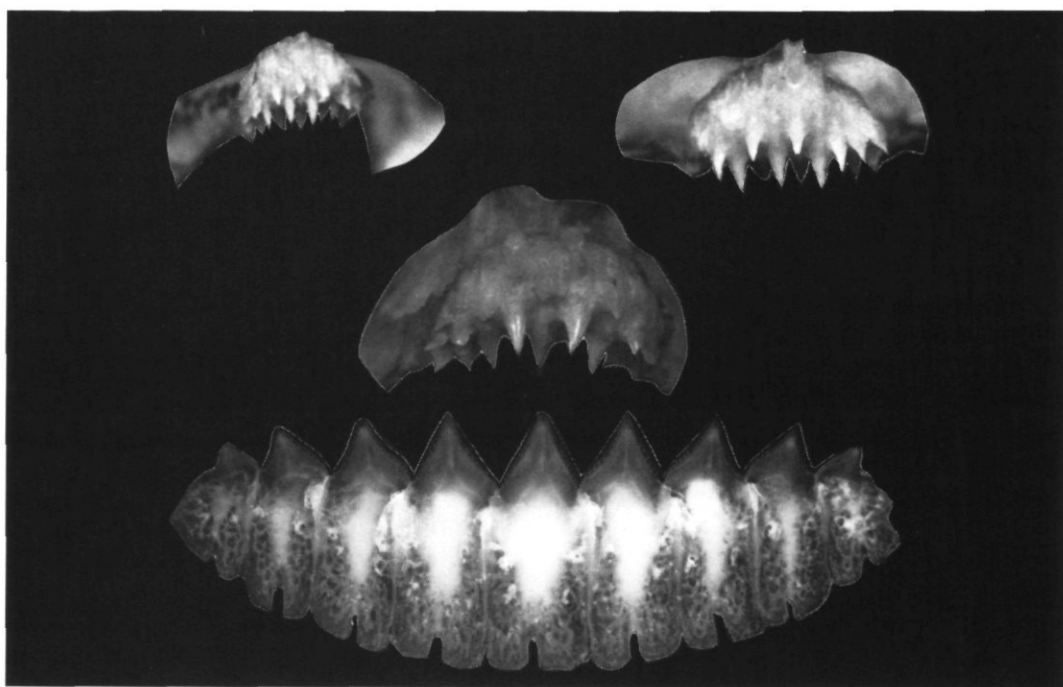
The crown has a distally strongly inclined principal cusp, which is mesio-basally rounded. Its long mesial cutting edge is weakly arched, while its short distal cutting edge joins a low distal blade in a notch. Serrations are absent on the cutting edges of the principal cusp are absent.

Except for some short basal costules, a true inner or outer ornamentation is absent.

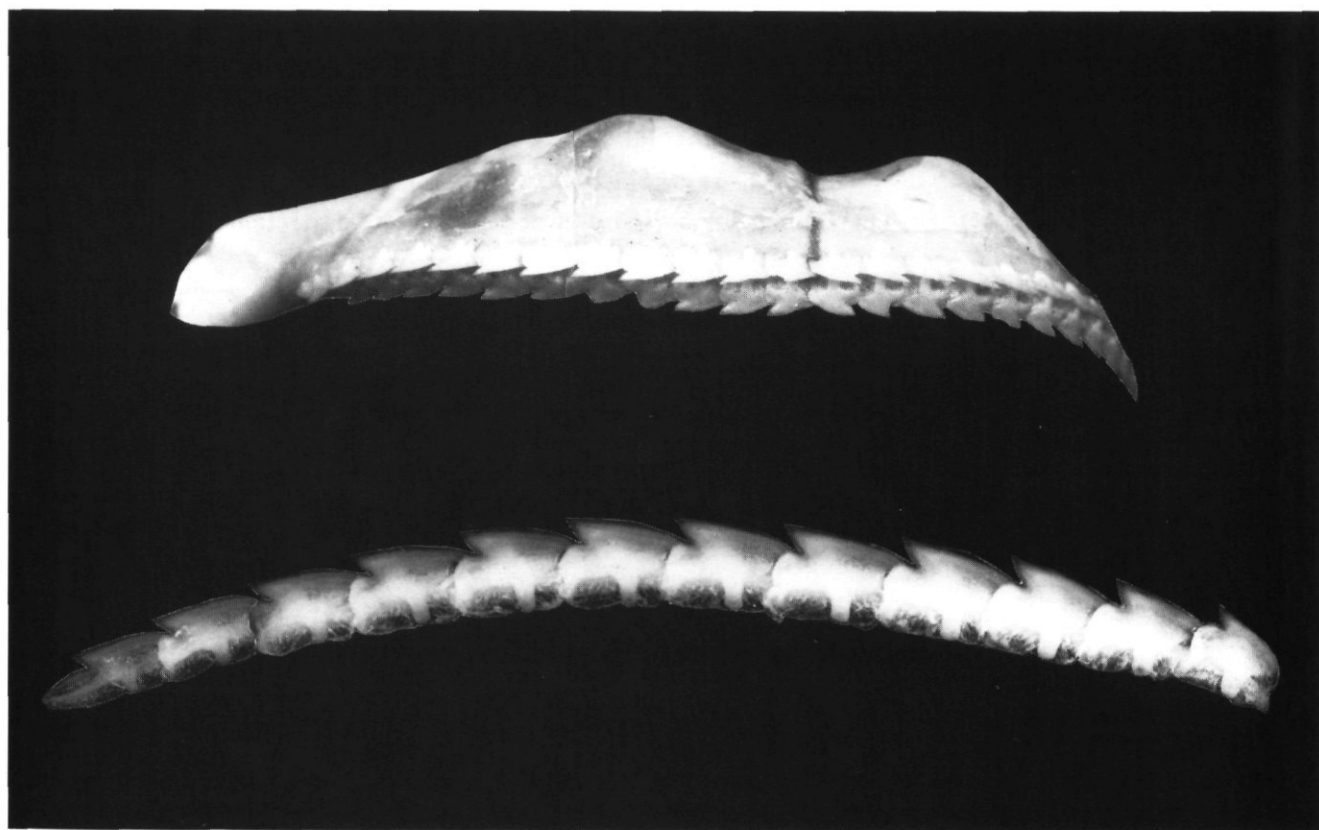
On the inner face, the principal cusp is weakly convex. A well developed, short central-basal uvula is present. On the outer face, both principal cusp and distal blade are weakly convex, showing a well developed central-basal apron, that strongly overhangs the root reaching its base. This apron is broad and more or less triangular with a rounded basal edge. The crown base overhangs the crown-root junction. The inner crown-root junction is depressed.

The anaulacorhizid root is very compressed.

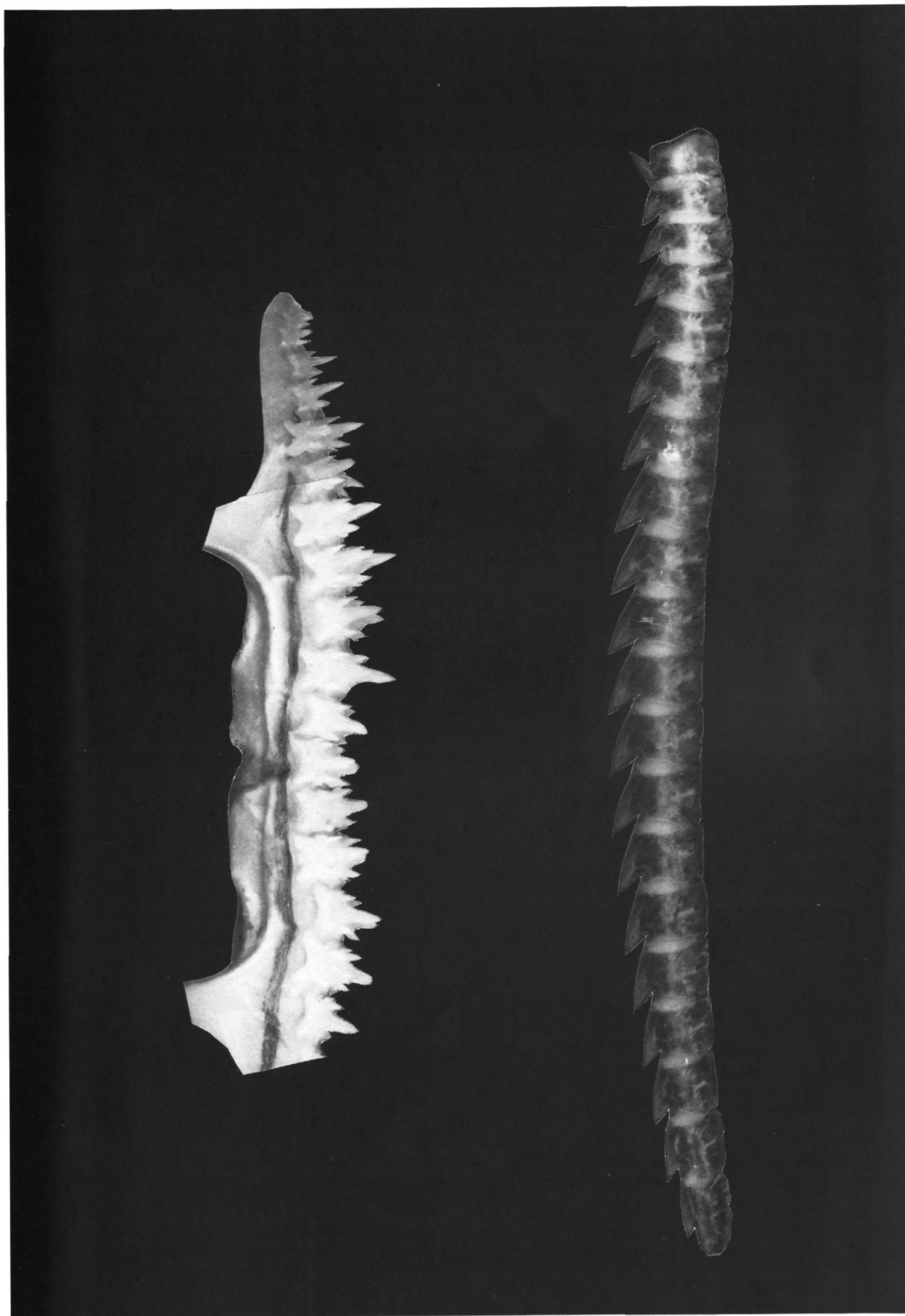
The inner face of the root is low and strongly convex longitudinally, more or less supporting the uvula. Several foramina are present along the crown-root junction. There is a large central-basal aperture present, that affects also the root base. The root base is



Text plate 2. *Oxynotus centrina* (LINNAEUS, 1758). Female 31 cm. t.l., Sète, France, Mediterranean Sea (left), female 36 cm. t.l., Dakar, Senegal (centre) and male 43 cm. t.l., Dakar, Senegal (right). All magnifications x 8.
Lower jaw : Female 46 cm. t.l. x 18 (Diagraph of the first non-functional file).



Text plate 3. *Squalus acanthias* (LINNAEUS, 1758). Female 90 cm. t.l., Belgium.
Upper jaw x 3 ; lower jaw x 10 (Diagraph of the outer most functional file).



Text plate 4. *Eimopterus spinax* (LINNAEUS, 1758). Female 55 cm. t.l., S. Lousy, N.E. Atlantic (upper jaw x 8). Lower jaw x 8 (Diagraph of the first non-functional file).

thickened centrally throughout its length. The outer face is a little higher than the inner face. One or two apertures with some foramina are present at both sides of the apron.

Genus : *Etmopterus* RAFINESQUE, 1810

After COMPAGNO (1984), this genus comprises sixteen species : *Etmopterus baxteri* GARRICK, 1957, *Etmopterus brachyurus* SMITH & RADCLIFFE, 1912, *Etmopterus bullisi* BIGELOW & SCHROEDER, 1957, *Etmopterus decacuspoidatus* CHAN, 1966, *Etmopterus gracilispinis* KREFFT, 1968, *Etmopterus granulatus* (GÜNTHER, 1880), *Etmopterus hillianus* (POEY, 1861), *Etmopterus lucifer* JORDAN & SNYDER, 1902, *Etmopterus polli* BIGELOW & SCHROEDER, 1953, *Etmopterus princeps* COLLETT, 1904, *Etmopterus pusillus* (LOWE, 1839), *Etmopterus schultzi* BIGELOW & SCHROEDER, 1953, *Etmopterus sentosus* BASS, d'AUBREY & KISTNASAMY, 1976, *Etmopterus unicolor* (ENGELHARDT, 1912), *Etmopterus villosus* GILBERT, 1905, *Etmopterus virens* BIGELOW & SCHROEDER, 1953 and the type species *Etmopterus spinax* LINNAEUS, 1758.

Etmopterus spinax (LINNAEUS, 1758)
Pl. 5, T. pl. 4.

Squalus spinax LINNAEUS, 1758, Syst. Nat., éd. 10, 1 : 233.

This species is extremely dignathic heterodont and gradient monognathic heterodont in both upper and lower teeth. The root is always anaulacorhizid.

Upper Jaw

The upper teeth are always multicuspid in having one principal cusp flanked by one to two cusplets. The teeth are not interlocked. The dimensions of the teeth are plurimillimetrical in range.

The crown has an erect, slender principal cusp with a weak basal constriction. Both, mesial and distal cutting edges therefore have a sigmoidal appearance. One or two cusplets always flank the principal cusp. If a second cusplet present, it is only one third as high as the first cusplet. The first cusplet can reach half the height of the principal cusp. The cusplets show the same basal constriction as the principal cusp. They become lower toward the commissure and disappear on the posterior teeth.

On inner face, the principal cusp and cusplets, are weakly convex.

Uvula and inner ornamentation are absent.

On outer face, the principal cusp and cusplets, are flat or slightly convex.

A strong basal ornamentation is present on principal cusp and cusplets by partly branched vertical custules. Apron is absent.

The high inner face of the root is falt, and a small central basal sulcus gives a pseudobilobate appearance to the anaulacorhizid root. A small central aperture is present near the crown-root junction.

The low outer face of the root is divided by the central basal sulcus. Several large foramina are scattered along the crown-root junction.

Lower jaw

The lower teeth are always strongly interlocked, presenting deep inner distal and outer mesial depressions affecting both, crown and root. The root is anaulacorhizid.

The crown has a very strongly inclined triangular principal cusp reaching sometimes beyond the distal root end in anterior teeth. The distal blade is short and joins the principal cusp in a notch. The cutting edges are always smooth.

The inner face of the crown is slightly convex. A flat uvula is present, covering also the upper central and mesial part of the root. There are two particular depressions on the uvula base. Inner ornamentation is absent.

The outer crown face is more or less flat, showing a flat apron reaching half of the root's height and covering the upper central and distal part of the root.

The uvula-root junction is mesio-distally straight. An outer ornamentation is absent.

The root is more or less rectangular.

The inner face is flat with a strong distal depression. There are three apertures present along the uvula-root junction, two under both mesial and distal lower ends of the uvula and one at deeper level in the central part. The outer face of the root shows a strong mesial depression. There are two apertures present, one under the mesial lower end of the uvula and one in the centre of the root. Along the uvula-root junction, there are up to 8 smaller foramina present.

Centroscyllium MÜLLER & HENLE, 1841

This genus comprises (after COMPAGNO, 1984) the following six species : *Centroscyllium fabricii* (REINHARDT, 1825), which is the type species, *Centroscyllium granulatum* GÜNTHER, 1887, *Centroscyllium kamoharai* ABE, 1966, *Centroscyllium nigrum* GARMAN, 1899, *Centroscyllium ornatum* (ALCOCK, 1889) and *Centroscyllium ritteri* JORDAN & FOWLER, 1903.

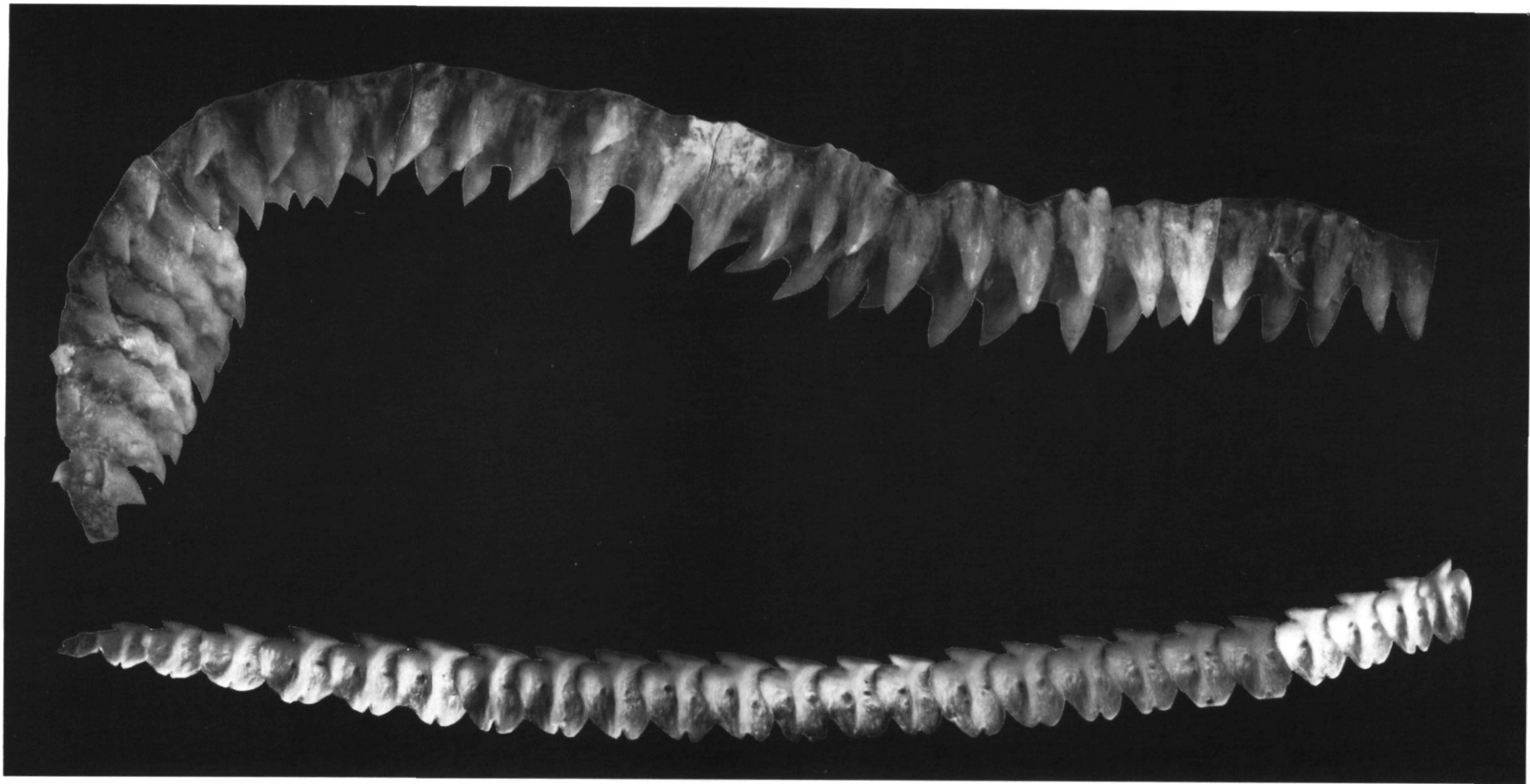
Centroscyllium fabricii (RHEINHARDT, 1825)
Pl. 6, T. pl. 5.

Spinax fabricii REINHARDT, 1825, Overs. K. danske Vidensk. Selsk. Forh., (1824-1825) : 3.

This species is almost homodont but shows a gradient weak monognathic heterodonty by reduction of tooth size toward the commissure. Sexual heterodonty is not existing. The teeth are plurimillimetrical in range.



Text plate 5. Centroscyllium fabricii (REINHARDT, 1825). Female 86 cm. t.l., W. George Bligh, N.E. Atlantic. Upper jaw x 6; lower jaw x 8.



Text plate 6. *Somniosus microcephalus* (BLOCH & SCHNEIDER, 1801). Female 470 cm. t.l., N. Lousy, N.E. Atlantic. Upper jaw x 1; lower jaw x 0.7.

The crown has an erect, slender and triangular principal cusp, flanked by a pair of also erect and slender but lower mesial and distal cusplets. The height of both cusplets is more than half of the height of the principal cusp on anterior and antero-lateral teeth, but only about half the height on latero-posterior teeth. Both, distal and mesial cutting edges of principal cusp and cusplets are smooth. The principal cusp becomes lower and broader based toward the commissure.

The inner face of principal cusp and cusplets is weakly convex, and they have a strong ornamentation. Vertical costules cover the basal half of the principal cusp and the entire length of the cusplets. Distinct reticulated, secondary ornamentation is present between the basal costules, uvula is absent.

The outer face of principal cusp and cusplets is flat to slightly convex and shows the same ornamentation with an extension. Vertical costules reach half the height of the principal cusp and are all over the cusplets and basal reticulation as on inner face.

The root is hemiaulacorhizid and bilobate. The root lobes are rounded at the mesial and distal basal ends. The inner root face shows a broad, deep central pseudo-groove in lower half of the root and a large central aperture near the crown-root junction. At the basal edges of each root lobe, numerous randomly scattered foramina are present.

The outer face shows ten or more foramina along the crown-root junction. The basal part of the inner pseudo-groove is visible.

Genus : *Aculeola* DE BUEN, 1959

The type species of this monotypic genus is *Aculeola nigra*.

Aculeola nigra DE BUEN, 1959
Pl. 7.

Aculeola nigra DE BUEN, 1959, Bol. Mus. Nac. Hist. Nat. Santiago, Chile, 27(3) : 180.

This species is almost homodont but shows a gradient weak monognathic heterodonty by reduction of tooth size toward the commissure. Sexual heterodonty is present in that females have a slightly lower, broader based crown with a more intensely reticulated outer ornamentation. The teeth are plurimillimetrical in range.

The crown has an erect, slender and symmetrical principal cusp. Mesial and distal cusplets are absent, and the cutting edges are smooth.

The principal cusp becomes slightly lower, a little broader based and curves stronger inward near the commissure.

The inner face of the principal cusp is convex and without ornamentation. Uvula is absent.

Outer face of principal cusp is slightly convex, and

shows a strong ornamentation. Long vertical costules reach half way up the principal cusp, or higher. A reticulated, secondary basal ornamentation is present between these costules. Apron is absent.

The root is hemiaulacorhizid but there is no true bilobation. The mesial and distal basal ends are rounded.

The inner face shows a broad shallow pseudo-groove in lower half of the root and a large central aperture near the crown-root junction. Some randomly scattered foramina are present at the basal edge of the root.

The outer face shows up to six foramina along the crown-root junction. The basal part of the inner pseudo-groove is visible.

Genus : *Somniosus* LESUEUR, 1818

This genus comprises the three species *Somniosus rostratus* (RISSO, 1826), *Somniosus pacificus* BIGELOW & SCHROEDER, 1944, and *Somniosus microcephalus* (BLOCH & SCHNEIDER, 1801), of which the latter is the type species. We will also describe, illustrate and discuss *Somniosus rostratus* (RISSO, 1826), because of the discussion amongst several authors on the species existing.

Somniosus microcephalus (BLOCH & SCHNEIDER, 1801)
Pl. 8, 9, T. pl. 6, 7.

Squalus microcephalus BLOCH & SCHNEIDER, 1801, Syst. Ichthyol., Berlin : 135.

This species shows a strong dignathic heterodonty and a weak gradient monognathic heterodonty.

The dimensions of the lower teeth are centrimetrical and those of the upper teeth are hemicentimetrical in range.

Upper jaw.

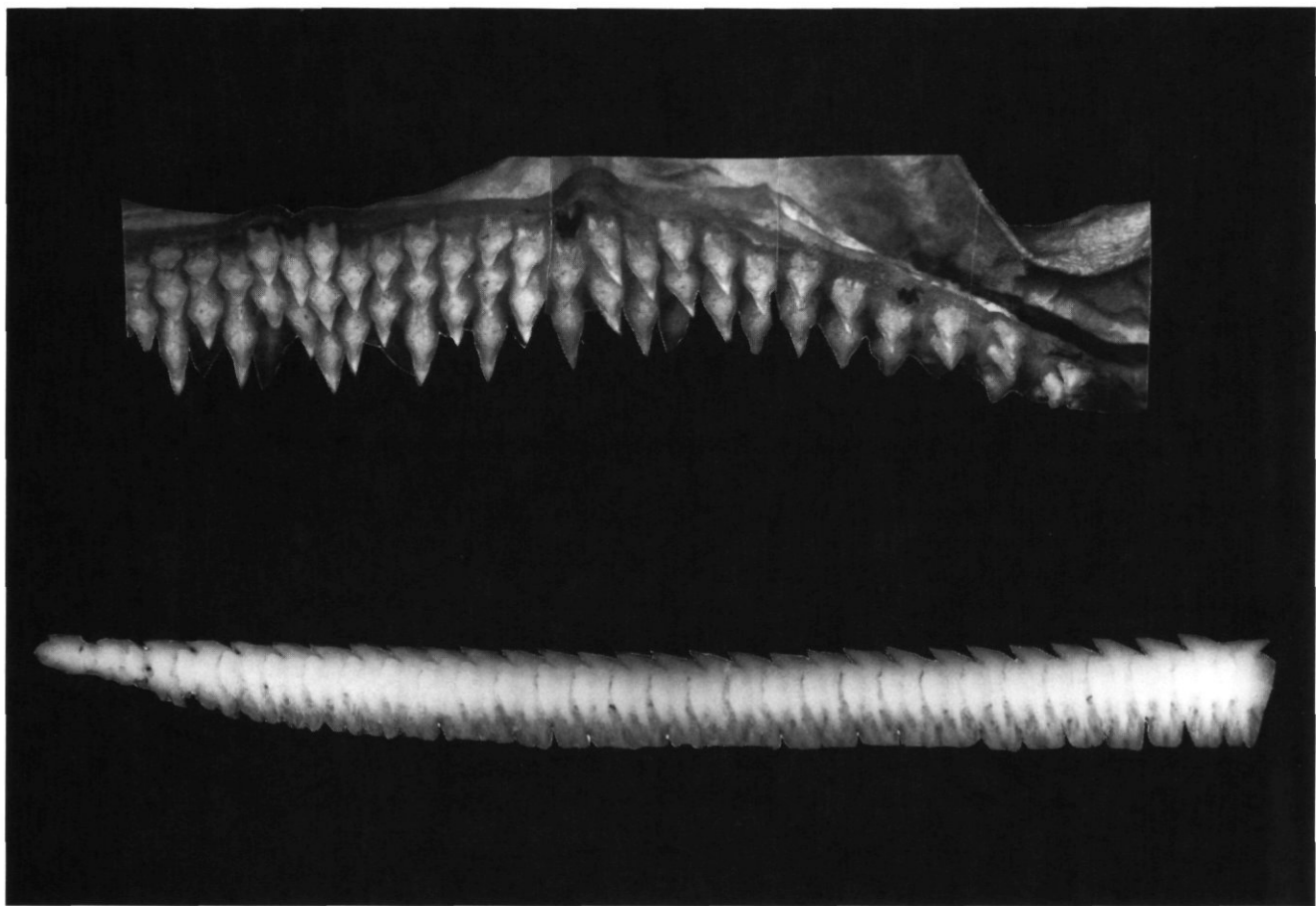
The teeth are slightly compressed, crown and root are vertically elongated.

The crown is twice as high as the crown base width. The teeth have an irregularly shaped, though more or less symmetrical erect crown, that is slightly inclining toward the commissure on latero-posterior teeth. Both mesial and distal cutting edges are undulated but not serrated.

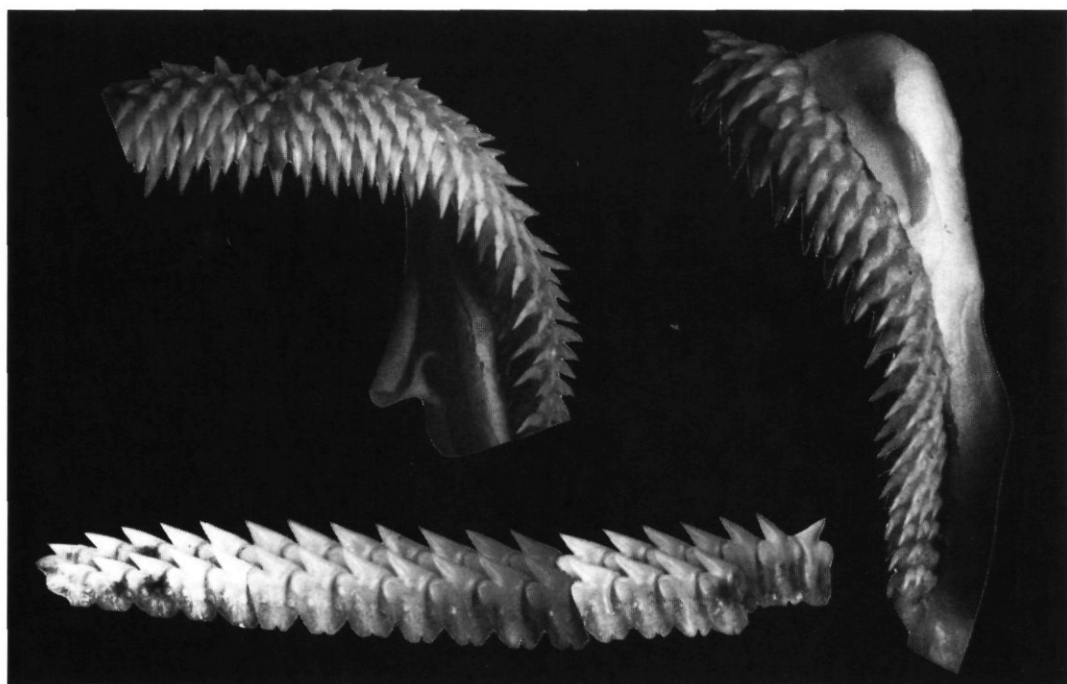
The inner face is strongly convex. Uvula and ornamentation are absent.

The outer face is slightly convex. A prominent, vertically elongated apron is present, forming one part with the root. Near the crown-root junction, some vertical protuberances are present. The pseudoholaulacorhizid root is elongated and divided into two root lobes. Both root lobes have a more or less rectangular appearance. The basal edges are slightly rounded.

The inner face is flat, showing a broad median groove, that includes a large central foramen with five or six



Text plate 7. *Somniosus microcephalus* (BLOCH & SCHNEIDER, 1801). Male 176 cm. t.l., E. Oseille, N.E. Atlantic. Upper jaw x 2; lower jaw x 2. (Diagram of the first non-functional file).



Text plate 8. *Somniosus rostratus* (RISSO, 1826). Male 109 cm. t.l., W. Hebrides, N.E. Atlantic. Upper jaw x 3; lower x 3.

smaller foramina. The root is slightly depressed mesio-distally. Some scattered foramina are present on the root lobes.

The outer face shows on both sides of the apron several randomly scattered foramina. The basal part of the inner median groove is visible.

Lower jaw.

The teeth are very compressed, with a strong distally inclined principal cusp. The mesial cutting edge is slightly arched, while the distal cutting edge joins the distal blade in a notch. The height of the crown is half to a quarter of the crown base width. Both mesial and distal cutting edges are smooth. A true ornamentation on the crown is absent.

The slightly convex, inner face of the crown shows a small, convex uvula, forming one part with the root.

The outer face shows a rather short, triangular apron, also forming one part with the root. The outer surface is a little more convex than the inner one.

The vertically expanded anaulacorhizid root has rounded mesio- and distal-basal ends and is constricted from just below the crown-root junction toward the basal root end. This constriction becomes much stronger toward the commissure.

On the inner face there is a large aperture situated distally besides the uvula. This aperture includes three large foramina. A broad, shallow median sulcus is present. Several foramina are randomly scattered on the flat inner face of the root. Interlocking has caused a strong inner distal depression.

The outer face shows some large apertures at each side of the apron. Near the junction of the apron and root, some vertical protuberances are present.

Interlocking has resulted in a mild outer mesial depression.

Somniosus rostratus (Risso, 1826)

Pl. 10, T. pl. 8.

Scymnus rostratus RISSO, 1826, Hist. nat. princip. prod. Europe Mérid., Paris 3 Poissons : 138.

This species also shows a strong dignathic heterodonty and a weak gradient monognathic heterodonty. The root, however, is always anaulacorhizid.

The dimensions of the lower teeth are hemicentimetrical and those of the upper teeth are plurimillimetrical in range.

Upper jaw.

The teeth are more or less compressed with the root short and the crown vertically elongated.

The triangular, symmetrical crown is three times as high as the crown base width and slightly inclining toward the commissure on latero-posterior teeth. Both, mesial and distal cutting edges are smooth.

The inner face is weakly convex. Uvula is absent. A weak ornamentation is presented by some basal costules.

The outer face is weakly convex. Apron is absent. A strong, reticulated basal ornamentation is present, in which a secondary much finer reticulated ornamentation is included.

The anaulacorhizid root is short and slightly constricted from below the crown-root junction downward. The basal ends are slightly rounded.

The inner face is flat, showing a large central foramen below the crown-root junction. Below this central foramen a second one is present from which a broad sulcus runs to the central basal end of the root.

The outer face is slightly concave and shows two or three large central foramina. Also two or three small scattered mesial and distal foramina are present. The basal part of the inner median groove is visible.

Lower jaw.

The teeth are very compressed, with a triangular, distally inclined principal cusp. The mesial cutting edge is straight and the distal cutting edge joins the distal blade in a notch. Both mesial and distal cutting edges and distal blade are smooth. There is no true ornamentation on the crown. The height of the crown has the dimensions of the crown base length.

The slightly convex inner face of the crown has no true uvula. The outer face shows a rather short, rectangular apron, forming one part with the root.

The vertically elongated anaulacorhizid root has rounded mesial and distal basal ends and is slightly constricted from just below the crown-root junction downward. Three large apertures are present on the inner face, situated on the central, distal and mesial parts along the crown-root junction.

From the central aperture, a broad shallow sulcus runs to the central basal end of the root. One or two small foramina are present in this sulcus. Interlocking has led to a strong inner distal depression.

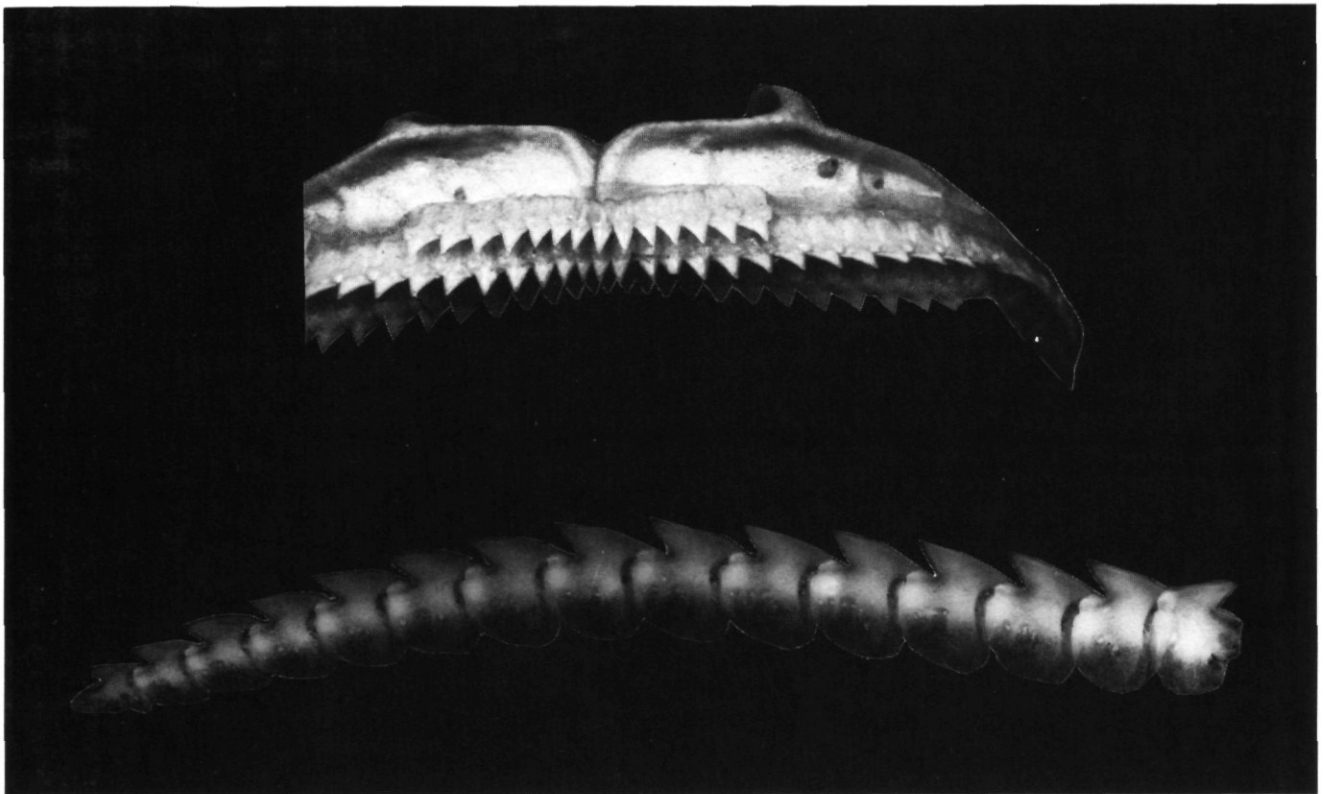
On the outer face, the apron is flanked by a pair of large apertures.

Five to six foramina are present along the crown-root junction. The basal part of the sulcus is visible. Interlocking has resulted in a mild outer mesial depression.

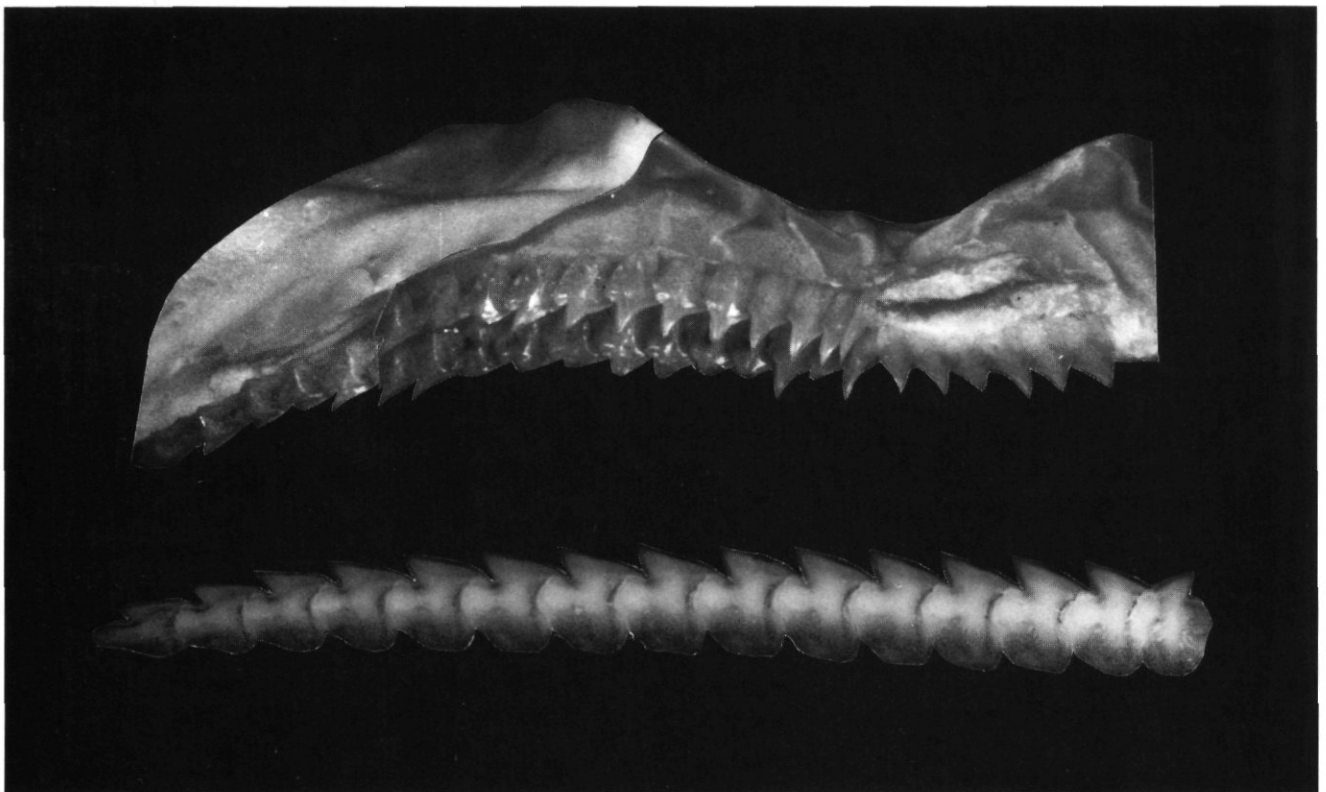
Genus : *Centrophorus* MÜLLER & HENLE, 1837

The genus *Centrophorus* comprises (after COMPAGNO, 1984) the following eight species : *Centrophorus acus* GARMAN, 1906, *Centrophorus granulosis* (BLOCH & SCHNEIDER, 1801), *Centrophorus harrissoni* McCULLOCH, 1915, *Centrophorus lusitanicus* BOCAGE & CAPELLO, 1864, *Centrophorus moluccensis* BLEEKER, 1860, *Centrophorus niaukang* TENG, 1959, *Centrophorus squamosus* (BONNATERRE, 1788), *Centrophorus tessellatus* GARMAN, 1906, and *Centrophorus uyato* (RAFINESQUE, 1810).

The type species is *Centrophorus granulosis* (BLOCH & SCHNEIDER, 1801).



Text plate 9. Centrophorus granulosus (BLOCH & SCHNEIDER, 1801). Male 86 cm., t.l. Nice, Mediterranean Sea. Upper jaw x 3. Female 97 cm. t.l. Motril, Mediterranean, Diagraph of the lower functional file (x 5).



Text plate 10. Centrophorus squamosus (BONNATERRE, 1788). Male 92 cm. t.l., S.W. Rockall, N.E. Atlantic. Upper jaw x 4; lower jaw : Diagraph of the functional file (x 5). Formerly Lepidorhinus squamosus (BONNATERRE, 1788).

Centrophorus granulosus (BLOCH & SCHNEIDER, 1801)
Pl. 11, T. pl. 9.

Squalus granulosus BLOCH & SCHNEIDER, 1801, Syst. Ichthyol. : 135.

This species shows a strong dignathic heterodonty and a weak gradient monognathic heterodonty. The root is always anaulacorhize.

The dimensions of the lower teeth are hemicentimetrical and those of the upper teeth are plurimillimetrical in range.

Upper jaw

The teeth have a triangular principal cusp and a small distal blade joins the distal cutting edge in a notch. The principal cusp inclines slightly toward the commissure on lateral and posterior teeth. Both distal and mesial cutting edges are smooth and slightly sigmoidal. A constriction from below the crown-root junction downward is stronger developed mesially. The mesial and distal basal ends are rounded.

The inner face of the crown is convex and is about as high as the crown base width. A small central basal uvula is present.

The outer face is slightly convex and narrow. A vertically elongated apron is present, reaching almost the central root end. The inner face of the root has a depressed crown-root junction. The root becomes strongly convex directly below this depression, forming a longitudinal ridge. A large central aperture is present on or just below the ridge and is the beginning of a broad, shallow sulcus running to the central root end. A few small foramina are on the crown-root junction and a large foramen is present in the mesial region.

The outer face of the root is flat with some small ridges near the apron. Along the apron, one major mesial aperture is present near the crown-root junction and another one on the mesio-central root end. Also one or two minor foramina are present along the apron.

Lower jaw

The teeth have a strong, distally inclined principal cusp, and a small distal blade joins the distal cutting edge in a notch. The arched mesial cutting edge is slightly serrated, while the distal one and the distal blade are smooth. A constriction from below the crown-root junction downward is stronger developed mesially. The mesial basal end is almost rectangular, while the distal basal end is rounded.

The inner face of the crown is convex, and its height is about half of the crown base width. A small central basal uvula is present.

The outer face is slightly convex, and a narrow, vertically elongated apron is present reaching half way toward the central root part.

The inner face of the root has a depressed crown-root junction. The root becomes strongly convex directly below this depression, forming a longitudinal ridge. A large semicentral aperture is present on the ridge,

situated mesially aside the apron. It is the origin of a broad, shallow sulcus running to the central root end. Few small foramina are on the distal region of the crown-root junction. On the mesial part, one large foramen and two or three minor foramina are present. The inner distal depression is only present in the region of the crown-root junction as a result of interlocking. The outer face of the root is flat with some small ridges near the apron. Along the apron, one or two major mesial apertures are present near the crown-root junction and eight to ten minor foramina. Two or three major apertures with some minor ones are on the distal part near the crown-root junction. The mesial depression is well developed as a result of interlocking.

Genus : *Deania* JORDAN & SNYDER, 1902

The genus *Deania* comprises (after COMPAGNO, 1984) the four species : *Deania calcea* (LOWE, 1839), *Deania histricosa* GARMAN, 1906, *Deania profundorum* (SMITH & RADCLIFFE, 1912) and *Deania quadrispinosum* (MCGULLOCH, 1915). The type species is *Deania calcea*.

Deania calcea (LOWE, 1839)

Pl. 13, Tpl. 11.

Acanthidium calceum LOWE, 1839, Trans. Zool. Soc. London, 3(1) : 19.

This species shows a strong dignathic heterodonty and a weak gradient monognathic heterodonty. The root is always anaulacorhizid.

The dimensions of lower and upper teeth are plurimillimetrical in range.

Upper jaw

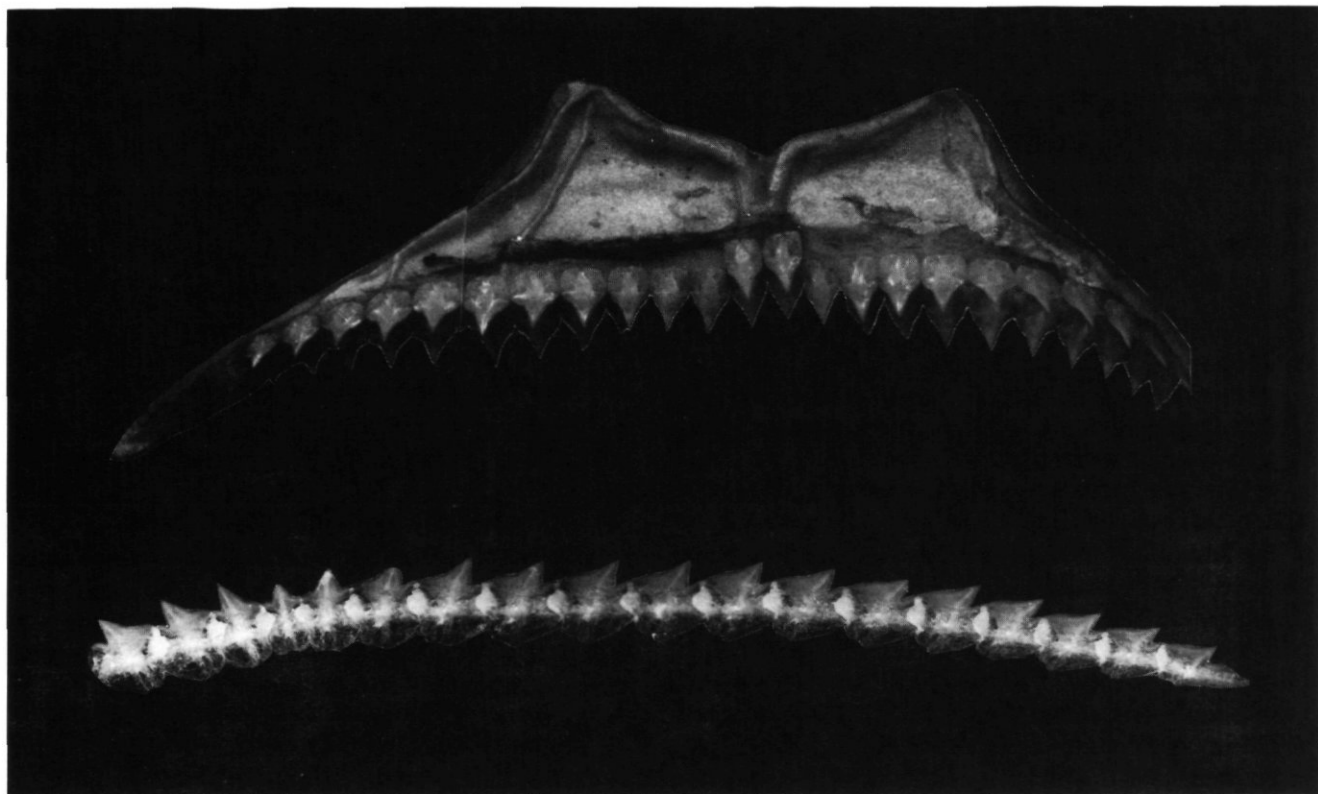
The teeth have a triangular principal cusp and a small distal and mesial blade both joining the principal cusp in a notch. The principal cusp inclines slightly toward the commissure on lateral and posterior teeth. Both distal and mesial cutting edges are smooth.

The inner face of the crown is convex and its height is about equal to the crown base width. A small central basal uvula is present.

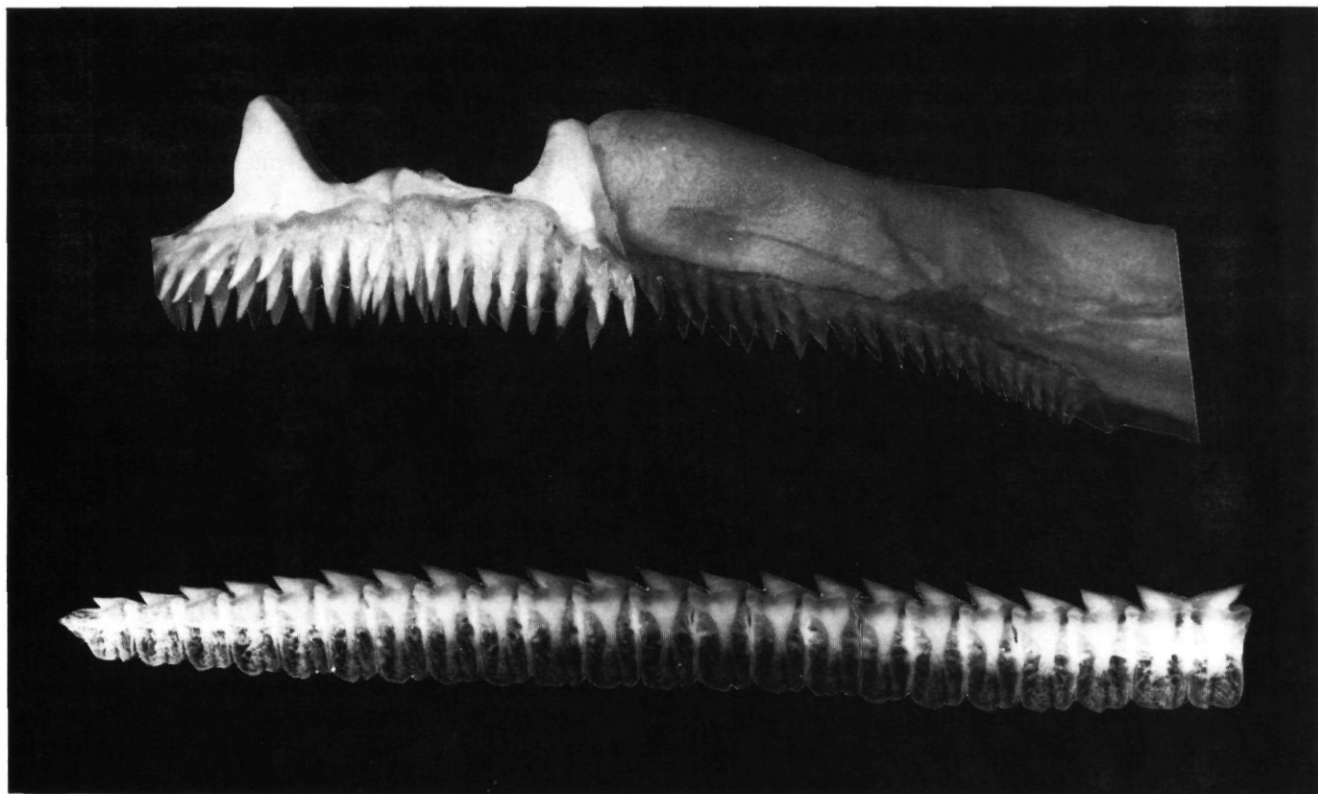
The outer face is slightly convex, and a triangular, vertically elongated apron with a rounded end is present, reaching almost the central root end.

The inner face of the root has a depressed crown-root junction. Directly below this depression the root becomes strongly convex, forming a longitudinal ridge. A large central aperture is situated on the ridge. A second aperture is present below this aperture, which is the origin of a broad, shallow sulcus running to the central root end. Two to four small foramina are on the crown-root junction at both sides of the central aperture.

The outer face of the root is flat. A major mesial and distal aperture is present along the apron near the crown-root junction.



Text plate 11. Deania calcea (LOWE, 1813). Female 107 cm. t.l., W. Hebrides, N.E. Atlantic. Upper jaw x 4; lower jaw : Diagraph of the first non-functional file (x 5).



Text plate 12. Centroscymnus coelolepis BOCAGE & CAPELLO, 1864. Male 85 cm. t.l., N. Bille Bailey, N.E. Atlantic. Upper jaw x 5; lower jaw : Diagraph of the first non-functional file (x 6).

Lower jaw

The teeth have a strong, distally inclined principal cusp and a small distal blade joining its distal cutting edge in a notch. The mesial and distal cutting edges are smooth. The low root has a constriction from below the crown-root junction downward, that is stronger mesially. The mesial basal end is narrower rounded than the distal basal end.

The inner face of the crown is convex, and its height is about half of the crown base width. A small central basal uvula is present.

The outer face is slightly convex, and a triangular, basally rounded apron is present reaching almost the central root end.

The inner face of the root has a depressed crown-root junction. Directly below this depression the root becomes strongly convex, forming a longitudinal ridge. Below the apron, a large central aperture is present on the ridge. A second aperture appears below this aperture, forming the origin of a broad, shallow sulcus running to the central root end. A few small foramina are on the distal region of the crown-root junction. One large foramen and three to six minor foramina are present on the mesial part.

The inner distal depression is only present in the region of the crown-root junction. Two or three major apertures are on the distal part near the crown-root junction. Interlocking has led to a strong mesial depression.

Genus : *Centroscymnus* BOCAGE & CAPELLO, 1864

The genus *Centroscymnus* comprises (after COMPAGNO, 1984) the following eight species : *Centroscymnus coelolepis* BOCAGE & CAPELLO, 1864, *Centroscymnus crepidater* (BOCAGE & CAPELLO, 1864, *Centroscymnus cryptacanthus* REGAN, 1906, *Centroscymnus macracanthus* REGAN, 1906, *Centroscymnus owstoni* GARMAN, 1906 and *Centroscymnus plunketi* (WAITE, 1900).

The type species is *Centroscymnus coelolepis*. Additionally *Centroscymnus crepidater* (BOCAGE & CAPELLO, 1864) was examined. Because so many remarkable differences were discovered between both species, also *Centroscymnus crepidater* will be described below, along with comments on its generic status.

Centroscymnus coelolepis BOCAGE & CAPELLO, 1864
Pl. 14, T. pl. 12.

Centroscymnus coelolepis, BOCAGE & CAPELLO, 1864,
Proc. Zool. Soc. London, 24 : 263.

This species has a strong dignathic heterodonty and a weak gradient monognathic heterodonty. The root is anaulacorhizid. Both upper and lower teeth are plurimillimetrical in range.

Upper jaw

The teeth have an elongated, basally constricted, narrow principal cusp. Cusplets are absent. The mesial and distal cutting edges are slightly sigmoidal. The root is bilobate. The inner face of the crown is convex. Ornamentation and uvula are absent.

The outer face of the crown is flat to slightly convex. Apron is absent. The crown base is strongly depressed, developing a mesial and distal vertical ridge on anterior teeth. On lateral teeth, from the "eye"-position toward the commissure, the basal depression is absent and mesial and distal ridges join in a pseudo-apron. A true ornamentation is absent.

The inner face of the root is flat, showing one large central aperture near the crown-root junction and one on the basal part of the root.

The outer face of the root has a strong central root depression. One or two mesial and distal apertures are present.

Lower jaw

The teeth are strongly compressed. The slightly sigmoidal principal cusp is strongly inclined toward the commissure, joining the distal blade in a notch. The crown is half as high as the crown base width. The rectangular root is constricted from the crown-root junction downward and is vertically elongated. The mesial and distal root ends are slightly rounded.

The inner face of the crown is flat to very weakly convex. The basal part is slightly depressed. A true uvula is absent.

The outer face of the crown is also weakly convex. A vertically elongated apron is present, that has a fair constriction at half of its length. The apron is not overhanging the root but forms one part together with it.

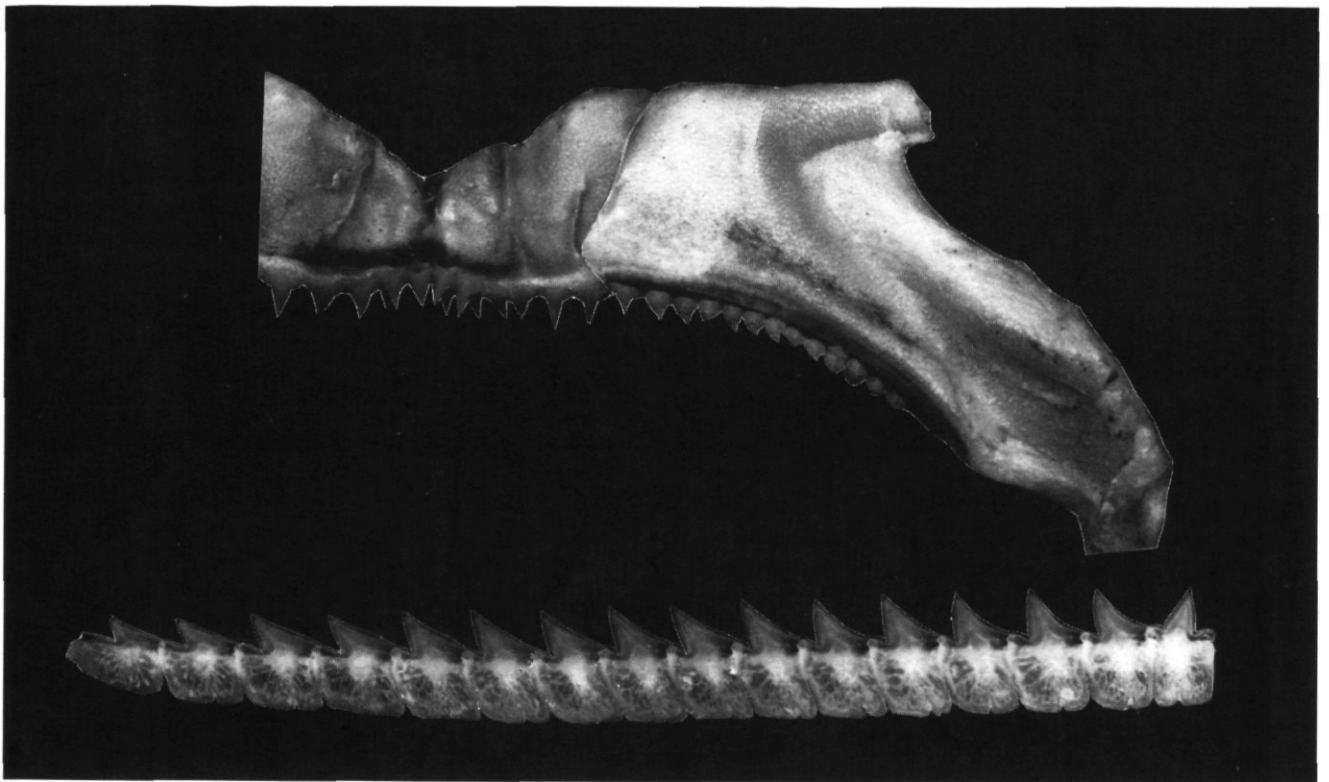
The inner face of the root shows near the crown-root junction a large central and large mesial aperture. One or two distal foramina are also present near the crown-root junction. A second large central aperture is present, in the middle of the root forming the origin of a broad, shallow sulcus running toward the central root base. A short distal depression is only present directly below the distal blade, as a result of interlocking.

The outer face of the root shows a very large mesial aperture and one or two smaller ones, as well as two or three large distal apertures along with one or two smaller ones. The latter are vertically arranged. The basal part of the sulcus is visible. The mesial depression is well developed.

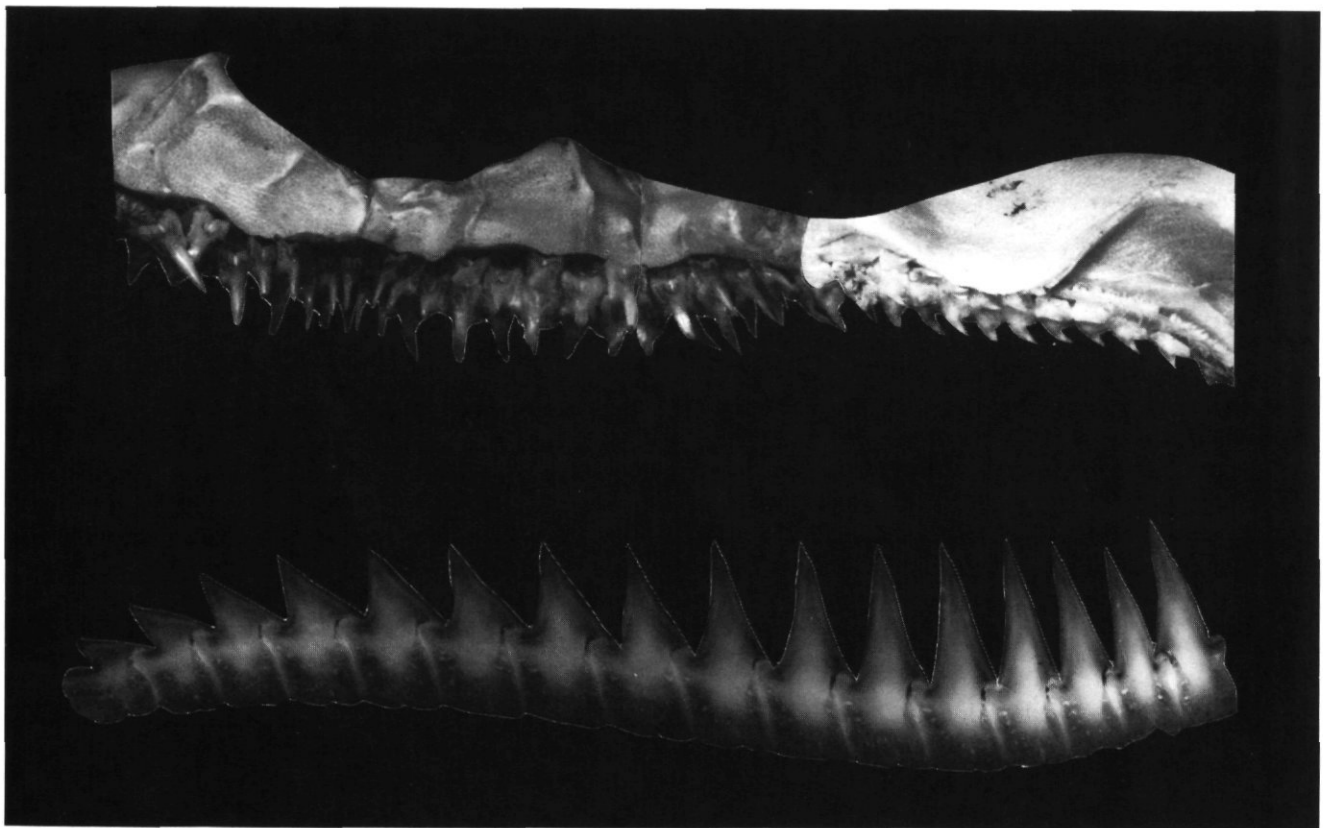
Centroscymnus crepidater (BOCAGE & CAPELLO, 1864)
Pl. 15, T. pl. 13.

Centrophorus crepidater BOCAGE & CAPELLO, 1864
Proc. zool. Soc. London, 24 : 262.

This species has a strong dignathic heterodonty and a weak gradient monognathic heterodonty. The root is



Text plate 13. *Centroscyrnus crepidater* (BOCAGE & CAPELLO, 1864). Female 84 cm. t.l., Porcupine, N.E. Atlantic. Upper jaw x 4; lower jaw : Diagram of the first non-functional file (x 6).



Text plate 14. *Scymnodon ringens* BOCAGE & CAPELLO, 1864. Female 102 cm. t.l., W. Hebrides, N.E. Atlantic. Upper jaw x 3; lower jaw : Diagram of the first non-functional file (x 4).

anulacorhizid. Both, upper and lower teeth are plurimillimetrical in range.

Upper jaw

The teeth have an elongated, narrow principal cusp. Cusplets are absent. The mesial and distal cutting edges are slightly sigmoidal. The root is quadrangular. The inner face of the crown is convex. Uvula is absent. An ornamentation is presented by short vertical costules. The outer face of the crown is flat to slightly convex. Apron is absent. The crown base is depressed with a mesial and distal vertical ridge on anterior teeth. On lateral teeth, from the "eye"-position toward the commissure, the basal depression is absent and mesial and distal ridges join in a pseudo-apron. A true ornamentation is absent, but some scattered basal costules are present.

The inner face of the root joins the crown surface in an angle. One large central aperture is present near the crown-root junction.

The outer face of the root has a central root depression. Three or four central apertures are present.

Lower jaw

The teeth are strongly compressed. The sigmoidal principal cusp is inclined toward the commissure, but its distal cutting edge tends to be almost vertical and joins the distal blade in a notch. The rectangular root is narrowing from just below the crown-root junction downward, becoming more oblique toward the commissure.

The inner face of the crown is flat to very weakly convex. The basal part is slightly depressed. A true uvula is absent.

The outer face of the crown is also weakly convex. A short quadrangular apron is present. The apron is not overhanging the root but forms one part with it. The crown is as high as the crown base width.

The inner face of the root is strongly convex near the crown-root junction, forming a longitudinal ridge. A central and mesial aperture is situated on the ridge. Sulcus is absent. A distal depression, as result of interlocking, is hardly developed.

The outer face of the root shows numerous foramina, mainly surrounding the apron. The upper mesial and distal foramina are much larger than the basal ones. A mesial depression, as result of interlocking, is hardly developed.

Genus : *Scymnodon* BOCAGE & CAPELLO, 1864

The genus *Scymnodon* comprises the three species *Scymnodon ringens* BOCAGE & CAPELLO, 1864, *Scymnodon obscurus* (VAILLANT, 1888) and *Scymnodon squamulosus* (GÜNTHER, 1877). The type species is *Scymnodon ringens*.

Scymnodon ringens BOCAGE & CAPELLO, 1864, Proc. zool. Soc. London, 24 : 263.

Pl. 16, T. pl. 14

This species has a strong dignathic heterodonty and a weak gradient monognathic heterodonty. The root is anulacorhizid. The upper teeth are hemicentimetrical and the lower teeth centrimetrical in range.

Upper jaw

The teeth have an elongated, narrow principal cusp. Cusplets are absent. The mesial and distal cutting edges are slightly sigmoidal. The root is quadrangular. The principal cusp inclines toward the commissure in latero-posterior teeth. The inner face of the crown is convex. Uvula is absent, as well as an inner ornamentation. The outer face of the crown is flat or slightly convex. Apron is absent. The crown base is depressed, with a mesial and a distal vertical ridges. An outer ornamentation is presented by some scattered basal costules on anterior and antero-lateral teeth and well developed vertical basal costules on lateral and commissural teeth.

The inner face of the root joins the crown surface in an angle. Apertures or foramina are absent. A short, narrow and deep basal sulcus is present.

The outer face of the root has a central root depression. Some randomly scattered foramina are present on latero-posterior and commissural teeth.

Lower teeth

The teeth are strongly compressed. The triangular crown is as high as the crown base wide.

The sigmoidal principal cusp is inclined toward the commissure but its distal cutting edge tends to be almost vertical and joins the distal blade in a notch. The rectangular root is narrowing from below the crown-root junction downward becoming more oblique toward the commissure.

The inner face of the crown is flat to very weakly convex. The basal part is slightly depressed. A true uvula is absent.

The outer face of the crown is also weakly convex. A short quadrangular apron is present. The apron is not overhanging the root but forms one part with it.

The inner face of the root is strongly convex near the crown-root junction, forming a longitudinal ridge. A central and mesial aperture is situated on the ridge. A short basal sulcus is present.

A distal depression, as result of interlocking, is poorly developed.

The outer face of the root shows numerous foramina, mainly surrounding the apron. The upper mesial and distal foramina are more or less vertically arranged and horizontally expanded, being much larger than the basal ones. The mesial depression is poorly developed.

Genus : *Scymnodalatias* GARRICK, 1956

The genus *Scymnodalatias* comprises the four species *Scymnodalatias albicauda* TANIUCHI & GARRICK, 1986, *Scymnodalatias oligodon* KUKUJEV & KONOVA-

LENKO, 1988, *Scymnodalantias garricki* KUKUJEV & KONOVALENKO, 1988 and *Scymnodon sherwoodi* (ARCHEY, 1921); Type species: *Scymnodon sherwoodi*. Because the type species was not available in time for examination, *Scymnodalantias albicauda* was used for description, which seems to have a similar tooth morphology.

Scymnodalantias albicauda TANIUCHI & GARRICK, 1986
Pl. 17, T. pl. 15.

Scymnodalantias albicauda, TANIUCHI & GARRICK, 1986, Japanese Journ. of Ichthyology 33(2) : 119-134.

This species has a strong dignathic heterodonty and a weak gradient monognathic heterodonty. The root is anaulacorhizid. The upper teeth are hemicentrimetrical and the lower teeth centrimetrical in range.

Upper jaw

The teeth have an elongated, narrow principal cusp, that has a slight constriction near the crown base. Cusplets are absent. The mesial and distal cutting edges are strongly sigmoidal. The root is bilobated on anterior and lateral teeth becoming quadrangular toward the commissure. The principal cusp inclines toward commissure in latero-posterior teeth. The inner face of the crown is strongly convex. Uvula is absent, as well as inner ornamentation. The outer face of the crown is slightly convex. Apron is absent. The crown base is depressed, with a mesial and distal vertical ridge. Outer ornamentation is absent.

The inner face of the root joins the crown surface in an angle. Apertures or foramina are absent. A short, narrow and deep basal sulcus is present.

The outer face of the root has a central root depression. Some randomly scattered foramina are present on latero-posterior and commissural teeth.

Lower teeth

The teeth are strongly compressed. The height of the triangular crown equals the crown base width.

The slightly arched principal cusp is inclined toward the commissure, joining the distal blade in a notch. The rectangular root is narrowing from below the crown-root junction downward becoming more oblique toward the commissure.

The inner face of the crown is flat to very weakly convex. The basal part is slightly depressed. A true uvula is absent.

The outer face of the crown is also weakly convex. A relatively narrow, short quadrangular apron is present. The apron is not overhanging the root but forms one part with it.

The inner face of the root is strongly convex near the crown-root junction, forming a longitudinal ridge. A central and mesial aperture is situated on the ridge. A

short basal sulcus is present.

A distal depression, as result of interlocking, is poorly developed. The outer face of the root shows numerous foramina, mainly surrounding the apron. The upper mesial and distal foramina are more or less vertically arranged and horizontally expanded, being much larger than the basal ones. The mesial depression is poorly developed.

Genus : *Isistius* GILL, 1864

This genus comprises the species *Isistius plutodus* GARRICK & SPRINGER, 1964 and *Isistius brasiliensis* (QUOY & GAIMARD, 1824), of which the latter is the type species.

Isistius brasiliensis (QUOY & GAIMARD, 1824)
Pl. 18, T. pl. 16.

Scymnus brasiliensis QUOY & GAIMARD, 1824, Zoologie, voy. Uranie et Physicienne, 1817-20 : 198.

This species has a strong dignathic heterodonty and a weak gradient monognathic heterodonty. The root is anaulacorhizid. The lower teeth are strongly interlocked. The upper teeth are plurimillimetrical and the lower ones are centrimetrical in range.

Upper jaw

The teeth have an elongated principal cusp. Cusplets are absent. The mesial and distal cutting edges are slightly curved. The root is pseudobilobated by a deep sulcus, having quadrangular pseudo-lobes. The root is constricted just below the crown-root junction downward. The crown is slightly distally inclined in lateral and posterior teeth and 50% higher than the width of its base.

The inner face of the crown is slightly convex. Uvula is absent, as well as inner ornamentation.

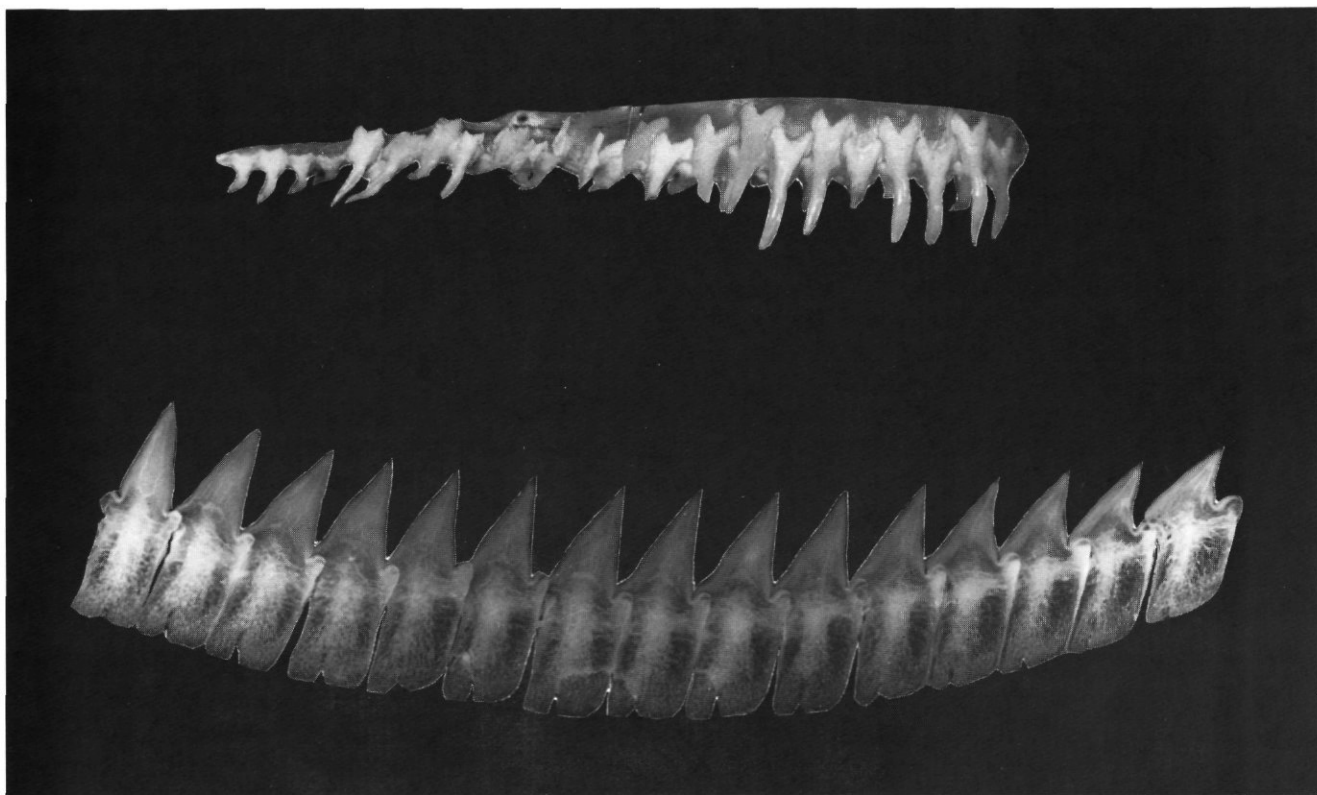
The outer face of the crown is flat to slightly convex and a triangular, basally rounded apron is present. Outer ornamentation is absent.

The inner face of the root shows a longitudinal ridge near the crown-root junction, on which a large central aperture is present. A narrow mesial depression is present below this ridge. A short, broad and deep basal sulcus is present.

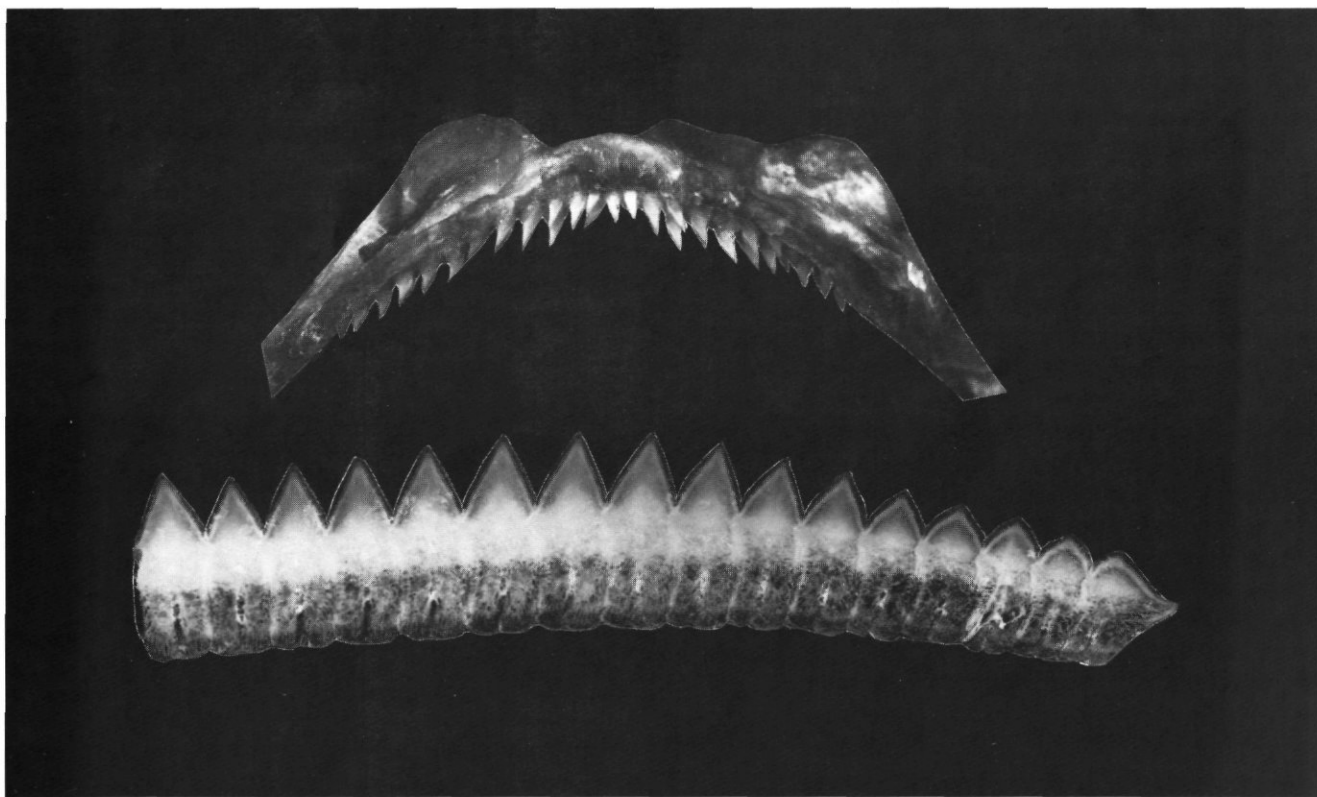
The outer face of the root has three foramina near the crown-root junction : two foramina flanking the apron and one central foramen below the apron. The central basal sulcus is also present on the outer face.

Lower jaw

The strongly compressed teeth are always interlocked, presenting deep, vertically long, inner distal and outer mesial depressions. Distal and mesial blades are absent. The crown inclines slightly toward the commissure in latero-posterior and posterior teeth.



Text plate 15. *Scymnodalatias albicauda* (TANIUCHI & GARRICK, 1986). Sex unknown 97.2 cm t.l., Hokitika Canyon, New Zealand. Upper jaw : uncomplete file x 3 ; lower jaw : Diagraph x 4 (The commissural tooth is missing).



Text plate 16. *Isistius brasiliensis* (QUOY & GAIMARD, 1824). Upper jaw : Female 41 cm t.l., Dakar, Senegal x 5. Lower jaw : Diagraph x 6, Female 24 cm t.l. Hawai Island.

The inner face of the crown is flat to very weakly convex and is as high as the crown base width. Uvula is absent.

The outer face of the crown is also weakly convex. A vertically long quadrangular apron covers the central and distal parts of the root. The apron is not overhanging the root but forms one part with it.

The inner face of the root is vertically long and very flat, showing a central aperture and another smaller distal foramen with sometimes a small mesial foramen near the crown-root junction, a large, elongated central aperture is present. A distal depression, as result of interlocking, is well developed. The outer face of the root shows a central aperture near the crown-root junction, that is the origin of a vertically long central depression. A smaller distal aperture is present also near the crown-root junction. A well developed mesial depression is present as a result of interlocking.

Genus : *Euprotomicroides* HULLEY & PENRITH, 1966

The type species of this monotypic genus is *Euprotomicroides zantedeschia* HULLEY & PENRITH, 1966.

Euprotomicroides zantedeschia HULLEY & PENRITH, 1966

Pl. 19, T. pl. 17.

Euprotomicroides zantedeschia HULLEY & PENRITH, 1966, Bull. mar. Sci., 16(2) : 222.

This species has a strong dignathic heterodonty and a weak gradient monognathic heterodonty. The root is anaulacorhizid. The lower teeth are strongly interlocked. Both upper and lower teeth are plurimillimetrical in range.

Upper jaw

The teeth have a very elongated, narrow principal cusp, that is symmetrical on the anterior positions and sigmoidal on lateral and posterior positions. Cusplets are absent.

The root is pseudobilobated by an arched root base, having rounded pseudo-lobes. The crown is more than five times higher than the width of its base.

The inner face of the crown is very convex. Uvula is absent, as well as an inner ornamentation.

The outer face of the crown is convex. Apron and outer ornamentation are absent.

The inner face of the root shows a convex crown-root junction, on which a large central aperture is present. Downward, the surface is flat, sometimes showing a short, shallow basal sulcus with one or two foramina in it.

The outer face of the root has a central aperture with two or three mesial and distal foramina along the crown-root junction. The central part between the root's pseudo-lobes is depressed.

Lower jaw

The strongly compressed teeth are always interlocked, presenting deep, vertically long, inner distal and outer mesial depressions. Distal and mesial blades are present on the symphyseal tooth. The mesial blade is absent on the other teeth. The crown inclines slightly toward the commissure in latero-posterior and posterior teeth. The principal cusp is over twice as high as its base width. The root has a slightly rounded base with rounded basal ends.

The inner face of the crown shows a slightly convex principal cusp. Uvula is absent.

The outer face of the crown is also weakly convex. A broad, vertically long rounded apron covers the central and distal parts of the root. The apron is not overhanging the root but forms one part with it.

The inner face of the root is vertically long and very flat, showing a central aperture flanked by one smaller mesial and one distal foramen near the crown-root junction. The distal depression, as a result of interlocking, is well developed.

The outer face of the root shows a large central aperture with two or three mesial and distal foramina along the crown-root junction. A well developed mesial depression is present as a result of interlocking.

Genus : *Euprotomicrus* GILL, 1864

The type species of this monotypic genus is *Euprotomicrus bispinatus* (QUOY & GAIMARD, 1824).

Euprotomicrus bispinatus (QUOY & GAIMARD, 1824)
Pl. 20, T. pl. 18.

Scymnus bispinatus QUOY & GAIMARD, 1924, Zoologie, Voy. Uranie et Physicienne, 1817-20 : 197.

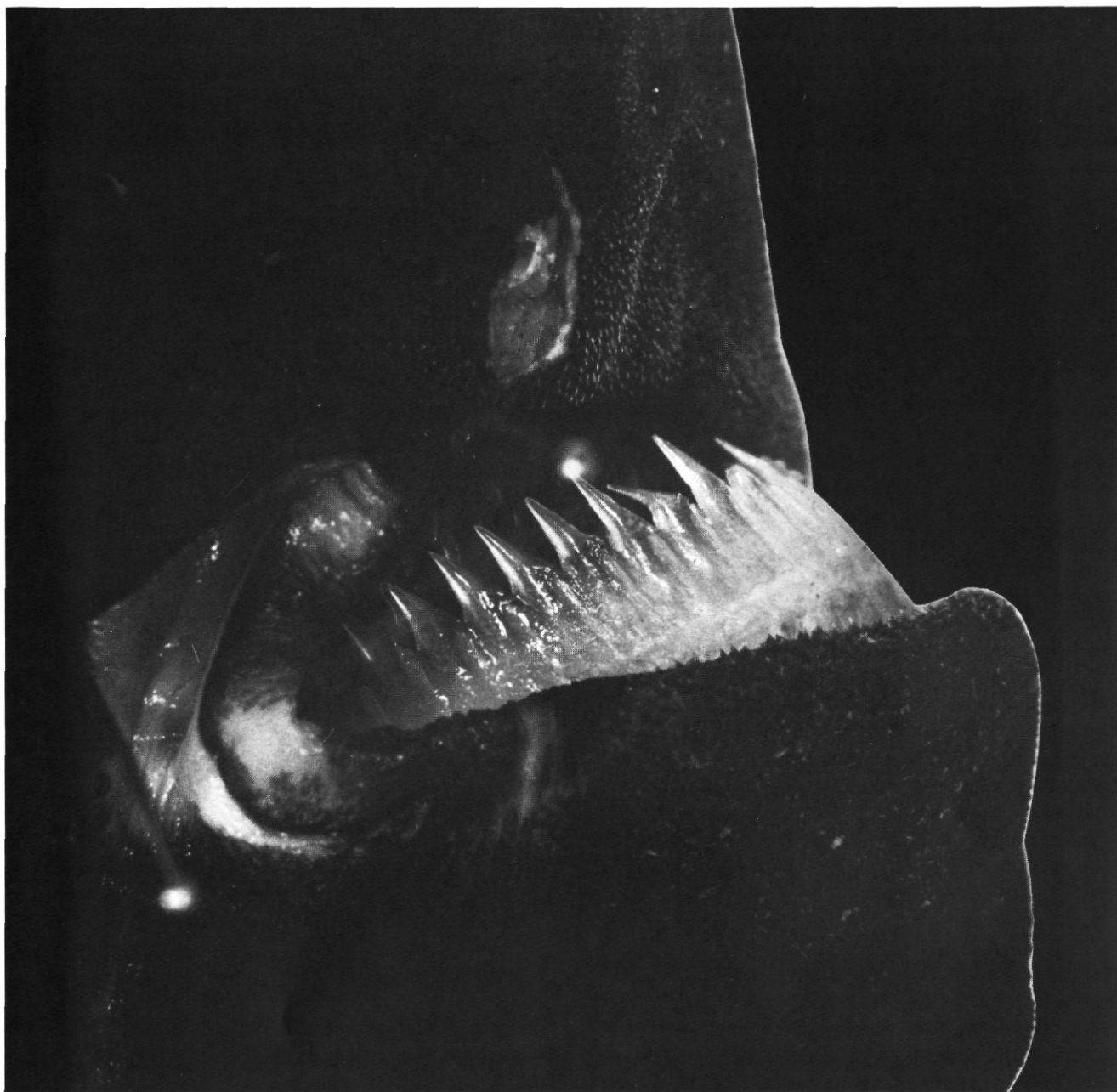
This species has a strong dignathic heterodonty and a weak gradient monognathic heterodonty. A weak sexual heterodonty is present in lower teeth by a slightly sigmoidal mesial cutting edge of the principal cusp in males and an arched mesial cutting edge in females. The root is anaulacorhizid. The lower teeth are strongly interlocked. Both upper and lower teeth are plurimillimetrical in range.

Upper jaw

The teeth have a very elongated, narrow principal cusp, that is constricted just above the crown-root junction. Mesial and distal cutting edges therefore are sigmoidal. Cusplets are absent. The teeth become lower and broader based toward the commissure.

The root is pseudobilobated by an arched root base, having rounded pseudo-lobes. The lateral teeth have a shorter distal pseudo-lobe. The crown is over three times as high as the width of its base.

The inner face of the crown is very convex. Uvula is absent. An inner ornamentation is present by fine, short basal costules.



Text plate 17. *Euprotomicroides zantedeschia* HULLEY & PENRITH, 1966. Male 41.6 cm. t.l., S.W. Atlantic. By courtesy of Dr. M. STEHMANN, I.S.H. Hamburg, Germany (x 5).

The outer face of the crown is convex. The basal constriction has caused a mesial and a distal ridges. The crown-root junction is strongly arched and the crown has formed an apron, which is divided into a mesial and a distal pseudolobe, that both are vertically long and narrow.

The inner face of the root is flat with a slight central, basal depression showing a large central aperture near the crown-root junction. One or two foramina are present on the root's pseudo-lobes.

The outer face of the root has a strong central depression, in which a very large central aperture is present. Both pseudo-lobes have a central foramen asides the apron.

Lower jaw

The strongly compressed teeth are always interlocked, presenting deep, vertically long, inner distal and outer mesial depressions. Distal and mesial blades are present on the symphyseal tooth. The mesial blade is absent on the other teeth. The crown inclines slightly toward the commissure in latero-posterior and posterior teeth. The principal cusp is over twice as high as its base width. Mesial and distal cutting edges are sigmoidal. The root has an arched base with rounded basal ends.

The inner face of the crown shows a slightly convex principal cusp. Uvula is absent.

The outer face of the crown is also weakly convex. The crown base is strongly arched; the apron is consequently

divided into a mesial and a distal pseudo-lobe. On lateral teeth the mesial apron is narrower than the distal one. Some basal, vertical costules are present.

The inner face of the root is vertically long and very flat, showing a central aperture. A distal depression, as a result of interlocking, is well developed.

The outer face of the root shows a very large central aperture. A foramen is present also at the junction of the pseudo-lobes and the root. A well developed mesial depression is present as a result of interlocking, in which one or two foramina are present along the crown-root junction.

Genus : *Squaliolus* SMITH & RADCLIFFE, 1912

The type species of this genus is *Squaliolus laticaudus* SMITH & RADCLIFFE, 1912. *Squaliolus aliae* TENG, 1959 has recently been revalidated from synonymy with *Squaliolus laticaudus* by SASAKI & UYENO (1987).

Squaliolus laticaudus SMITH & RADCLIFFE, 1912
Pl. 21.

Squaliolus laticaudus SMITH & RADCLIFFE, 1912,
Proc. U. S. nat. Mus., 41 : 684.

This species has a strong dignathic heterodonty and a weak gradient monognathic heterodonty. A weak sexual heterodonty is present in lower teeth by a slightly sigmoidal mesial cutting edge of the principal crown in males and a straight mesial cutting edge in females. The root is anaulacorhizid. The lower teeth are strongly interlocked. Both upper and lower teeth are plurimillimetric in range.

Upper jaw

The teeth have a very elongated, narrow principal cusp, that is constricted just above the crown-root junction. Mesial and distal cutting edges therefore are sigmoidal. Cusplets are absent. The teeth become lower and broader based toward the commissure.

The root is pseudobilobated by an arched root base having rounded pseudo-lobes. The lateral teeth have a shorter distal pseudo-lobe. The crown is over three times as high as its base width.

The inner face of the crown is very convex. Uvula is absent. An inner ornamentation is present by fine, short basal costules.

The outer face of the crown is convex. The basal constriction has caused a mesial and distal ridge. The crown-root junction is strongly arched and the crown has formed an apron, which is divided into a mesial and distal pseudo-lobe, that both are vertically long and narrow.

The inner face of the root is flat, with a slight central, basal depression, showing a large central aperture near the crown-root junction. On the pseudo-lobes one or two foramina are present.

The outer face of the root has a strong central depression, in which a very large central aperture is present. Both pseudo-lobes may have a central foramen aside the apron.

Lower jaw

The strongly compressed teeth are always interlocked, presenting deep, vertically long, inner distal and outer mesial depressions. Distal and mesial blades are present on the symphyseal tooth. The mesial blade is absent on the other teeth. The crown inclines slightly toward the commissure in latero-posterior and posterior teeth. The principal cusp is over twice as high as its base width. Mesial and distal cutting edges are sigmoidal. The root has an arched root base with rounded basal ends.

The inner face of the crown shows a slightly convex principal cusp. Uvula is absent.

The outer face of the crown is also weakly convex. The crown base is strongly arched, presenting an apron divided into a mesial and a distal pseudo-lobe. On lateral teeth, the mesial pseudo-lobe is narrower than the distal one.

The inner face of the root is vertically long and very flat, showing a large central aperture. A distal depression, as result of interlocking, is well developed.

The outer face of the root shows a very large central aperture. Another foramen is present at the junction of pseudo-lobes and root. A well developed mesial depression is present as a result of interlocking, in which one or two foramina are present along the crown-root junction.

Genus : *Heteroscymnoides* FOWLER, 1934

The type species of this monotypic genus is *Heteroscymnoides marleyi* FOWLER, 1934.

Heteroscymnoides marleyi FOWLER, 1934
Pl. 22.

Heteroscymnoides marleyi FOWLER, 1934, Proc. Acad. nat. Sci. Philad., 85 : 239.

This species has a strong dignathic heterodonty and a weak gradient monognathic heterodonty. The mesial cutting edge of the lower teeth is almost straight, reaching beyond the crown base and joining with it in a short rounding.

The root is anaulacorhizid. The lower teeth are strongly interlocked. Both upper and lower teeth are plurimillimetric in range.

Upper jaw

The teeth have a very elongated, narrow principal cusp, that is constricted just above the crown-root junction. Mesial and distal cutting edges therefore are sigmoidal. Cusplets are absent. The teeth become lower and broader based toward the commissure.

The root is pseudobilobated by an arched root base,

having rounded pseudo-lobes. The lateral teeth have a shorter distal pseudo-lobe. The crown is over three times as high as its base width.

The inner face of the crown is very convex. Uvula is absent. An inner ornamentation is present by fine, short basal costules.

The outer face of the crown is convex. The basal constriction has caused a mesial and a distal ridge. The crown-root junction is strongly arched, and the crown has formed a mesial and a distal apron, that both are vertically long and narrow.

The inner face of the root is flat with a slight central, basal depression, showing a large central aperture near the crown-root junction. One or two foramina are present on the pseudo-lobes.

The outer face of the root has a strong central depression, in which a very large central aperture is present. Both pseudo-lobes can have a central foramina side the apron.

Lower jaw

The strongly compressed teeth are always interlocked, presenting deep, vertically long, inner distal and outer mesial depressions. Distal and mesial blades are present on the symphyseal tooth. The mesial blade is absent on the other teeth. The crown inclines slightly toward the commissure at latero-posterior and posterior teeth. The principal cusp is over twice as high as its base width. Mesial and distal cutting edges are sigmoidal. The root has an arched base with rounded basal ends.

The inner face of the crown shows a slightly convex principal cusp. Uvula is absent.

The outer face of the crown is also weakly convex. The crown base is strongly arched, presenting an apron which is divided into a mesial and a distal pseudo-lobe. On lateral teeth the mesial pseudo-lobe is narrower than the distal one.

The inner face of the root is vertically long and very flat, showing a central aperture. A distal depression, as a result of interlocking, is well developed.

The outer face of the root shows a very large central aperture. Another foramen is present at the junction of pseudo-lobes. A well developed mesial depression is present as a result of interlocking, in which one or two foramina are present along the crown-root junction.

Genus : *Dalatias* RAFINESQUE, 1810

The type species of this monotypic genus is *Dalatias licha* (BONNATERRE, 1788).

Dalatias licha (BONNATERRE, 1788)

Pl. 23, T. pl. 19.

Squalus licha BONNATERRE, 1788, Tabl. encyclop. méthod. trois règ. nat., Ichthyol., Paris : 12.

This species has a strong dignathic heterodonty and a weak gradient monognathic heterodonty. The root is anaulacorhizid. The lower teeth are strongly inter-

locked. The upper teeth are subcentimetrical and the lower ones centimetrical in range.

Upper jaw

The teeth have an elongated principal cusp, that is broad based and constricted just above the crown base. Cusplets are absent. The principal cusp is always slightly directed toward the commissure, still more so in lateral and posterior teeth. The root is pseudobilobated by a deep sulcus, having slightly rounded pseudo-lobes. The crown height is twice or more the crown base width.

The inner face of the crown is slightly convex. Uvula is absent. Also an inner ornamentation is absent.

The outer face of the crown is slightly convex. Apron and outer ornamentation are absent.

The inner face of the root shows a low longitudinal ridge near the crown-root junction, on which a large central aperture with a mesial and a distal foramen is present. A short, broad and deep basal sulcus originates just below the central aperture, in which a second central foramen is present.

The short outer face of the root sometimes has one or two foramina scattered below the crown-root junction. The central basal sulcus is also present on the outer face.

Lower jaw

The strongly compressed teeth are always interlocked, presenting deep, vertically long, inner distal and outer mesial depressions. Small distal and mesial blades are present at the symphyseal tooth. The lateral teeth have a small distal blade only, that becomes more distinct on posterior teeth. The crown inclines slightly toward the commissure in lateral and posterior teeth.

Mesial and distal cutting edges and distal blade are serrated. This fine serration is very regular, reaching almost the apex of the principal cusp and half way on the cutting edge of the distal blade.

The rectangular root is vertically long and pseudobilobated with rounded pseudo-lobes. The root becomes more oblique in lateral and posterior teeth.

The inner face of the crown is flat to very weakly convex and as high as the crown base width. Uvula is absent.

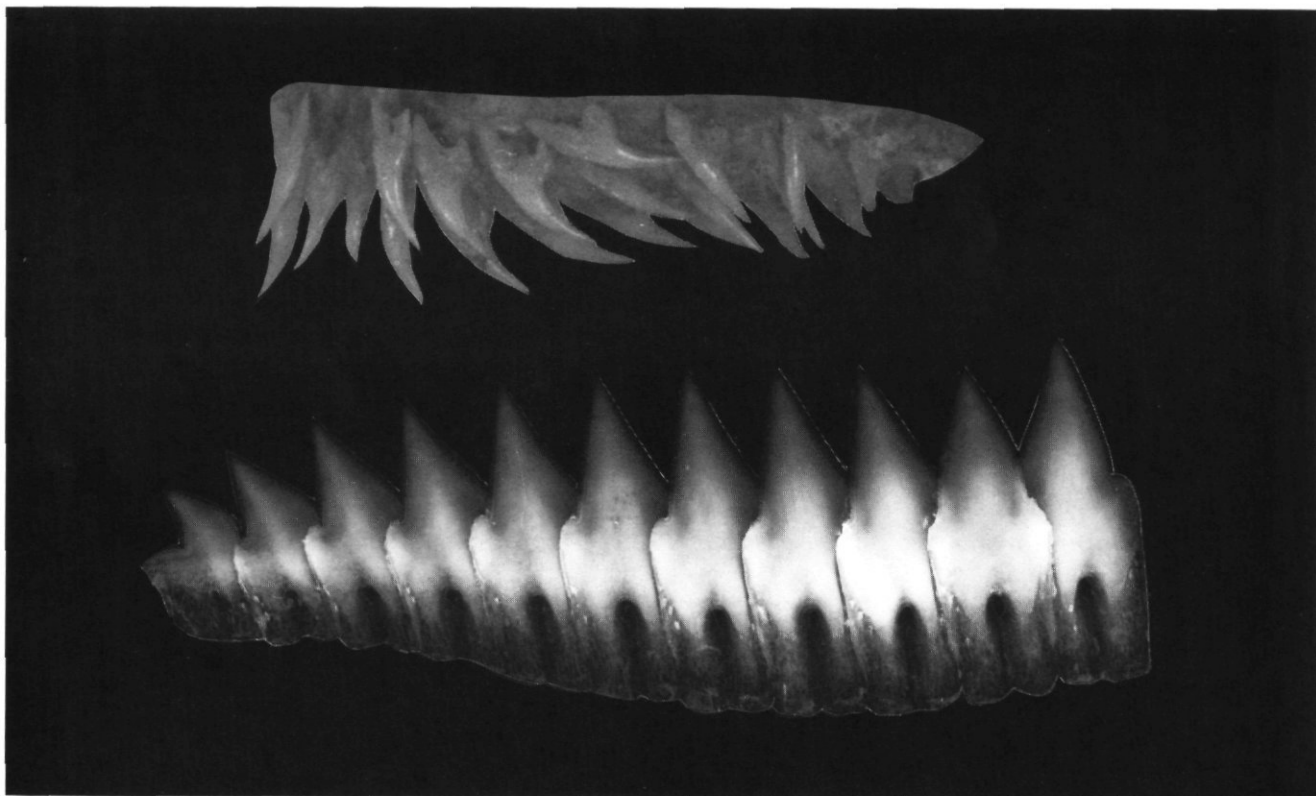
The outer face of the crown is also weakly convex. Vertically long mesial and distal aprons are present. The aprons are not overhanging the root but form one part with it. Ornamentation is absent.

The inner face of the root is vertically long and very flat, showing a central aperture and a mesial and a distal foramen. Just below the central aperture, a vertically long, broad, deep sulcus divides the root into two pseudo-lobes.

The outer face of the root shows the sulcus, running from the crown-root junction between both pseudo-lobes of the apron to the basal end. Foramina are absent.



Text plate 18. *Euprotomicrus bispinatus* (QUOY & GAIMARD, 1824). Female 22 cm. t.l., Indian Ocean. Upper jaw x 10 ; lower jaw x 10.



Text plate 19. *Dalatias licha* (BONNATERRE, 1788). Female 84 cm. t.l., W. Hebrides, N.E. Atlantic. Upper jaw x 4 ; Lower jaw : Diagraph of the functional file. (x 5).

Both pseudo-lobes have irregularly scattered depressions.

Differential diagnosis

Squaliform and hexanchiform teeth are derived from the anaulacorhizid root type. Their compressed and vertical expanded shape is the result of a long evolution, which has led to several forms of vascularisation and developed the tooth types as displayed in Hexanchiform and Squaliform species.

The following remarkable features were noted during our examinations :

- Both species of *Echinorhinus* show an hexanchiform root type of jaw teeth, and their odontology does not give any evidence of a relationship with Squaliformes.
 - There is hardly any morphological difference in teeth of the genera *Squalus* and *Cirrhigaleus*, nor is there any evidence in their external morphology to maintain two separate genera.

- A similar situation exists for *Squaliolus*, *Euprotomicrus* and *Heteroscymnoides*, all with one or two species only. Despite their strong dignathic heterodonty and sexual heterodonty, there is not any morphological evidence to maintain three separate genera.

- The genera *Scymnodon* and *Scymnodalatias* are odontologically very similar. We examined one species of the genus *Scymnodalatias*, but the minor differences in tooth morphology are covered by the natural variability within the genus *Scymnodon*.

- The morphological differences between teeth of *Somniosus microcephalus* and *Somniosus rostratus* are that extreme, that each could represent a separate supraspecific taxon.

Upper teeth <i>C. coelolepis</i> root pseudobilobated sulcus present mesial and distal foramina	<i>C. crepidater</i> root rectangular sulcus absent central foramen only
Lower teeth apron long foramina horizontally expanded and situated aside the apron sulcus present root ends rounded	apron short and broad foramina surrounding the apron sulcus absent root ends angled

The degree of vacularisation in squaliform tooth roots has led to several typical tooth types. (see text-plate 1). These tooth types will be described below and the genera grouped accordingly into 8 subfamilies :

1. - Lower and upper teeth homodont : crown low, apron and uvula well developed and root low (text fig. 1, fig. 1)
 *Squalus*
 *Cirrhigaleus*
2. - Lower teeth : similar to type 1 but higher root ; uvula less developed and sulcus longer
 - Upper teeth : principal cusp erect, uvula absent, root rectangular and apron flanked by two foramina (text fig. 1, fig. 2)
 *Deania*
 *Centrophorus*

3. - Lower teeth : root narrowing, apron flanked by two large apertures, short but broad uvula and a long vertical sulcus
 - Upper teeth : numerous foramina scattered around the apron, sulcus very long and broad (text fig. 1, fig. 3)
 *Somniosus*
 (*microcephalus*-form)
 *Somniosus*
 (*rostratus*-form)
4. - Lower teeth : apron broadly rounded, surrounded by several foramina, root rectangular and equally broad
 - Upper teeth : uvula absent, short sulcus (text fig. 1, fig. 4)
 *Oxynotus*
5. - Lower teeth : apron flanked by several horizontally expanded foramina that are arranged in a vertical row, respectively, or numerous small foramina randomly arranged around the apron
 - Upper teeth : entire tooth well developed and elongated with outer basal ridges on the principal cusp, root pseudobilobated (text fig. 1, fig. 5)
 *Scymnodon*
 *Scymnodalatias*
 *Centroscymnus*
 (*coelolepis*-form)
 *Euprotomicroides*
 *Centroscymnus*
 (*crepidater*-form)
6. - Lower teeth : apron divided into a mesial and a distal part, uvula absent
 - Upper teeth : crown elongated and outer root centre depressed with either one large, or up to three smaller foramina (text fig. 1, fig. 6)
 *Dalatias*
 *Isistius*
 *Squaliolus*
 *Euprotomicrus*
 *Heteroscymnoides*
- Lower teeth : extremely broad apron covering the central and distal root parts
7. - Upper teeth : branched root and multicuspid crown (text fig. 1, fig. 7)
 *Etmopterus*
8. - Lower and upper teeth almost homodont : elongated crown, unicuspid (text fig. 1, fig. 8)
 *Aculeola*

Conclusions

Despite its relative dignathic homodonty, the strong ontogenetic heterodonty, the absence of an anal fin and 5 pairs of gill slits only, all in contrast to the hexanchiform genera, the genus *Echinorhinus* based on odontological features does not have a relationship to squaliforms but rather to hexanchiforms. However, the differences to both orders are otherwise extreme, and therefor we rather tend to follow the palaeontologists PFEIL (1983) and CAPPETTA (1987) in their proposal to place Echinorhinidae in a separate order : Echinorhiniformes.

Odontologically the genus *Oxynotus* has the typical characteristics of Squalidae, and thus no additional arguments are offered to support some authors in holding a separate familie Oxynotidae.

Odontologically no differences exist between *Cirrhigaleus* and *Squalus*.

Only minor odontological differences exist between *Euprotomicrus*, *Squaliolus* and *Heteroscymnoides*, which thus might be congeneric.

Subdivision of the genus *Somniosus* into two subgenera has often been proposed by authors. The present odontological result supports this view as expressed by QUERO (1976) and COMPAGNO (1984 : 102), to group *S. microcephalus* and *S. pacificus* into one subgenus *Somniosus (Somniosus)* and *S. rostratus* into another subgenus *Somniosus (Rhinoscymnus)*.

The species of *Centrosymnus* share a characteristic external morphology. However *Centrosymnus crepidater* differs so markedly in its tooth morphology from its congeners, that GARMAN's (1913) introduction of a separate genus *Centroselachus* for this species appears justified.

Although *Centrosymnus* and *Scymnodon* have the same type of root vascularisation, all their odontological characters differ that extreme that generic distinction should remain.

However the distinction of *Scymnodon* and *Scymnodalatias* by odontology is of minor importance only and therefore both may be congeneric.

Lepidorhinus squamosus has been reassigned to the genus *Centrophorus* by COMPAGNO (1984). This decision is supported by odontological characters as illustrated for *C. squamosus* in the present paper (Pl. 12, Tpl. 10).

The degree of development of vascularisation in tooth roots is a significant indication of phylogenetic relationships and would allow to group the squalid genera in subfamilies. COMPAGNO (1973) had subdivided the Squalidae, as then understood by him, into four subfamilies but withdrew this concept (1984 : 29) pending his further completion of work on squaloid morphology, and he considered separate families for *Echinorhinus* and *Oxynotus*. Though based on other characters, COMPAGNO's (1973) concept of squalid subfamilies is generally in accordance with the present odontological results to group squalid genera into 8 subfamilies as indicated in the differential diagnosis above.

Remark : *Centrosyllium fabriccii* and *Aculeola nigra*

in general show odontological similarities with the family Scyliorhinidae. These will be discussed in the forthcoming contributions on scyliorhinid odontology.

Key to the squalid genera based on odontological characters :

- 1. Principal cusp blade-like and broad based :
 - a - Uvula present :
 - Sulcus absent
 - Apron and uvula cover the whole upper part of the root
 - *Etmopterus*
(lower teeth)
(Pl. 5).
 - Sulcus short
 - Apron narrow and short
 - Uvula small
 - Crown strongly directed distally
 - *Squalus*
(upper and lower teeth)
(Pl. 3).
 - Apron broad
 - Uvula broad
 - Crown erect, with serrated cutting edges
 - *Oxynotus*
(lower teeth)
(Pl. 2).
 - Sulcus long
 - Crown strongly directed distally
 - Uvula very small
 - Root always broader than high
 - *Deania*
(lower teeth)
(Pl. 13).
 - Uvula narrow and small
 - Width and height of root base about equal
 - *Centrophorus*
(lower teeth)
(Pl. 11).
 - Uvula broad and short
 - Root base narrower than the height of the root
 - a-Apron short
 - *Somniosus*
(*Somniosus*)
(lower teeth)
(Pl. 8, 9).
 - b-Apron long
 - *Centrosymnus*
(lower teeth)
(Pl. 14).
- A pair of large foramina flanking the apron
 - *Somniosus*
(*Rhinoscymnus*)
(lower teeth)
(Pl. 10).
- Several horizontally expanded foramina flanking the apron
 - *Scymnodon*
(lower teeth)
(Pl. 16).
- b-Uvula absent
 - Short apron flanked by two main foramina
 - Root high, strongly narrowing from just below the crown-root junction downward
 - *Centrophorus*
(upper teeth)
(Pl. 11).

- Root low, almost equally wide from just below the crown-root junction downward
 *Deania*
 (upper teeth)
 (Pl. 13).
- Long apron surrounded by foramina
- Crown height twice the crown base width. Root long
 *Euprotomicroides*
 (lower teeth)
 (Pl. 19).
- Crown height equals the crown base width
- a-Root low
 *Centroselachus*
 (lower teeth)
 (Pl. 15).
- b-Root very high
 *Oxynotus*
 (upper teeth)
 (Pl. 2).
- Long and broad apron, divided into a mesial and a distal part
- Sulcus long apron dividing from crown-root junction downward
 Cutting edges serrated
 *Dalatias*
 (lower teeth)
 (Pl. 23).
- Sulcus short
 Crown triangularly shapes
 Apron divided at apron base only
 *Isistius*
 (lower teeth)
 (Pl. 18).
- Sulcus absent
 Apron divided in lower half only
 *Euprotomicrus*
 (lower teeth)
 (Pl. 20).
- Apron prominent and long
 *Somniosus*
 (*Somniosus*)
 (upper teeth)
 (Pl. 8, 9)
- Apron absent
- Fine reticulated ornamentation present on the outer crown base
 *Somniosus*
 (*Rhinoscyrnus*)
 (upper teeth)
 (Pl. 10)
- 2. Principal cusp vertically long and slender :
 Root hemiaulacorhizid
- Cusplets present
 *Centrosyllium*
 (upper and lower teeth)
 (Pl. 6).
- Cusplets absent
 *Aculeola*
 (upper and lower teeth)
 (Pl. 7).
- Root anaulacorhizid
- Cusplets present
 *Etmopterus*
 (upper teeth)
 (pl. 5).
- Cusplets absent
- Outer crown base slightly depressed
 Crown strongly constricted at base
 Root mesio-distally wide
 Slightly rounded root lobes
 *Dalatias*
 (upper teeth)
 (Pl. 23).
- Outer crown base not depressed
 Crown not constricted
 Root mesio-distally narrow, with quadrangular root lobes
 *Isistius*
 (upper teeth)
 (Pl. 18).
- Outer crown base strongly depressed, with a large central foramen
 Root mesio-distally narrow with rounded root ends
 *Euprotomicrus*
 (upper teeth)
 (Pl. 20).
- Basal ridge on the outer part of the principal cusp present
- Root bilobate
 One broad, outer mesial and another distal foramen present
 *Centroscyrnus*
 (upper teeth)
 (Pl. 14).
- Root more or less quadrangular
- a-Sulcus present
 Outer mesial and distal foramina absent
 (some outer scattered foramina present on posterior teeth)
 *Scymnodon*
 (upper teeth)
 (Pl. 16).
- b-Sulcus absent
 Three to four outer central foramina present
 Root shape quadrangular
 *Centroselachus*
 (upper teeth)
 (Pl. 15).
- Basal ridge on the outer part of the principal cusp present
- Root bilobate
 One broad, outer mesial and another distal foramen present
 *Centroscyrnus*
 (upper teeth)
 (Pl. 14).
- Root more or less quadrangular
- a- Sulcus present
 Outer mesial and distal foramina absent
 (some outer scattered foramina present on posterior teeth)
 *Scymnodon*
 (upper teeth)
 (Pl. 16).
- b-Sulcus absent
 Three to four outer central foramina present
 Root shape quadrangular
 *Centroselachus*
 (upper teeth)
 (Pl. 15).
- Basal ridge on the outer part of the principal cusp absent
- One or two outer central foramina and two or three mesial and distal foramina present
 Root more or less bilobate
 *Euprotomicroides*
 (upper teeth)
 (Pl. 19)

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Glossary (also applying to previous issues of this series)

An-, Hemi-, Hol- and Poly-aulacorhizid
Considering their vascularisation, E. Casier (1947) recognised and described 4 phylogenetically characteristic root forms of elasmobranch teeth :

Anaulacorhizid
Vascularisation through scattered foramina of equal size on both outer and inner faces.
(like Hexanchidae)

Hemiaulacorhizid
Vascularisation through a median and 1 or 2 lateral foramina on inner face.
(like Squatinidae and Orectolobidae)

Holaulacorhizid
Vascularisation through many small foramina concentrated in a median groove running from outer to inner face.
(like Carcharhinidae, Lamnidae, Rajidae etc.)

Polyaulacorhizid
Vascularisation through many small foramina concentrated in several grooves running parallel from outer to inner face and near crown-root junction on both inner and outer faces. (like Myliobatidae, etc.)

Anterior
Tooth positions close to junction of left and right jaw part.

- Apron**
Expansion of the central part of the outer crown base.
- Basal**
Bottom face concerned.
- Commissural**
Tooth positions near the end of jaw.
- Costule**
Short, vertical ridges sometimes present on inner and/or outer crown base.
- Dignathic**
Heterodont by having different tooth morphology in upper and lower jaw.
- Distal**
Tooth row from symphysis toward end of jaw. (longitudinally)
- Heterodonty**
Different tooth morphology within a tooth file.
- Homodonty**
Equal tooth morphology within a tooth file.
- Inner face**
View from inside the mouth.
- Lateral**
Tooth positions half way along the jaw.
- Median keel**
Transversal ridge dividing crown into inner and outer face.
- Mesial**
Toward junction (symphysis) of left and right jaw parts.
- Outer face**
View from outside the mouth.
- Parasymphysial**
First anterior tooth row if a symphysial tooth row is absent
- Pseudoapron**
Apron-like vertical ridges that appear sometimes on lateral and posterior teeth
- Pseudosymphysial**
One of the parasymphysial tooth rows becomes the character of a symphysial tooth row (symmetry). This phenomenon is sometimes present in species.
- Posterior**
Tooth positions toward end of jaw.
- Row**
Tooth row from inner face to outer face of jaw (transversally).
- Striae**
Vertical ridges running from crown base toward apex.
- Sulcus**
Groove developed by the main vascularisation string leading from root base to the main foramen on analacorhizid root types.
It differs from the median groove of the holaulacorhizid root type and the parallel grooves of the polyaulacorhizid root type, in which several foramina are concentrated, respectively.
- Symphysial**
Teeth at junction of both halves of a jaw.
- Uvula**
Lobate extension of the inner crown base.

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Compositions of the plates

As far as possible, for all the genera and subgenera, one plate of the complete tooth file of upper and lower jaw and another plate with SEM-photographs or macro-photographs of isolated teeth are presented.

Both plates have the same composition : the upper part shows always the upper jaw or teeth and the lower part the lower jaw or teeth.

The outer and inner view of the isolated teeth (macro- or SEM-photographs) always are symmetrically presented.

Only the outer view of the jaw halves or tooth files is presented, because it is our intention to show the number of tooth rows, their dispositions and the variations in form and size of the teeth. There are two techniques of photographing used : diagraphs (the tooth file used as negativ) and composition of photographs that partly overlap every previous one tot form one complete jaw half.

The choice of left or right jaw half depends of quality of preservation of the specimens's tooth files only.

The upper scale bar refers to the upper teeth, the lower scale bar to the lower teeth. Photographs of posterior and commissural teeth mostly are enlarged and have their own scale bar.

Legend

- s = Symphysial position
- ps = Parasymphysial position
- a = Anterior position
- al = Antero-lateral position
- l = Lateral position
- lp = Latero-posterior position
- p = Posterior position
- c = Commissural position

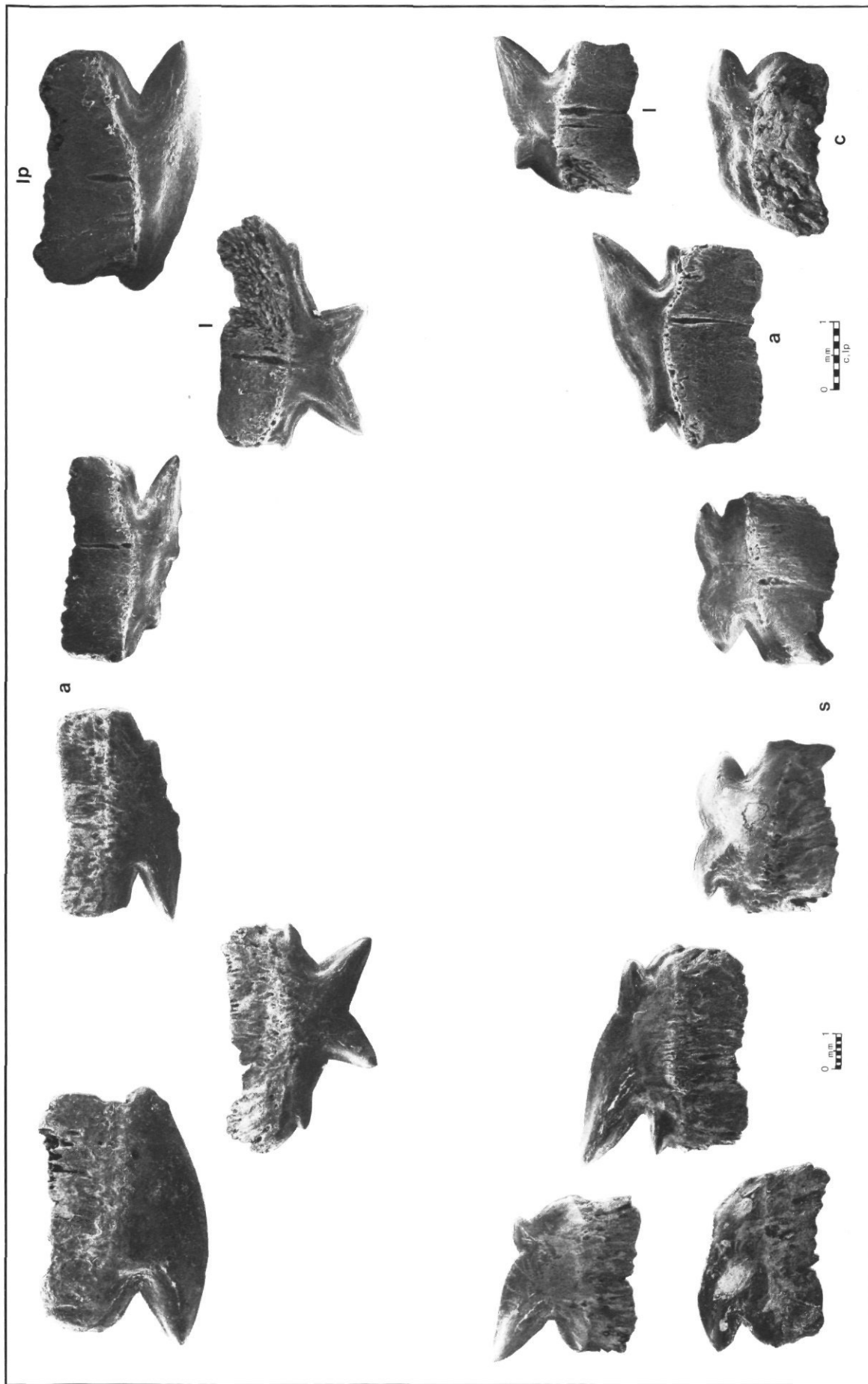


Plate 1. *Echinorhinus brucus* (BONNATERRE, 1788). Female 240 cm. t.l., Belgium, North Sea. Upper lateral tooth abnormal.

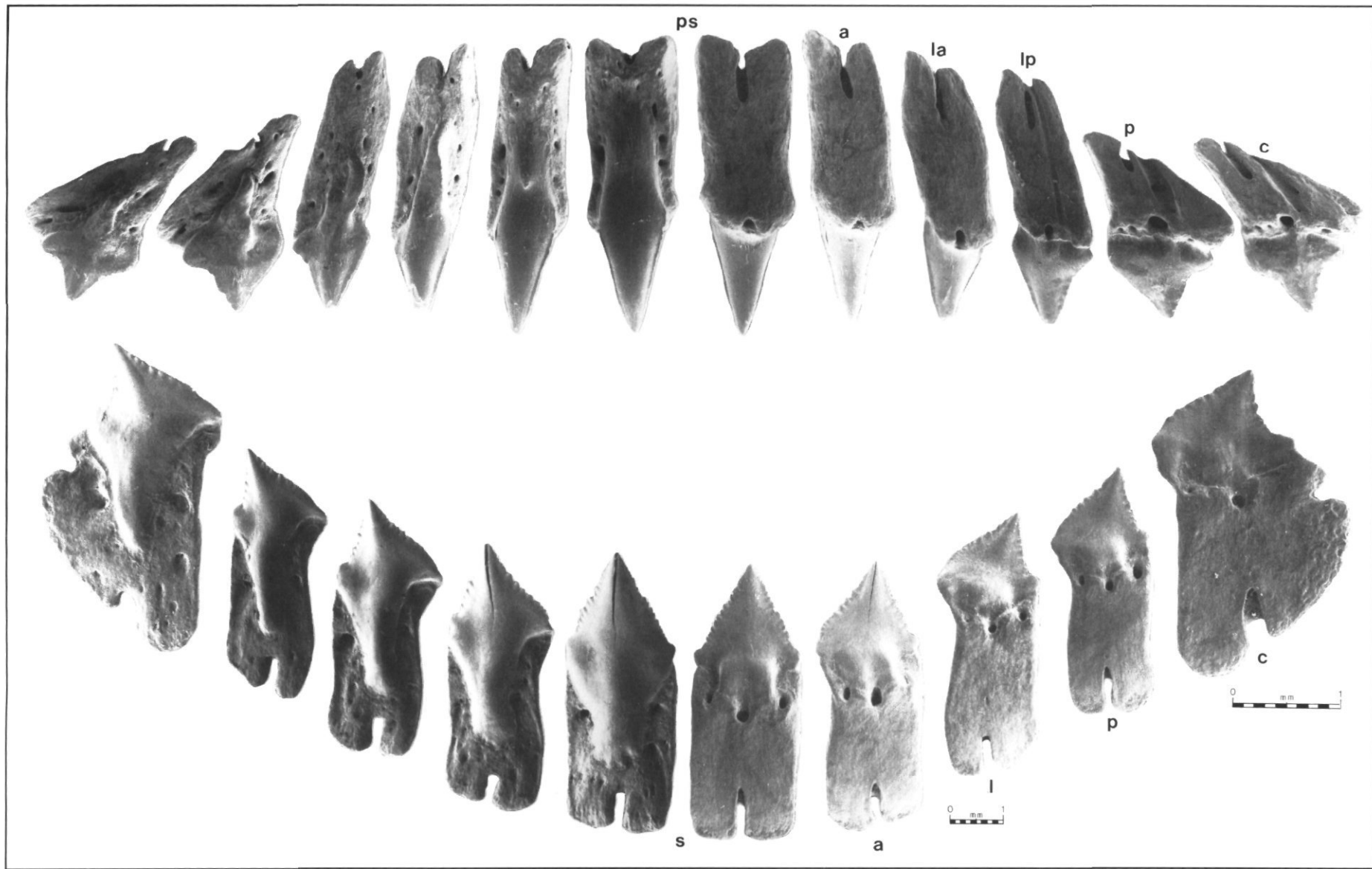


Plate 2. *Oxynotus centrina* (LINNAEUS, 1758). Female 46 cm. t.l., Dakar, Senegal.
(only the lower commissural tooth refers to the large scale).

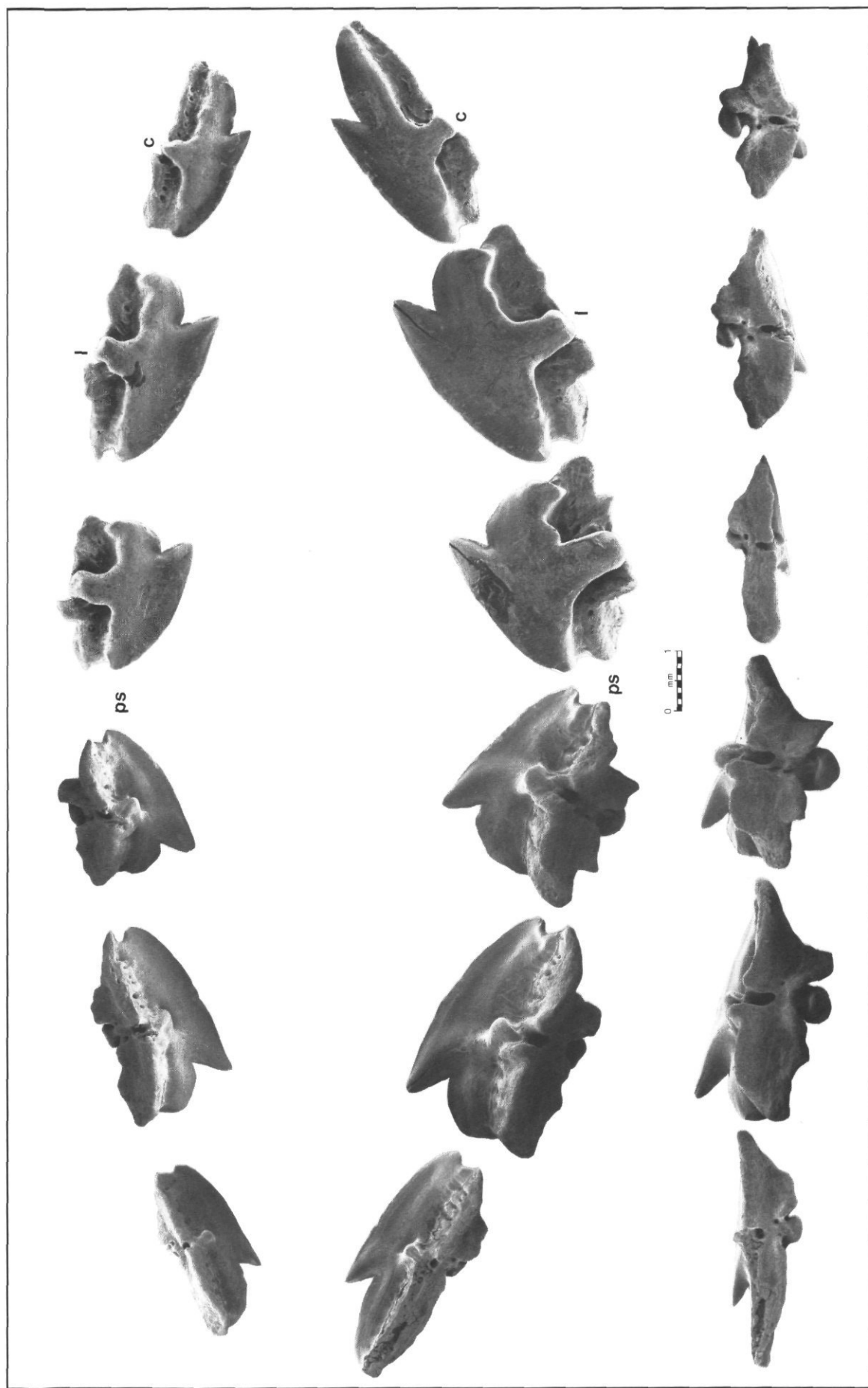


Plate 3. *Squalus acanthias* (LINNAEUS, 1758). Female 100 cm. t.l., E. Orelle, N.E. Atlantic.

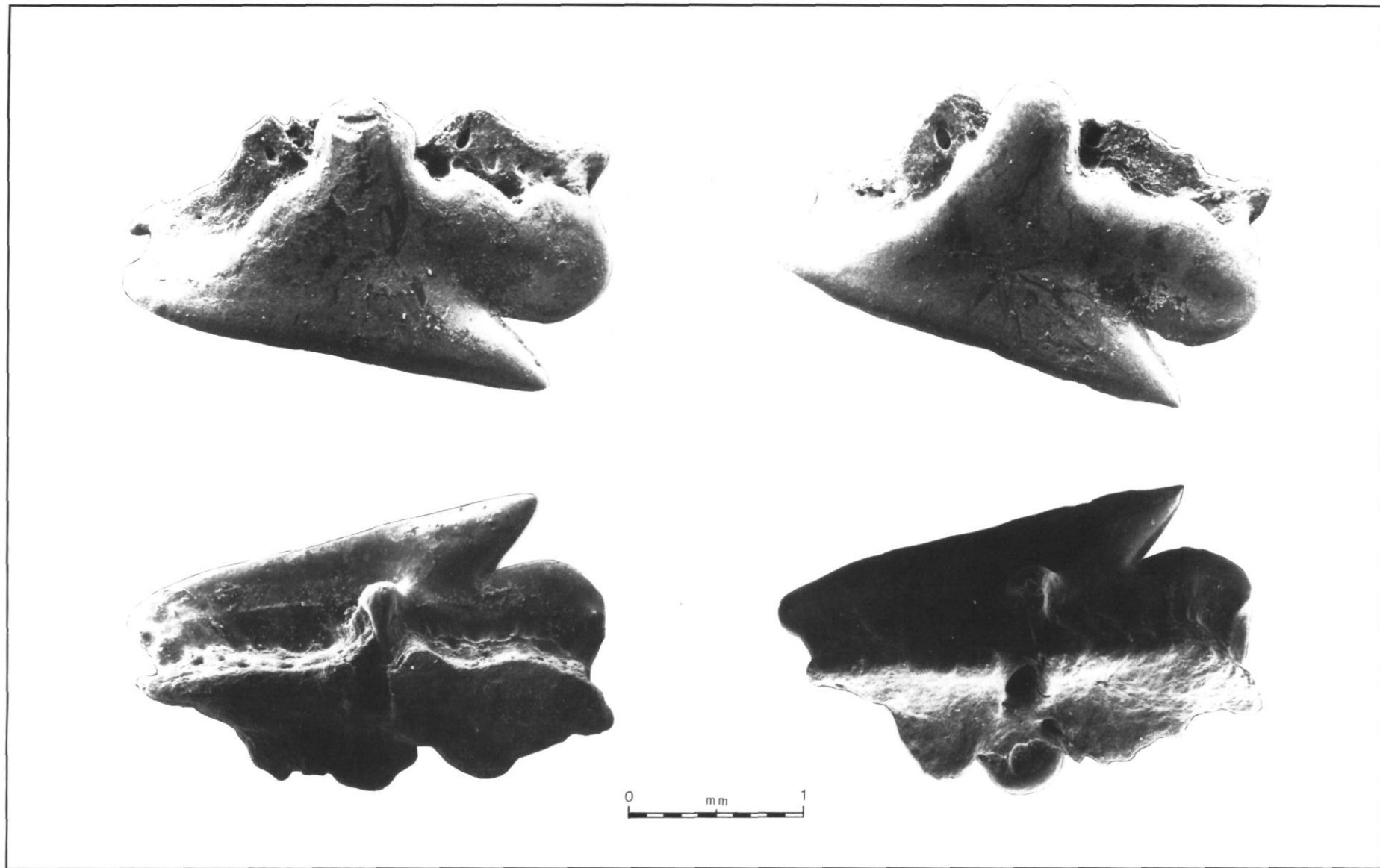


Plate 4. *Squalus barbifer* (TANAKA, 1912). Female 82 cm. t.l., Sagami Bay, Japan (lateral teeth). Formerly *Cirrhigaleus barbifer* (TANAKA, 1912).

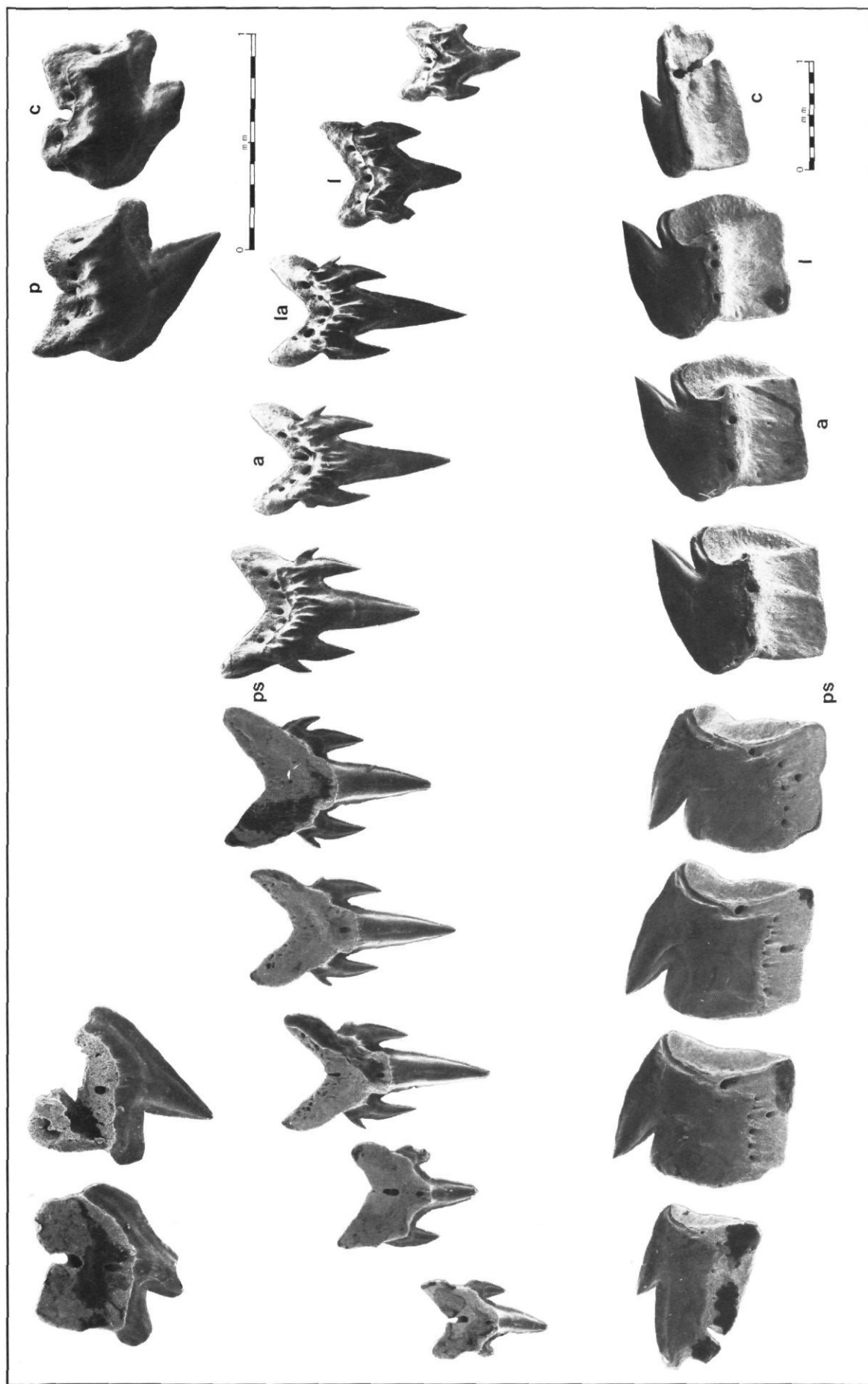


Plate 5. *Etmopterus spinax* (LINNAEUS, 1758). Female 29 cm. t.l., Nice, Mediterranean Sea.

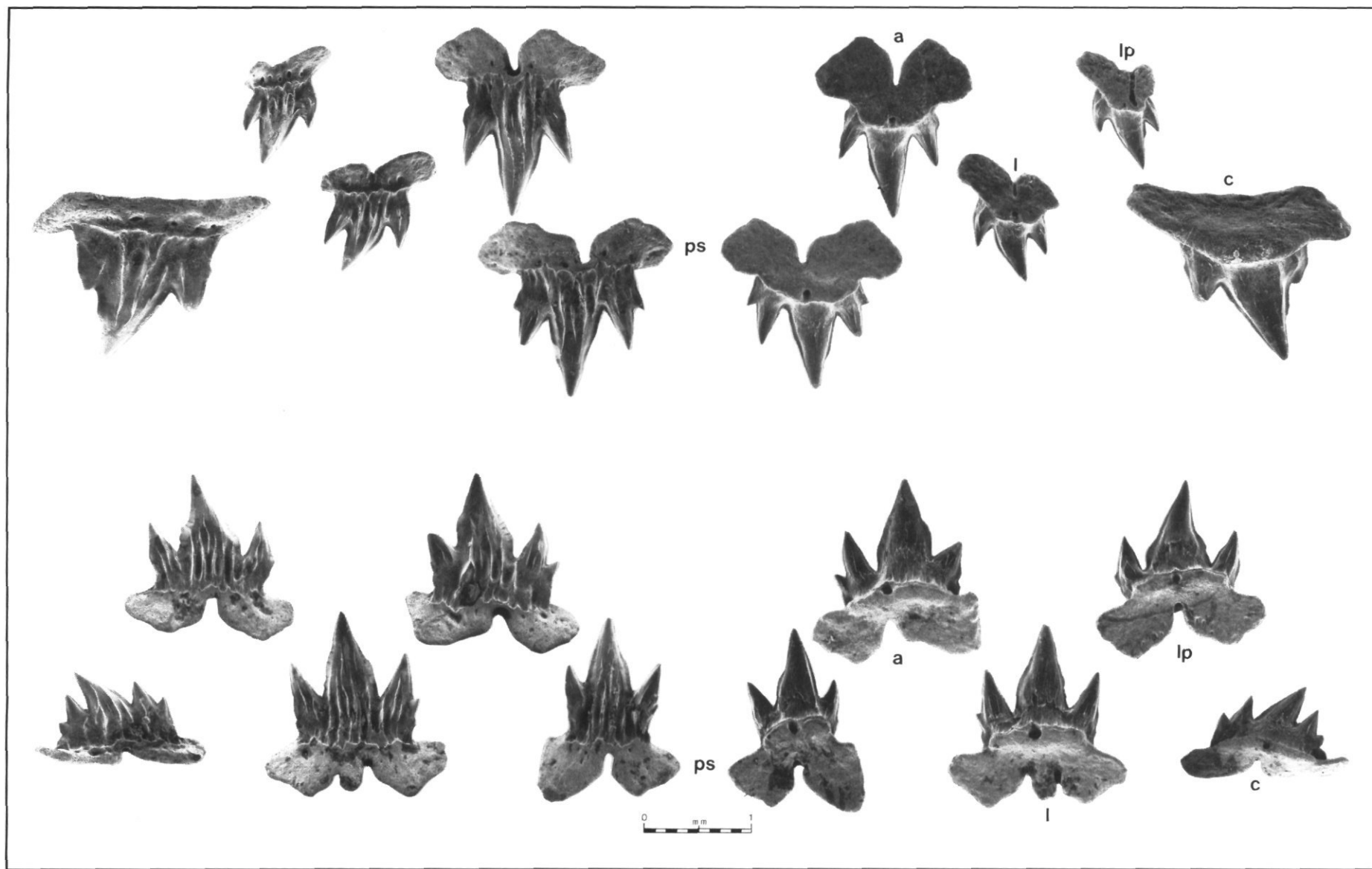


Plate 6. *Centroscyllium fabricii* (REINHARDT, 1825). Female 85 cm. t.l., N. Bill Bailey, N.E. Atlantic. Upper commissural tooth is 3 times more enlarged than the other teeth. Lower lateral tooth has an abnormal root structure.

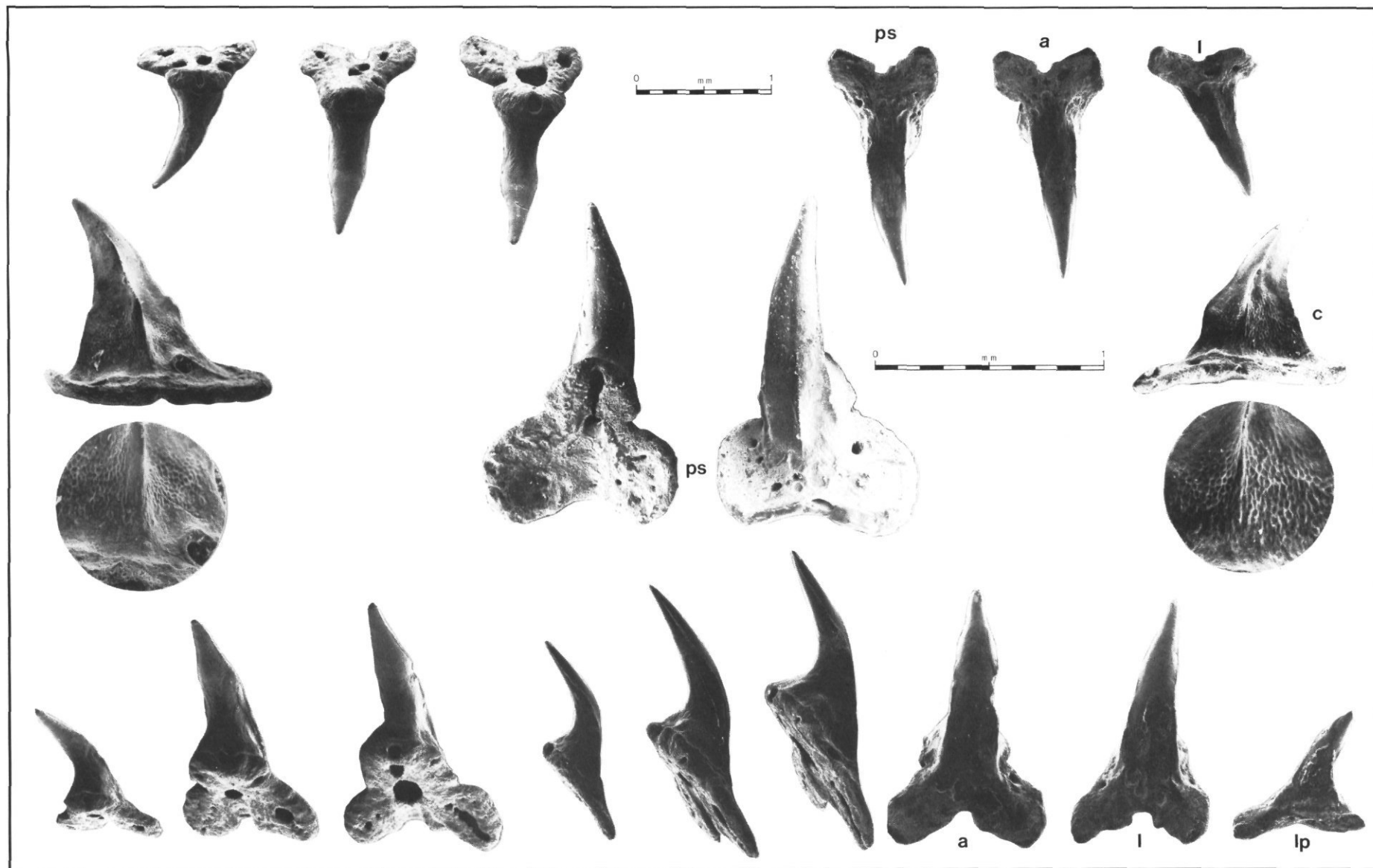


Plate 7. *Aculeola nigra* DEBUEN, 1959. Upper photo series : male 44.5 cm. t.l., Peru. Central photo series : male 40 cm t.l., Chile. (Details of the micro-ornamentation of the commissural teeth x 90). Lower photo series : female 38 cm. t.l., Chile. All these SEM-photos by courtesy of Mr. F. CIGALA-FULGOSI, Parma, Italy.

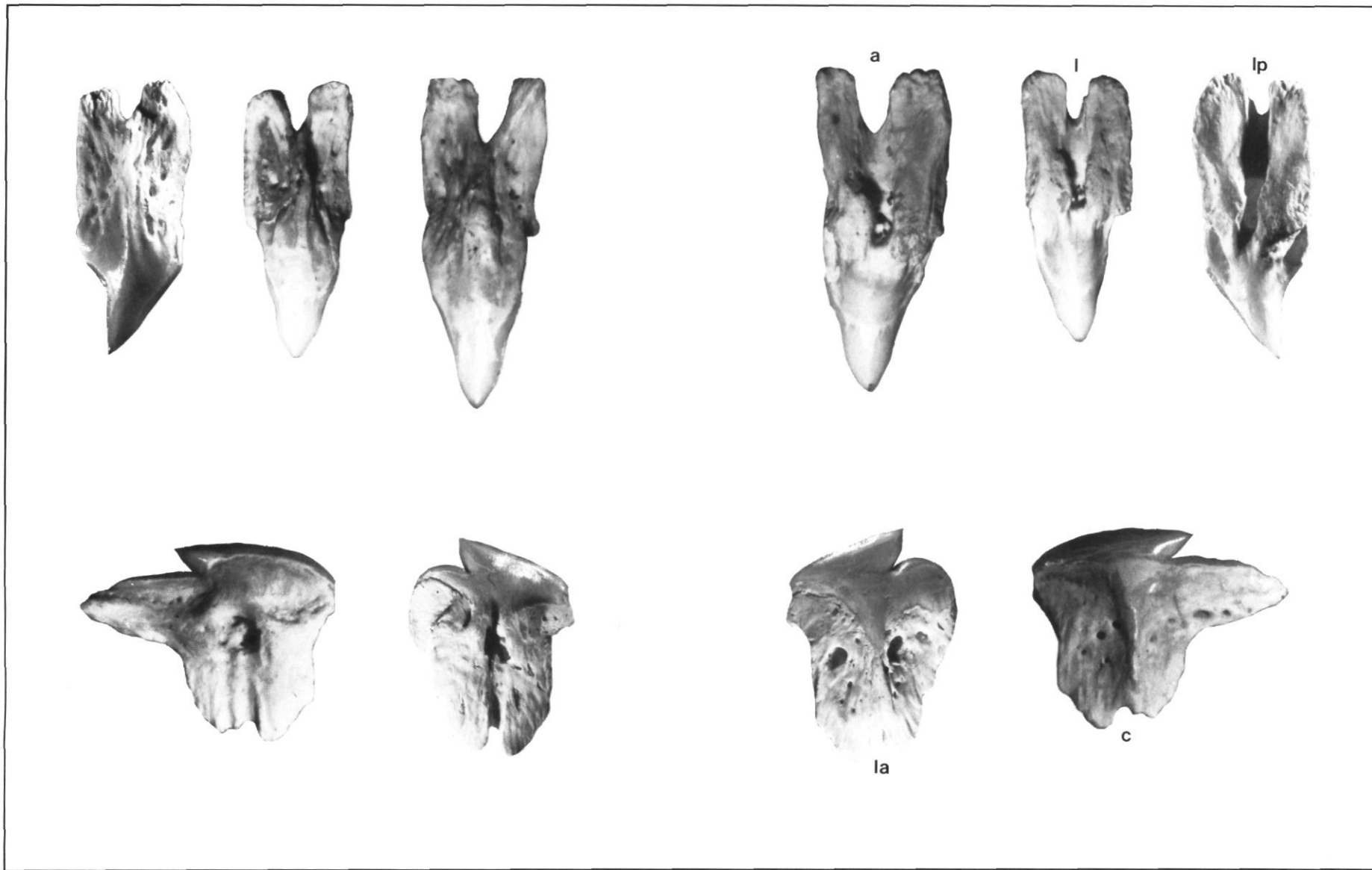


Plate 8. *Somniosus microcephalus* (BLOCH & SCHNEIDER, 1801). Female 470 cm. t.l., N. Lousy N.E. Atlantic. Upper teeth x 35 ; lower antero-lateral tooth x 2.5 ; lower commissural tooth x 7. Macro-photographs were taken by K. Jansen, Oudembosch, The Netherlands. New taxonomic proposition : *Somniosus* (*Somniosus*) *microcephalus* (BLOCH & SCHNEIDER, 1801).

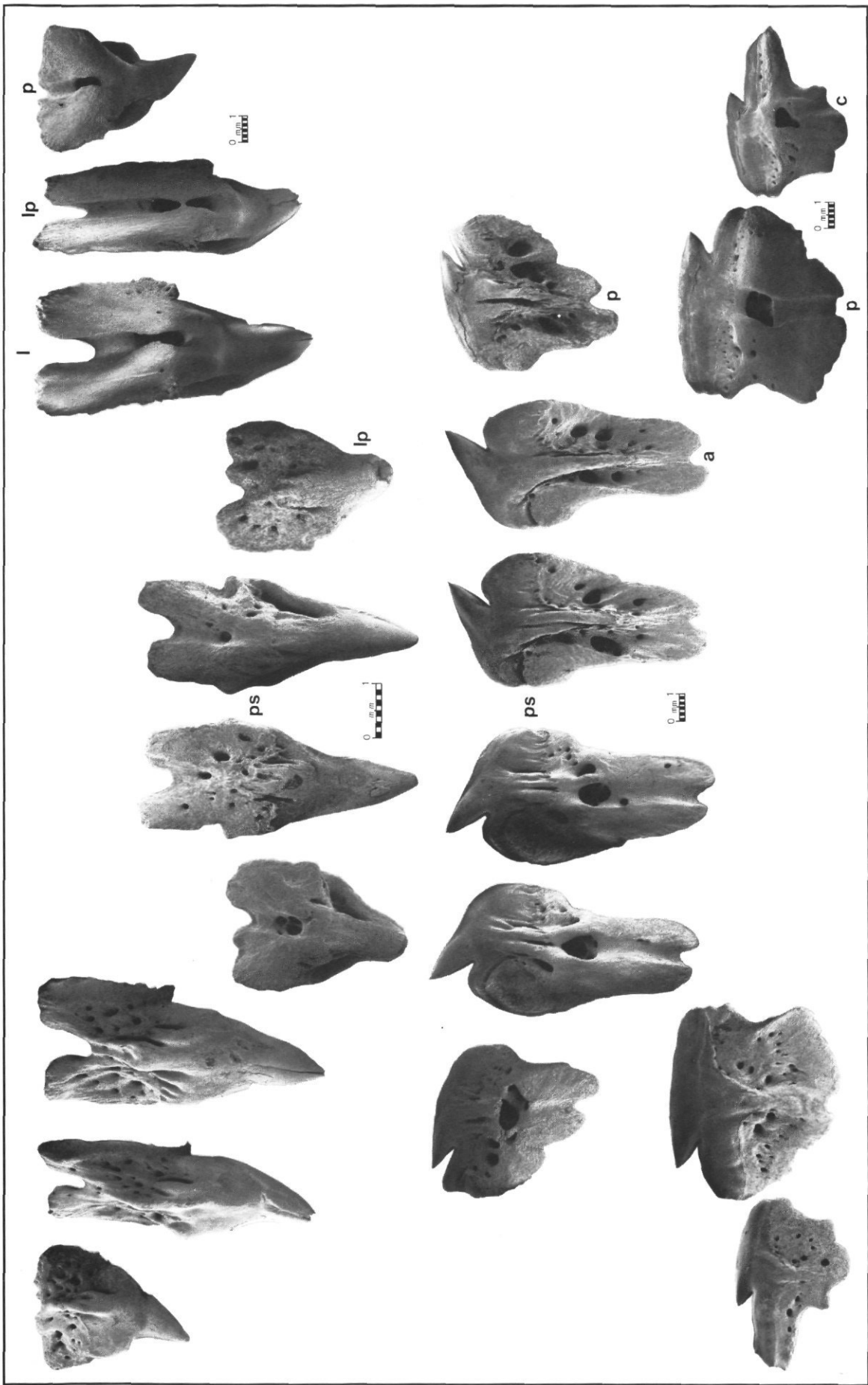


Plate 9. *Somniosus microcephalus* (BLOCH & SCHNEIDER, 1801). Central part : male 176 cm. t.l., E. Océan, N.E. Atlantic. Outer parts : female 470 cm. t.l., N. Lousy, N.E. Atlantic. New taxonomic proposition : *Somniosus* (*Somniosus*) *microcephalus* (BLOCH & SCHNEIDER, 1801).

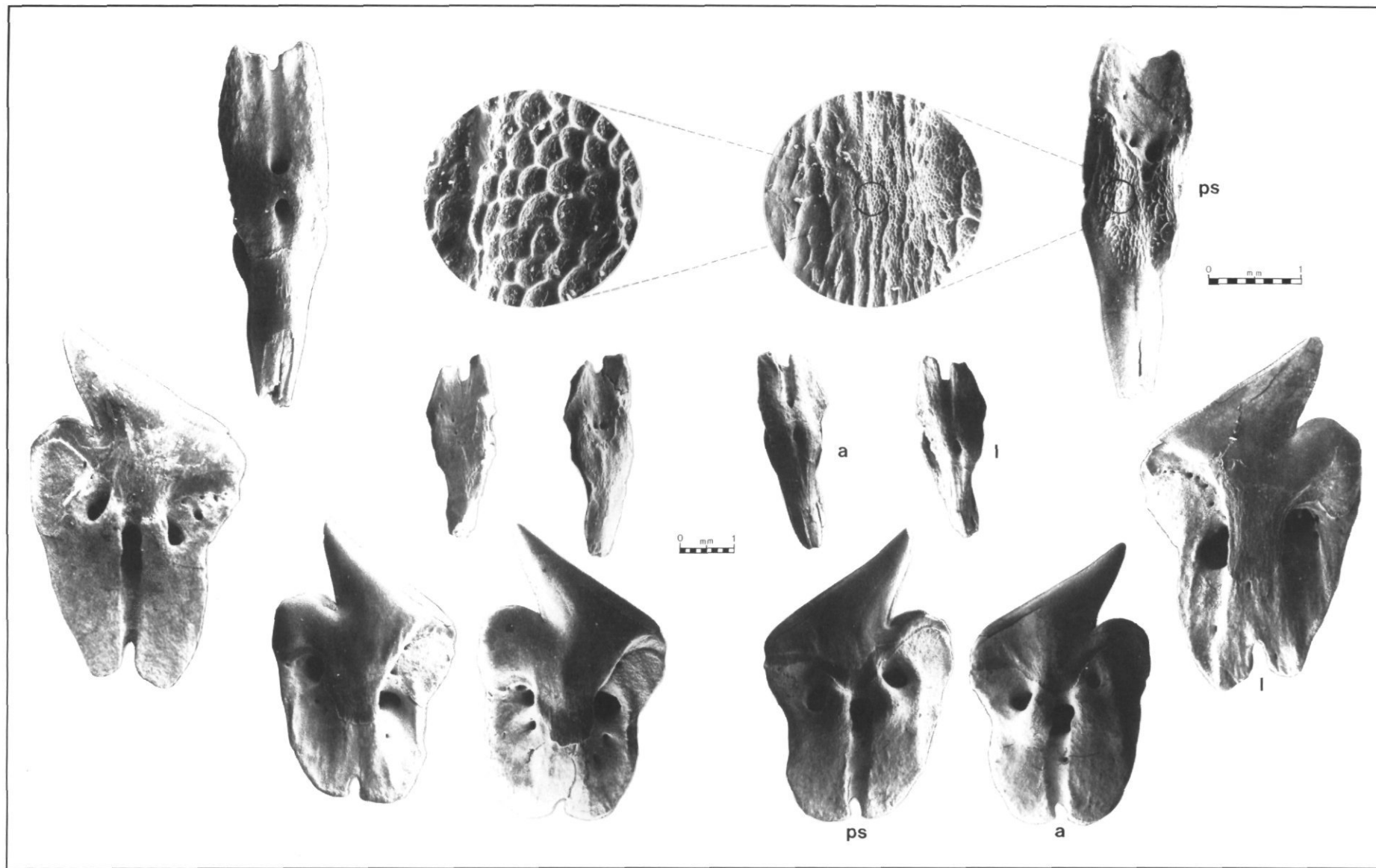


Plate 10. *Somniosus rostratus* (Risso, 1826). Male 109 cm. t.l., W. Hebrides, N.E. Atlantic. The micro-ornamentation of the upper parasymphysial tooth x 90 and x 650, respectively. New taxonomic proposition: *Somniosus* (*Rhinoscyrnus*) *rostratus* (Risso, 1826).

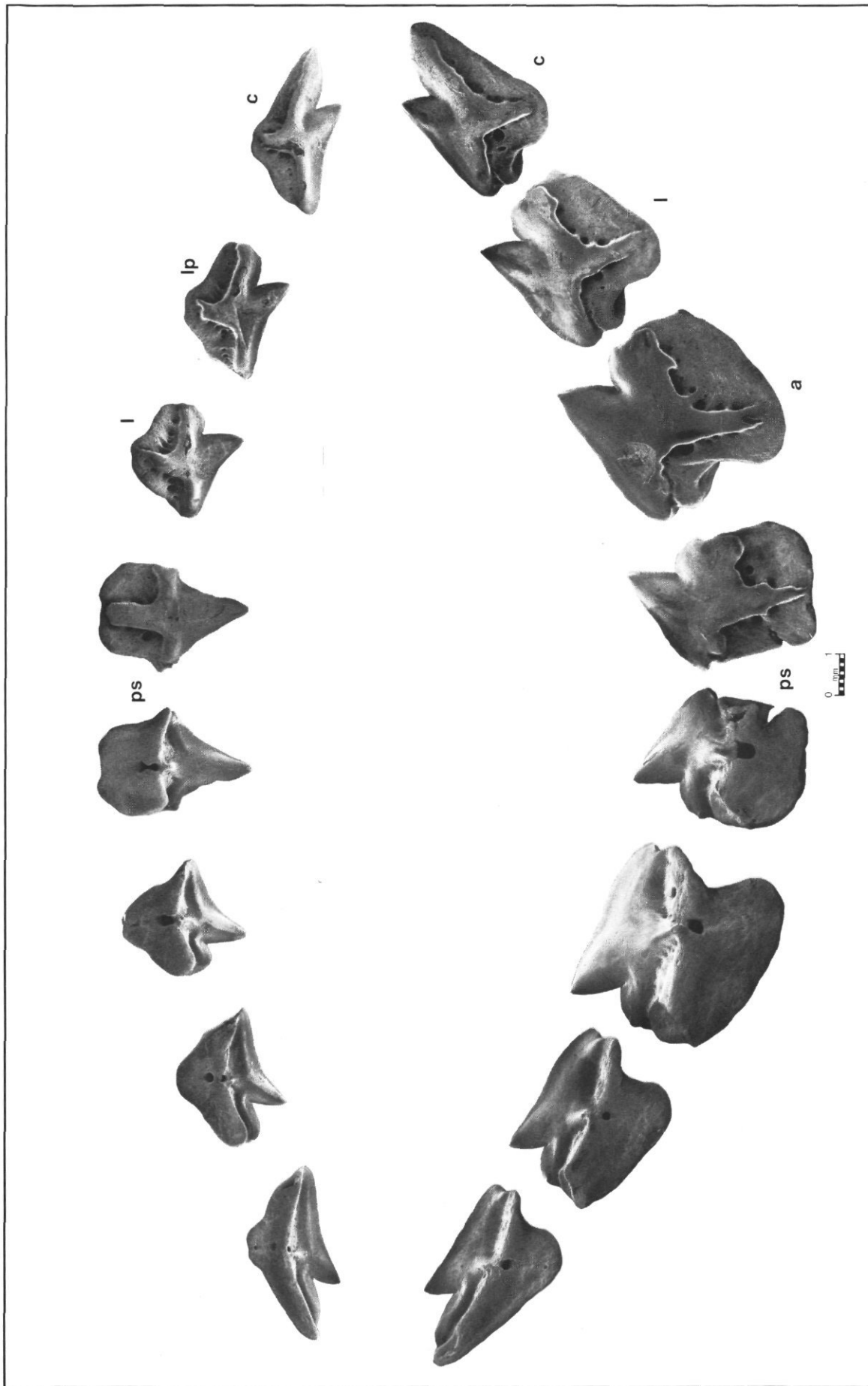


Plate 11. *Centrophorus granulosus* (BLOCH & SCHNEIDER, 1801). Female 97 cm. t.l., Motril, Mediterranean Sea.

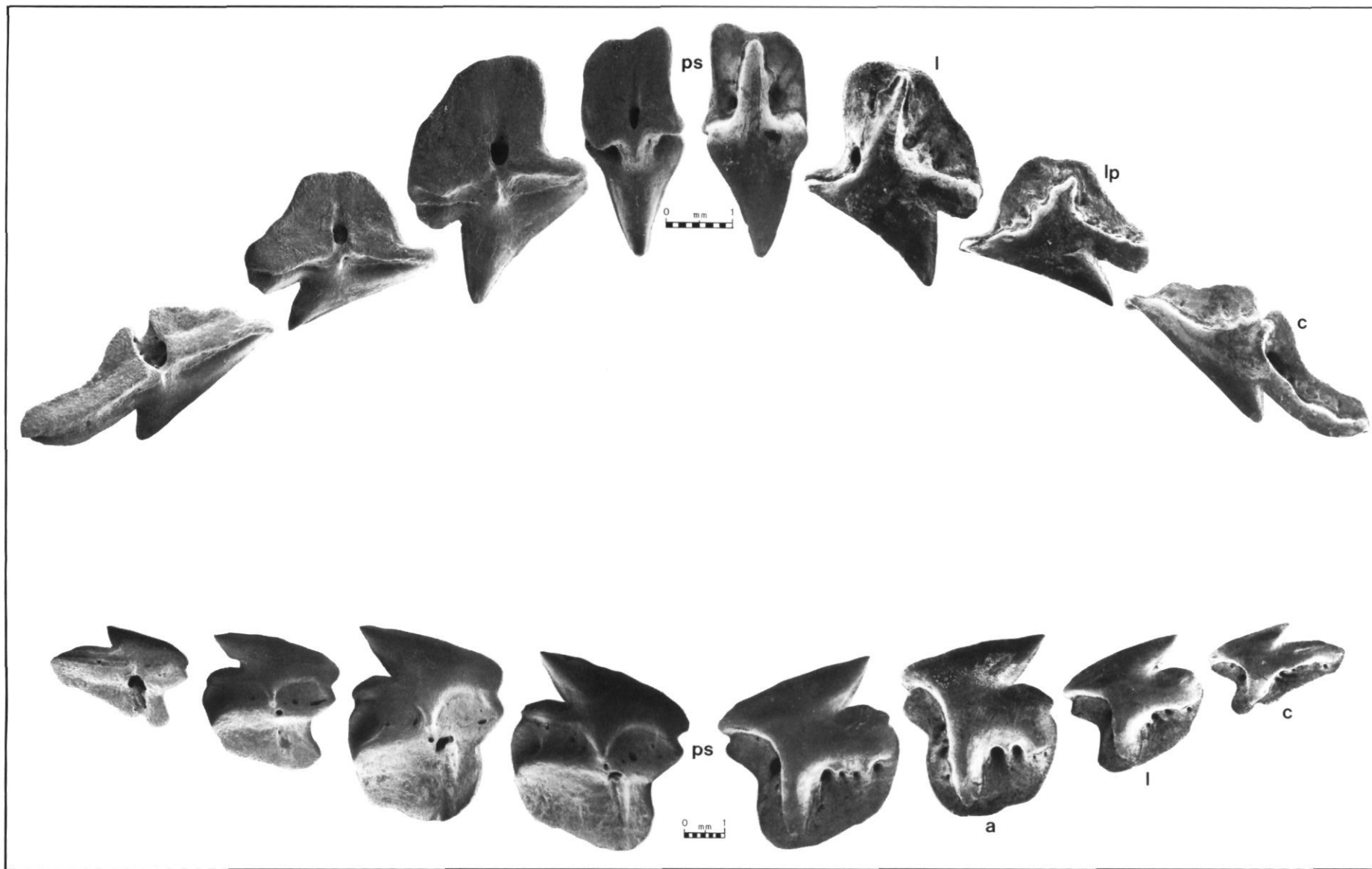


Plate 12. *Centrophorus squamosus* (BONNATERRE, 1788). Male 92 cm. t.l., S.W. Rockall. N.E. Atlantic. Formerly *Lepidorhinus squamosus* (BONNATERRE, 1788).

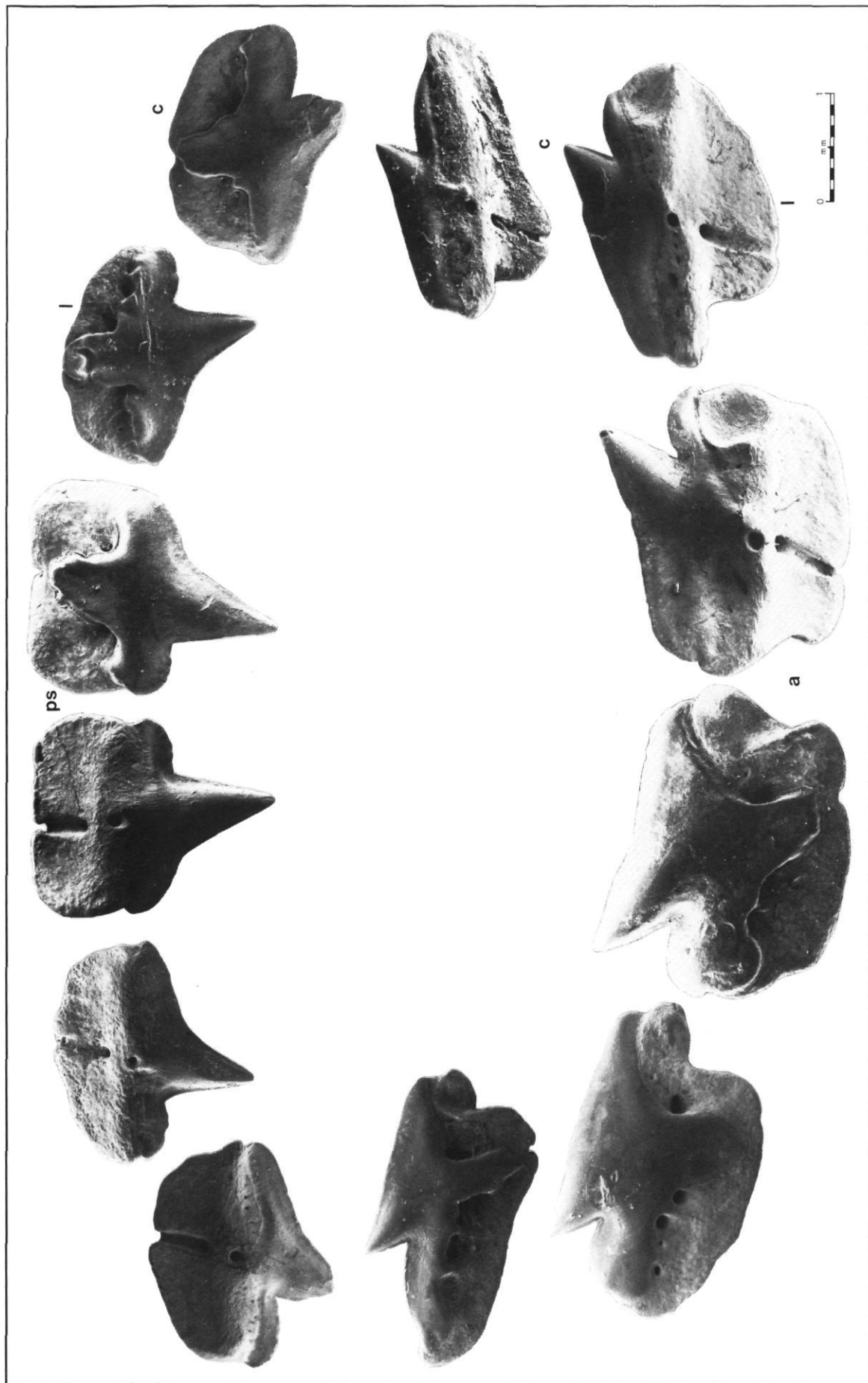


Plate 13. *Deania calcea* (LOWE, 1813). Female 107 cm. t.l., W. Hebrides, N.E. Atlantic.

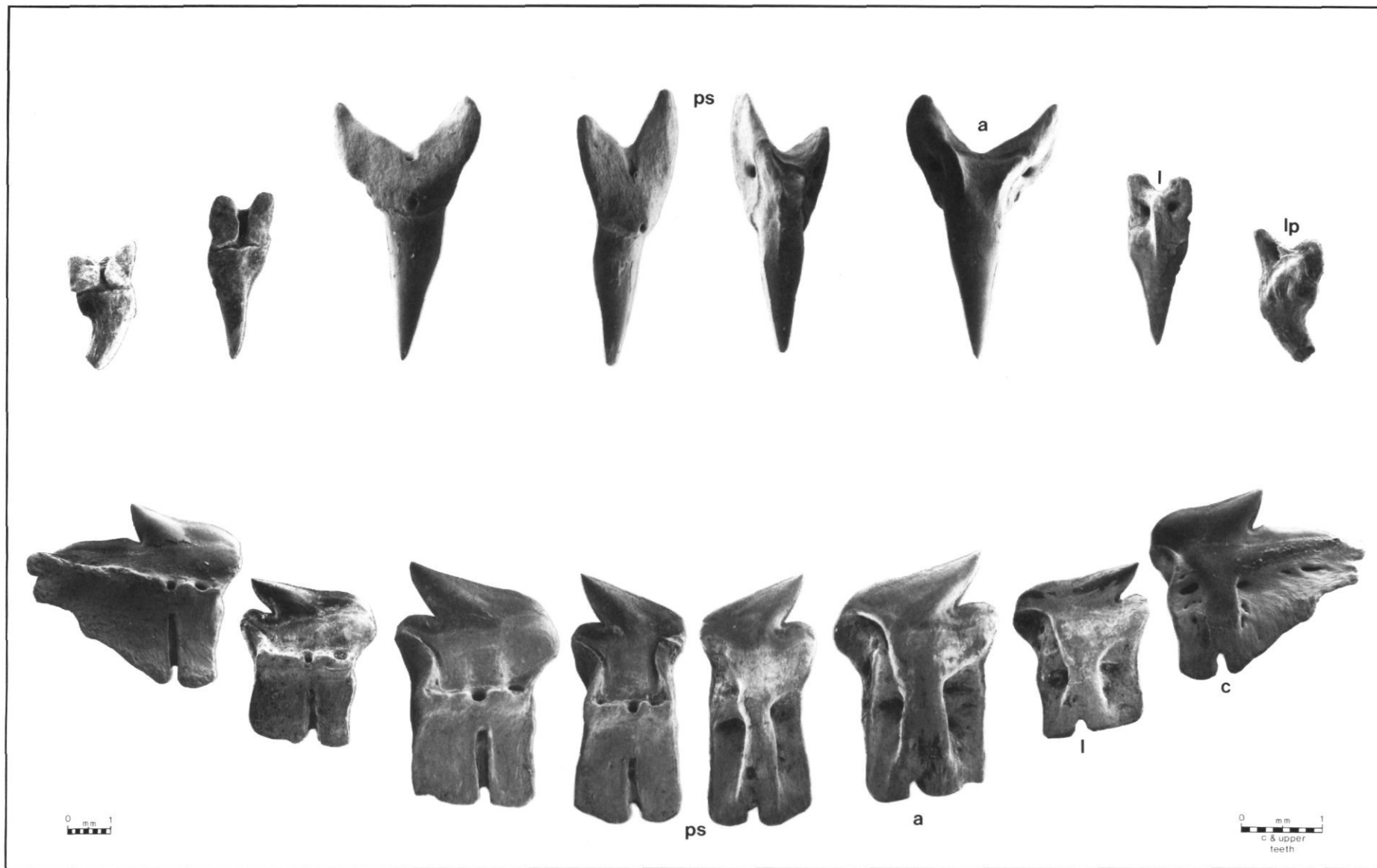


Plate 14. *Centroscyrnus coelolepis* BOCAGE & CAPELLO, 1864. Female 110 cm. t.l., N. Bill Bailey, N.E. Atlantic. Both upper parasymphysial tooth and anterior tooth are from a female 102 cm. t.l., Nice Mediterranean.

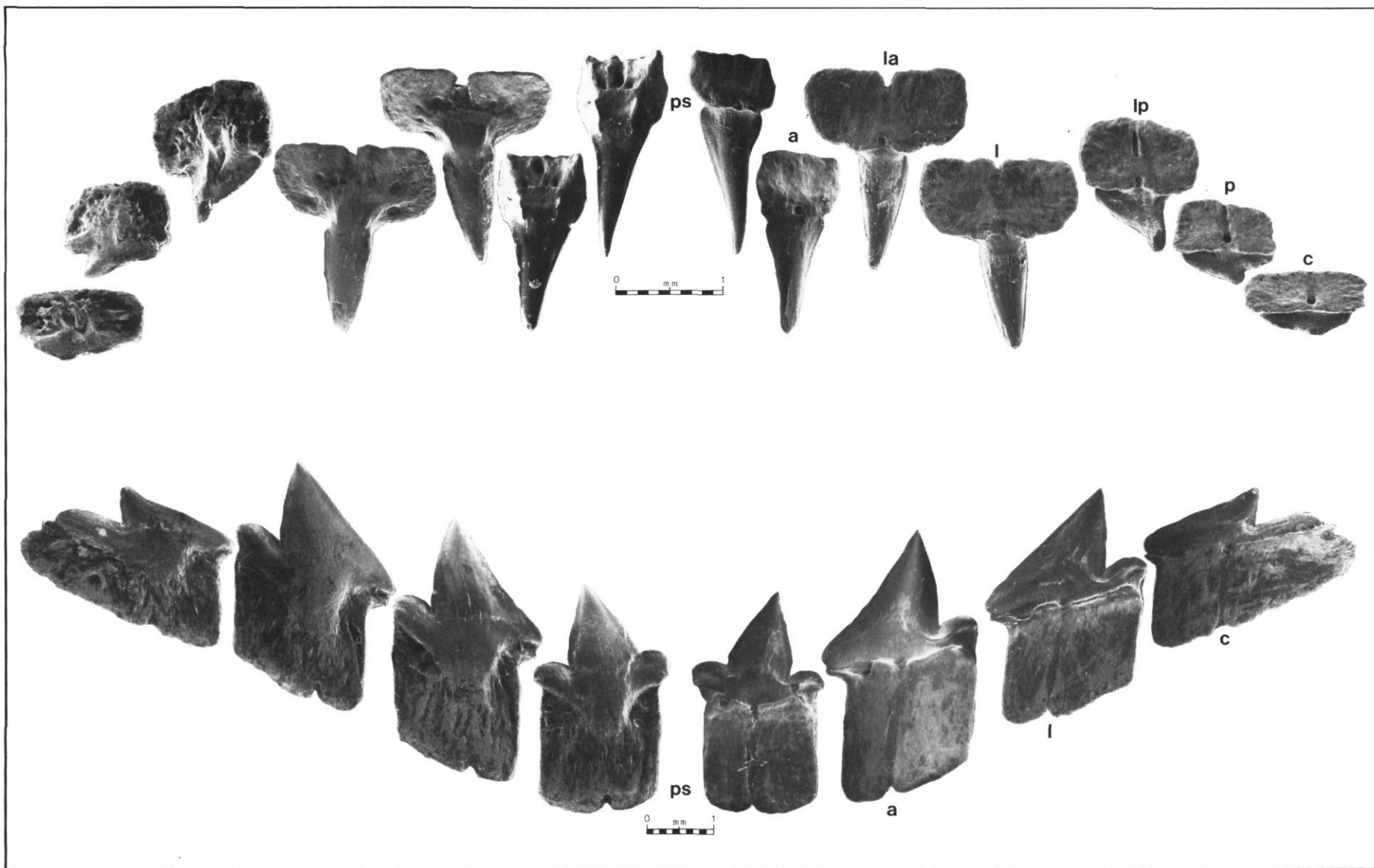


Plate 15. *Centroselachus crepidater* (BOCAGE & CAPELLO, 1864). Female 84 cm. t.l., Porcupine, N.E. Atlantic. Both upper parasymphysial and anterior teeth are from a male 61 cm. t.l., N. Bill Bailey, N.E. Atlantic. New taxonomic proposition: *Centroselachus crepidater* (BOCAGE & CAPELLO, 1864) such as proposed by GARMAN (1913).



Plate 16. *Scymnodon ringens* BOCAGE & CAPELLO, 1864. Female 102 cm. t.l., W. Hebrides, N.E. Atlantic. (Upper teeth). Lower teeth: Male 61 cm. t.l., N. Bill Bailey, N.E. Atlantic.

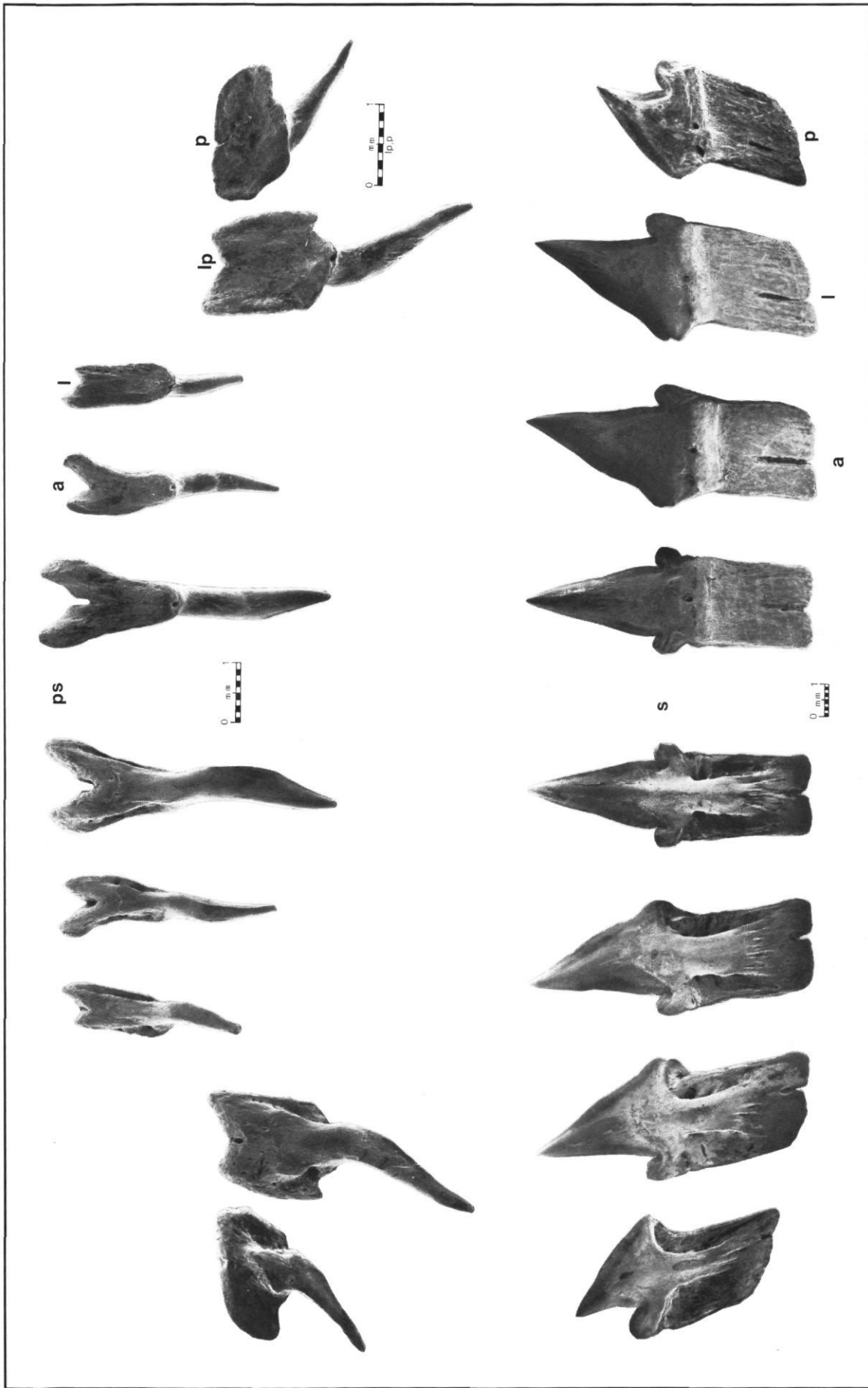


Plate 17. *Ssymnodalarias albicauda* TANIUCHI & GARRICK, 1986. Sex unknown 97.2 cm. t.l., Hokitika Canyon, New Zealand. New taxonomic proposition : *Ssymnodon albicauda* (TANIUCHI & GARRICK, 1986).

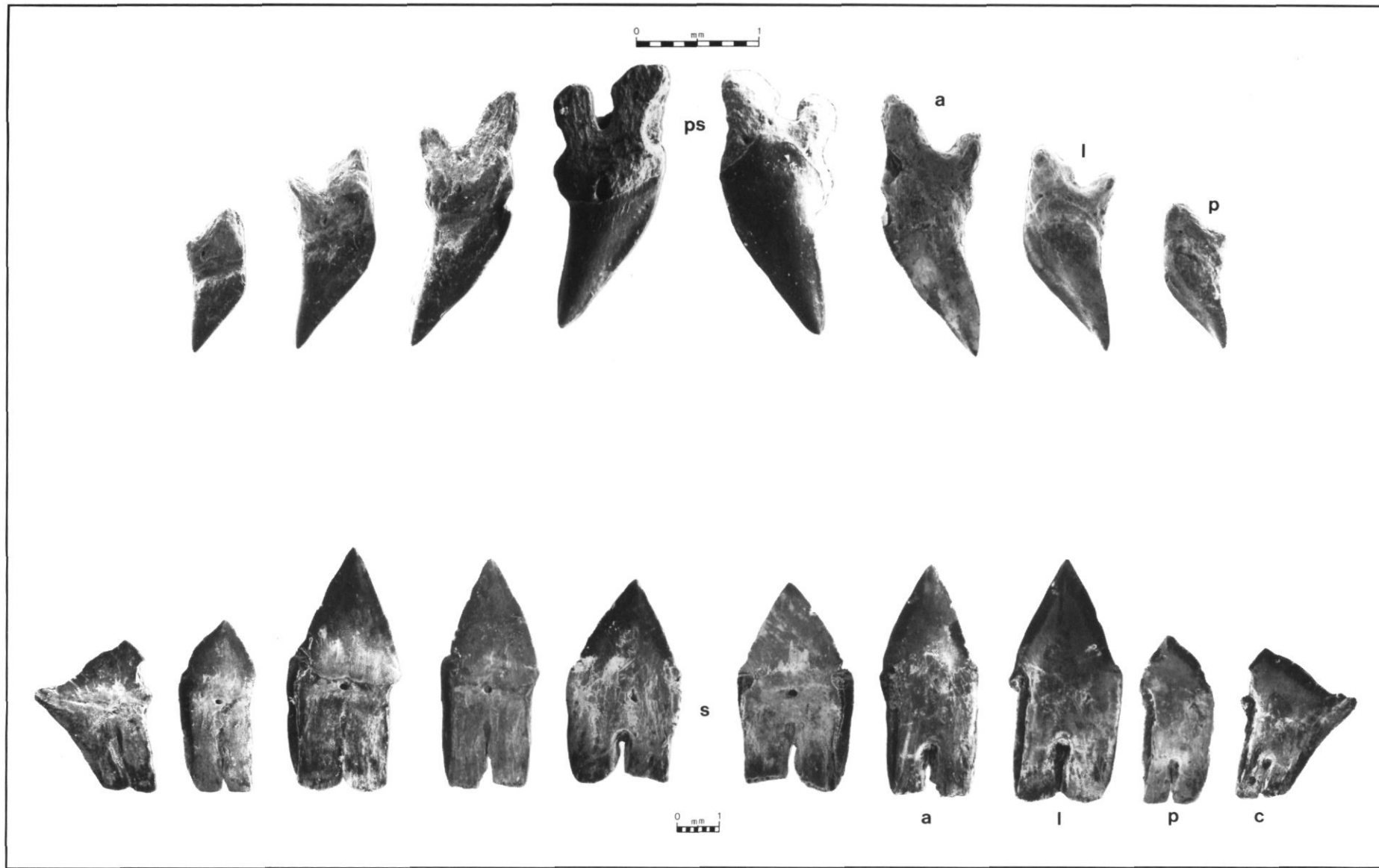


Plate 18. *Isistius brasiliensis* (QUOY & GAIMARD, 1824). Female 41 cm. t.l., Dakar, Senegal. The parasymphysial tooth from a female 24 cm. t.l., Hawai Island (2 x more enlarged).

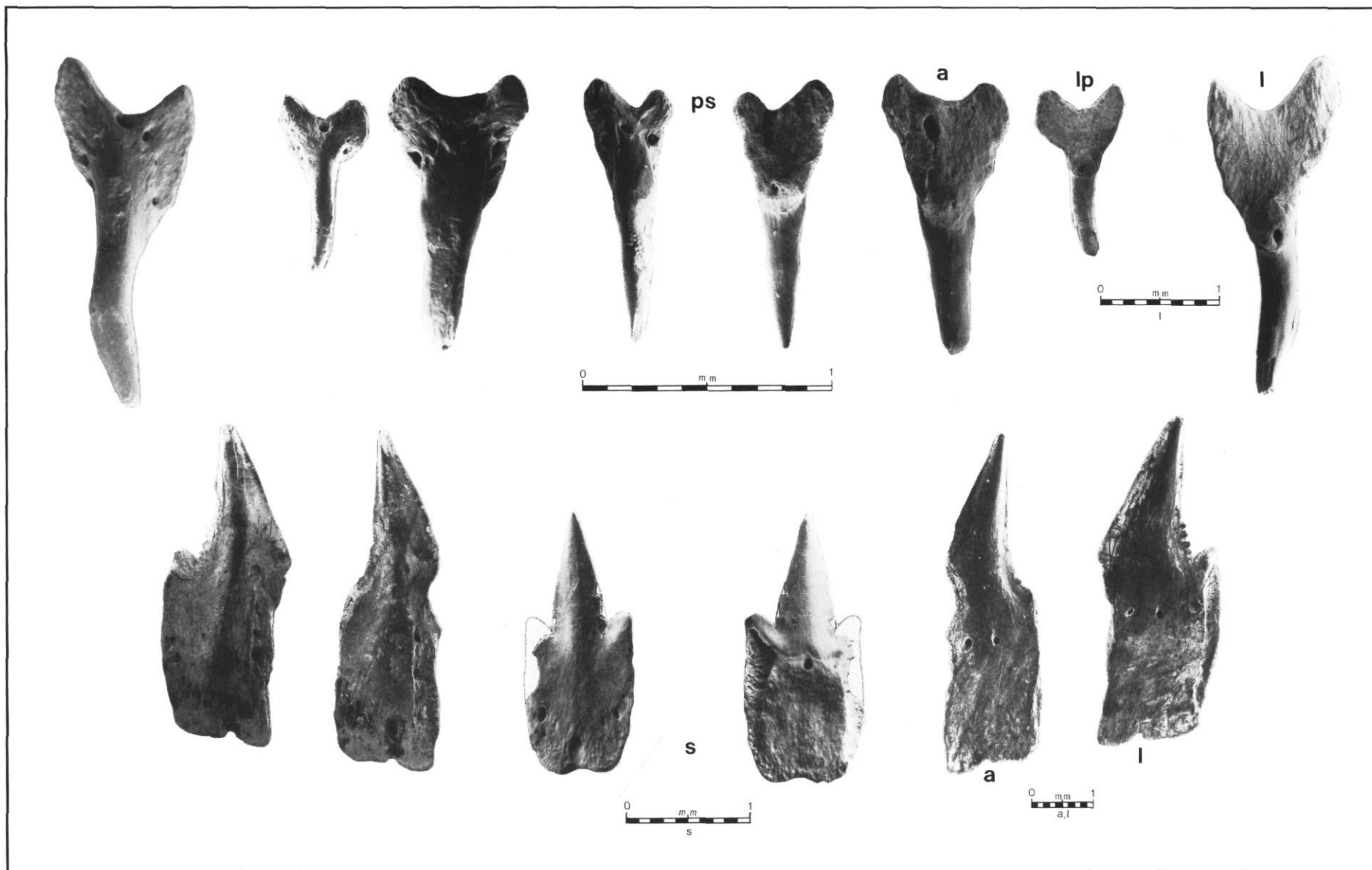


Plate 19. *Euprotomicroides zantedeschia* HULLEY & PENRITH, 1966. Female (Holotype) 17.6 cm. t.l., S. Africa: lower symphysial and upper teeth. (except the lateral one). The lower anterior and lateral teeth, as well as upper lateral are from a male 41.6 cm. t.l., S.W. Atlantic. (I.S.H.).

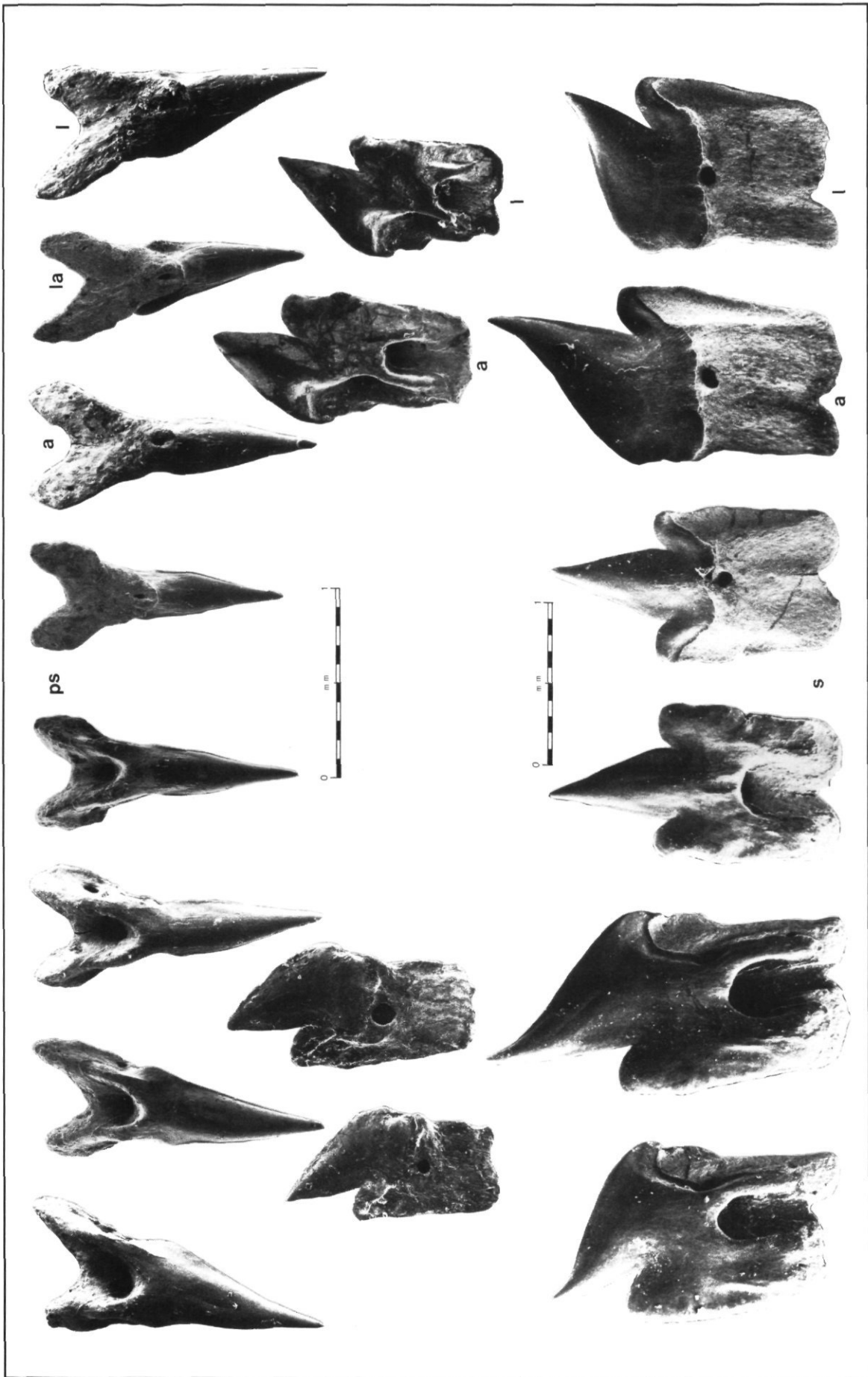


Plate 20. *Euprotomicrus bispinatus* (QUOY & GAIMARD, 1824). Male 20 cm. t.l., Mauritius Island. Centre of the plate. Female 11.5 cm. t.l., near Ascension Island, Central Atlantic.

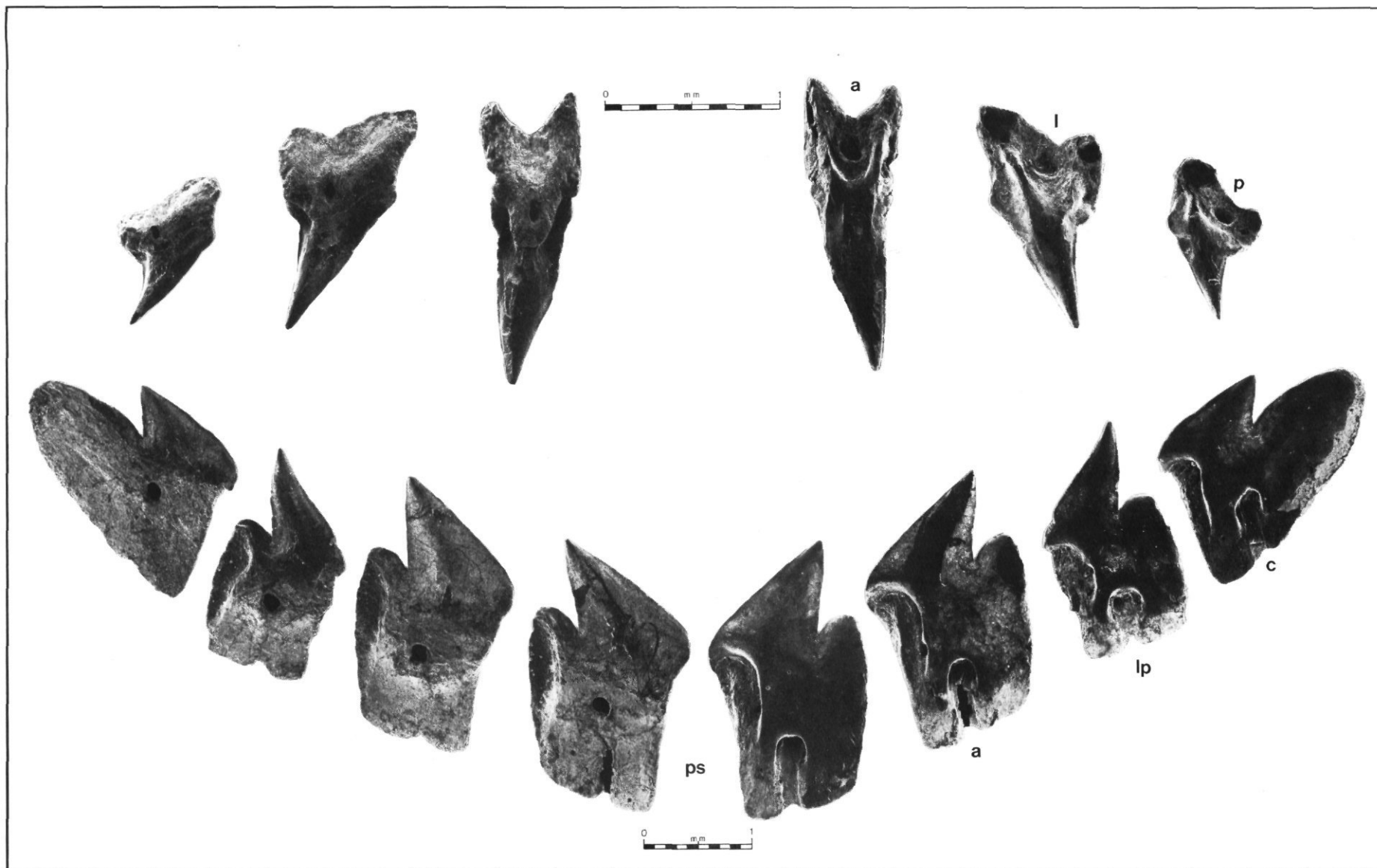


Plate 21. *Squaliolus laticaudus* (SMITH & RADCLIFFE, 1912). Female 22.7 cm. t.l., N.E. Atlantic. By courtesy of Dr. M. Stehmann I.S.H. Hamburg, Germany. New taxonomic proposition : *Euprotomicrus laticaudus* (SMITH & RADCLIFFE, 1912).

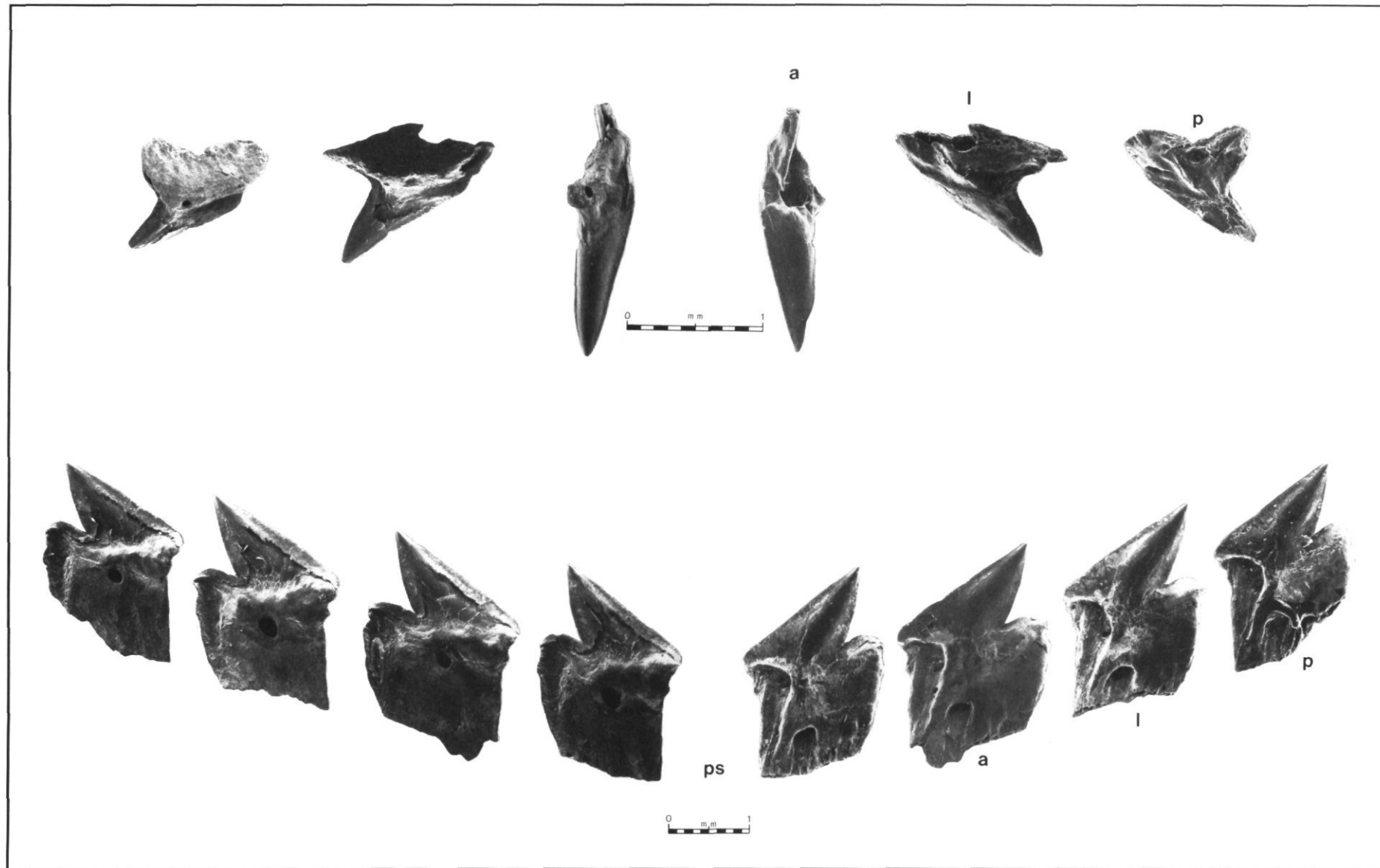


Plate 22. *Heteroscymnoides marleyi* (FOWLER, 1934). Female 28.4 cm. t.l., S.E. Atlantic. By courtesy of Dr. M. Stehmann I.S.H. Hamburg, Germany. New taxonomic proposition: *Euprotomicrus marleyi* (FOWLER, 1934).

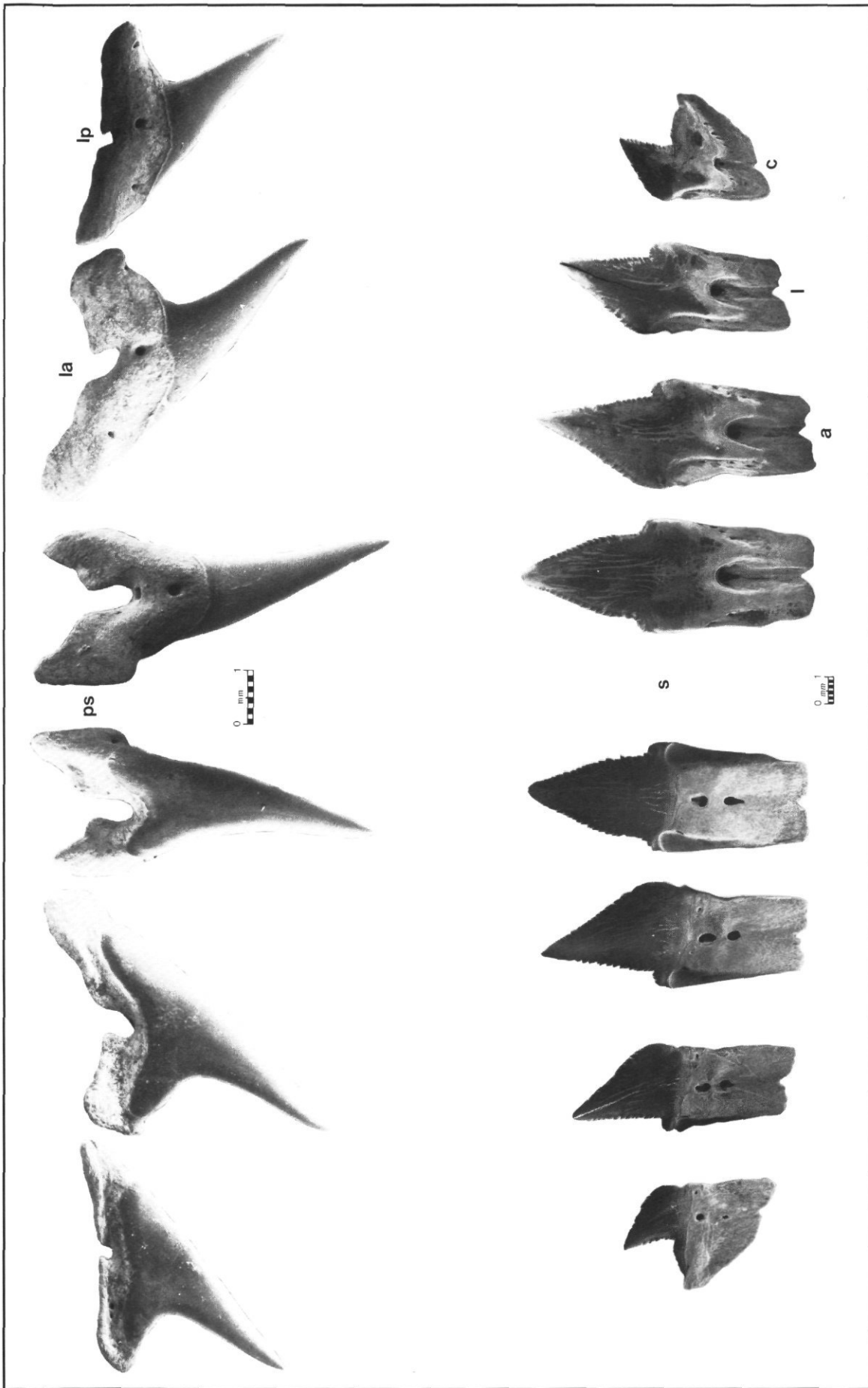


Plate 23. *Dalatias licha* (BONNATERRE, 1788). Female 147 cm. t.l. (upper teeth), Female 84 cm. t.l. (lower teeth), both from W. Hebrides, N.E. Atlantic.

