

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

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Part A : Selachii. No. 2a :

Order : Carcharhiniformes - Family : Triakidae

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Abstract

The teeth of all genera of the Triakidae are described and illustrated with SEM-photographs. Their morphology allows a direct generic assignment.
Key-words : Elasmobranchii - Selachii - Triakidae - Odontology.

Résumé

La morphologie des dents de tous les genres des Triakidae est décrite et figurée (clichés MEB), elle permet une identification générique.
Mots-clefs : Elasmobranchii - Selachii - Triakidae - Odontologie.

Kurzfassung

Die Zähne aller Gattungen der Triakidae werden beschrieben und mit REM-Photos abgebildet. Ihre Morphologie erlaubt eine direkte generische Zuordnung.

Schlüsselwörter : Elasmobranchii - Selachii - Triakidae - Odontologie.

Introduction

The teeth of the Triakidae in general never have been described nor properly been illustrated, including their roots.

A careful examination was initiated of the teeth of all living genera of the family Triakidae : *Triakis*, *Hemitriakis*, *Furgaleus*, *Mustelus*, *Scylliogaleus*, *Galeorhinus*, *Hypogaleus*, *Gogolia* and *Iago*.

Thus it was required to ascertain, whether or not tooth morphology is a reliable generic or specific character within this family.

Description of the odontological morphotypes

ORDER : CARCHARHINIFORMES sensu COMPAGNO 1984

This order comprises, after COMPAGNO (1984), eight families : the Triakidae, Proscylliidae, Leptochariidae, Scyliorhinidae, Pseudotriakidae, Sphyrnidae, Carcharhinidae and the Hemigaleidae. Besides the Triakidae, the tooth morphology of which will be described and illustrated in detail in this fascicle, the remaining families include the following genera :

Family : Proscylliidae

<i>Proscyllium</i>	HILGENDORF,	1904
<i>Eridacnis</i>	SMITH,	1913
<i>Ctenacis</i>	COMPAGNO,	1973
<i>Gollum</i>	COMPAGNO,	1973

Family : Leptochariidae

<i>Leptocharias</i>	SMITH, in MUELLER & HENLE,	1838
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Family : Scyliorhinidae

<i>Apristurus</i>	GARMAN,	1913
<i>Asymbolus</i>	WHITLEY,	1939
<i>Atelomycterus</i>	GARMAN,	1913
<i>Cephaloscyllium</i>	GILL,	1862
<i>Cephalurus</i>	BIGELOW & SCHROEDER,	1941
<i>Galeus</i>	RAFINESQUE,	1810
<i>Halaalurus</i>	GILL,	1862
<i>Holohalaalurus</i>	FOWLER,	1934
<i>Aulohalaalurus</i>	FOWLER,	1934
<i>Parmaturus</i>	GARMAN,	1906
<i>Haploblepharus</i>	GARMAN,	1913
<i>Pentanachus</i>	SMITH & RADCLIFFE,	1912
<i>Poroderma</i>	SMITH,	1837
<i>Schroederichthys</i>	SPRINGER,	1966
<i>Scyliorhinus</i>	BLAINVILLE,	1816

Family : Pseudotriakidae		
<i>Pseudotriakis</i>	GILL,	1893
Family : Sphymidae		
<i>Eusphyra</i>	GILL,	1862
<i>Sphyrna</i>	RAFINESQUE,	1810
Family : Carcharhinidae		
<i>Carcharhinus</i>	BLAINVILLE,	1816
<i>Scoliodon</i>	MUELLER & HENLE,	1837
<i>Galeocerdo</i>	MUELLER & HENLE,	1837
<i>Triaenodon</i>	MUELLER & HENLE,	1837
<i>Loxodon</i>	MUELLER & HENLE,	1838
<i>Glyphis</i>	AGASSIZ,	1843
<i>Prionace</i>	CANTOR,	1849
<i>Nasolamia</i>	COMPAGNO & GARRICK,	1983
<i>Isogomphodon</i>	GILL,	1862
<i>Lamiopsis</i>	GILL,	1862
<i>Rhizoprionodon</i>	WHITLEY,	1929
<i>Negaprion</i>	WHITLEY,	1940
Family : Hemigaleidae		
<i>Hemipristis</i>	AGASSIZ,	1843
<i>Hemigaleus</i>	BLEEKER,	1852
<i>Chaenogaleus</i>	GILL,	1862
<i>Paragaleus</i>	BUDKER,	1935

Family : Triakidae GRAY, 1851

This family, after COMPAGNO (1984), includes the following genera :

- Triakis* MUELLER & HENLE 1838, type species : *Triakis scyllium*
Hemitriakis HERRE 1923, type species : *Hemitriakis leucoperiptera*
Furgaleus WHITLEY 1951, type species : *Furgaleus ventrosa*
Mustelus LINCK 1790, type species : *Squalus mustelus*
Scylliogaleus BOULENGER 1902, type species : *Scylliogaleus quecketti*
Galeorhinus BLAINVILLE 1816, type species : *Squalus galeus*
Hypogaleus SMITH 1957, type species : *Hypogaleus zanzibarensis*
Gogolia COMPAGNO 1973, type species : *Gogolia filewoodi*
Iago COMPAGNO & SPRINGER 1971, type species : *Eugaleus omanensis*.

Most species of the Triakidae show a holaulacorhizid type of root. This means, a median groove with one, sometimes two central foramina and several lateral foramina, that are near both the inner and outer crown-root junctions.

Genus *Triakis* MUELLER & HENLE, 1838

The genus *Triakis* was defined in 1838 by MUELLER & HENLE (Charlesworth's Mag. Nat. Hist., 2 p. - Archiv. Naturg. Jahrg. 4, 1, p. 84) based on the type species *Triakis scyllium* MUELLER & HENLE, 1839 (Syst. Besch. Plagiost. : p. 63). Various authors later included many more species. The recentmost complete review of this genus was achieved by COMPAGNO (1984), who assigned the following species to the genus *Triakis* :

<i>Triakis scyllium</i>	MUELLER & HENLE,	1839
<i>Triakis semifasciata</i>	GIRARD,	1854
<i>Triakis megalopterus</i>	SMITH,	1849
<i>Triakis maculata</i>	KNER & STEINDACHNER,	1849
<i>Triakis acutipinna</i>	KATO,	1968

Furthermore, COMPAGNO also grouped *Triakis scyllium* and *Triakis semifasciata* in the subgenus *Triakis* (*Triakis*) and *Triakis megalopterus*, *Triakis maculata* and *Triakis acutipinna* in the subgenus *Triakis* (*Cazon*).

The present authors consider the genera *Triakis* and *Mustelus* as a continuous evolutionary development (see below). As COMPAGNO doesn't present arguments for his grouping, we cannot argue against that. Also, we don't want to change classification here.

T. maculata and *T. acutipinna* have developed a tooth morphology intermediate between *T. scyllium*, *T. semifasciata* and *T. megalopterus* and *Mustelus sensu stricto*.

Triakis scyllium MUELLER & HENLE, 1839
(Plate 1)

In the type species of the genus *Triakis*, the jaws show a weakly dignathic tooth morphology, that is expressed by an inclining principal cusp, a constriction near the outer crown-root junction, and the ornamentation of the crown. The dimensions of the teeth are in submillimetrical to plurimillimetrical range.

THE UPPER JAW

The teeth of the upper jaw present a well developed slender principal crown, that inclines more toward the commissure. The principal cusp of the anterior teeth is flanked by two mesial and two distal cusplets, of which the distal ones are more developed and pronounced than the mesial ones. There is only one distal cusplet left on the lateral teeth, that disappears on the commissural teeth.

The mesial cutting edge of the anterior teeth is slightly sigmoid, while on the lateral teeth it is stronger sigmoid and bends toward the commissure on the commissural ones.

At the outer side, the crown is strongly convex near the junction with the root and overhangs strongly the root.

The outer ornamentation consists of a well developed principal costulation. About five to eight longitudinal costules on the anterior teeth incline toward the commissure in about the same orientation as the cutting edge of the principal cusp on the lateral and commissural teeth. On the anterior and latero-anterior teeth the costules reach the height of the secondary cusplets, whereas on the extreme lateral and commissural ones they meet at the apex of the principal cusp and secondary cusplets, respectively. They all arise at the base of the crown, except for two or three intermediate ones.

There is no intermediate micro-ornamentation, nor a reticulation. The inner face has a similar, but less pronounced ornamentation.

The teeth of both upper and lower jaws have strongly holaulacorhizid roots with a broad and deep median groove, that divides the root into two subequal lobes. The mesial lobes are always slightly more voluminous than the distal ones. There are only a few lateral foramina on both inner and outer faces. The basal face is narrow on the inner part.

THE LOWER JAW

The teeth of the lower jaw present the same principal morphology as the teeth of the upper jaw, with the following differences :

- a. Outer ornamentation vaguely present.
- b. Inner ornamentation totally absent.
- c. Principal cusp less sigmoid and less inclining.
- d. The constriction near the outer crown-root junction is stronger, so that the whole crown base forms a pseudo-apron that presents a slight median depression.

Only a few specimens were examined. We were not able to detect evidence for a sexual dimorphism. Also none of the previous authors has ever mentioned it.

We observed an ontogenetic heterodonty in that the secondary cusplets gradually are reduced in size, much more so for the mesial than the distal ones (personal observations J. Herman).

Also the outer ornamentation on the crown diminishes during ontogeny.

Triakis semifasciata GIRARD, 1854 (Plate 2)

Proc. Acad. nat. Sci. Philad., 7 (6) : 196.

This species presents a weak dignathic heterodonty, that is limited to the inclining of the principal cusp, which is more pronounced in the upper teeth. Also is the presence of secondary cusplets more accentuated in the upper teeth. The dimensions of the teeth are millimetrical to hemicentimetrical in range.

The tooth morphology is very similar to that in *Triakis scyllium*. Therefore we restrict the description to the differences we have observed.

The following features distinguish *T. semifasciata* from *T. scyllium* :

- a. The mesial and distal secondary cusplets in both upper and lower jaws are less developed and lower, diminishing toward the commissure.
- b. The outer ornamentation on the crowns is absent, or hardly perceptible even at teeth of juvenile specimens. The costules are very short and less pronounced, but more numerous than on the teeth of *T. scyllium* (their number varies between 10 and 24).
- c. The inner ornamentation on the crowns is less pronounced even in juvenile specimens, and adults only preserve remains of it.

- d. The anterior cutting edge of the principal cusp bends in all teeth strongly toward the commissure in juvenile specimens and becomes nearly suberect in adult specimens.
- e. A pronounced outer constriction is present near the crown-root junction in both upper and lower teeth and in both juvenile and adult specimens.
- f. The root is lower and the median groove slightly broader.

Although numerous specimens were observed, we could not discover a true sexual dimorphism in isolated teeth. We observed an ontogenetic heterodonty in the gradual disappearance of the outer ornamentation, the disappearance of the inner ornamentation and the reduction of the mesial bending of the principal cusp. The latter becomes more and more suberect.

The odontological similarity of *T. scyllium* and *T. semifasciata* confirms their general similarity (COMPAGNO, 1984) and underlines the strong affinities between both species.

Triakis acutipinna KATO, 1968 (Plate 3)

Copeia, 1968 (2) : 320, figs. 1-2.

In this species we could hardly observe any dignathic heterodonty. The very small teeth are millimetrical to hemicentimetrical in size range.

Although the crown is broad based, it carries an erect, strong and slender cusp, that is rather low. Instead of secondary cusplets, there is a mesial and distal extension of the cutting edges. The distal extension has sometimes a serrulation.

There is a basal outer ornamentation, that consists of numerous short longitudinal costules. A similar inner ornamentation is less pronounced.

All teeth have a fair-sized median protuberance at the inner base of the crown, which on its surface presents also the same kind of costules as does the inner ornamentation. This particular protuberance, or uvula, is well known of teeth of Squatiniformes, most of the Orectolobiformes, Pristiophoriformes and most of the Squaliformes. Concerning the Triakidae, the uvula is only present on teeth of *T. acutipinna*, *T. maculata*, and *Mustelus sensu stricto*. It is absent on teeth of *T. scyllium* and *T. semifasciata*.

The outer face of the crown, medially at its lower part, presents the appearance like an apron.

Both outer and inner faces present a constricted crown-root junction, with the crown base overhanging the root, what we also observed in *Triakis maculata*, *Rhinotriakis henlei* and *Mustelus sensu stricto*.

The root is always strongly holaulacorhizid with a deep, broad median groove. The root lobes are more or less subequal although the mesial one is slightly more developed.

There is no sexual dimorphism apparent in the tooth morphology.

Triakis megalopterus SMITH, 1849

Pisces, III. Zool. S. Africa, 4 : 4, pl. 2.

Unfortunately we were not able to examine any specimen. However it seems to us, that the information of BASS, D'AUBREY & KISTNASAMY (1975), concerning the teeth of their specimen, is helpful.

Their observations were restricted to one female of nearly 140 cm TL.

Their figures show a strongly inclined single cusp and give the impression of a possible serration on the distal cutting edge extension. Considering all growth stages of other *Triakis* species investigated, this serration may be stronger in juvenile specimens. Also the mesial cutting edge may tend to incline slightly in a bow, and a microstructure as an outer basal ornamentation may be present.

Triakis maculata KNER & STEINDACHNER, 1867
(Plates 4, 5)

Sitzber. Akad. Wiss. Wien, 54 : 391.

This species has a very weak dignathic heterodonty. The dimensions of the teeth are plurimillimetrical to subcentimetric in range. The broad based cusp has a *Squatina*-like appearance : high but massive and subconical with a mesial and distal basal extension, respectively, that are slightly depressed.

The distal extension presents always a shape like a cusplet. All cusps of the teeth incline slightly toward the commissure including the very lateral ones.

Both, inner and outer basal ornamentation of the crown are of the type observed on the teeth of *T. acutipinna*. However the costules are always finer.

An outer median pseudoapron is also present, but less pronounced than in *T. acutipinna* or sometimes even hardly perceptible. The uvula is strong but less protruded than in *T. acutipinna*.

The outer constriction near the crown-root junction is very deep.

The holaulacorhizid root presents a deep median groove, and secondary lateral foramina are abundant. The root lobes are subequal, though the mesial lobe is generally slightly more developed (except for the teeth of the symphysial region).

The teeth of this species present a close similarity with those of *T. acutipinna*.

Conclusion on the genus *Triakis*

Although our original intention now as before is to restrict the tooth descriptions to the generic type, the heterogeneous tooth morphologies presented by the four species examined made it necessary to review them here.

Like COMPAGNO (1984) did, odontologically the four species can also be divided into two groups :

T. scyllium and *T. semifasciata* as one group *Triakis* (*Triakis*).

T. maculata and *T. acutipinna* as the other group *Triakis* (*Cazon*).

Key to the two groups :

- Principal cusp relatively compressed and fairly inclined toward the commissure.
- Secondary cusplets present but weakly developed.
- The crown has no true basal median apron or median uvula.
- The outer and inner ornamentation of the crown consists of fine elongate striae.
..... *T. scyllium* & *T. semifasciata*
- Principal crown suberect and *Squatina*-like.
- Secondary cusplets absent.
- The crown with a vague median apron and a basal median uvula.
- The outer and inner ornamentation of the crown consists of the same kind of strong basal costules.
..... *T. maculata* & *T. acutipinna*

The numerous morphological differences indicate the long independent evolution of each of the two groups.

Because of a constricted crown-root junction on both inner and outer faces with the outer crown overhanging the root and the presence of an uvula but also because of the *Squatina*-like principal cusp (all archaic features), we suppose that the latter group is the most primitive type of the genus *Triakis*.

Because of insufficient data on *T. megalopterus* it is not possible to ascertain its status here.

Genus *Hemitriakis* HERRE, 1923

This genus comprises two species : *Hemitriakis japonica* (MUELLER & HENLE, 1839) and *Hemitriakis leucoperiptera* HERRE, 1923. It was not possible to obtain material of the type species *H. leucoperiptera*, but as *H. japonica* is supposed to be conspecific (COMPAGNO, 1973) we therefore use *H. japonica* to define the tooth morphology of the genus *Hemitriakis*.

Hemitriakis japonica (MUELLER & HENLE, 1839)
(Plates 6, 7)

Syst. Besch. Plagiost. : 58, pl. 22.

This species presents a weak dignathic heterodonty. The teeth of the lower jaw differ from those in the upper by :

- a. An inner mesio-basal ornamentation on the lateral and commissural teeth.
- b. The presence of mesial secondary cusplets on anterior teeth.
- c. The slight inclination toward the commissure of the symphysial teeth.

The dimensions of all teeth are millimetrical to hemicentimetric in range.

Generally, they are strongly compressed (in inner-outer direction), presenting a fair-sized principal cusp, that is erect to suberect on anterior teeth and strongly inclined toward the commissure on lateral and commissural ones. Except for some basal costules, there is no true outer ornamentation.

THE UPPER JAW

The teeth of the upper jaw present a crown, that has a principal cusp with a well developed mesial cutting edge, strongly inclined toward the commissure. This anterior cutting edge is smooth and weakly sigmoid. Only the parasymphysial teeth and very anterior ones present one or sometimes two fairly developed mesial secondary cusplets. One to three distal secondary cusplets are present, inclining strongly toward the commissure.

The outer face of the crown is smooth and slightly depressed in the lower part. At the fair constriction of the crown-root junction the crown overhangs the root distinctly and shows reduced basal costules. These are easier to recognize on teeth of juvenile specimens.

The inner face of the crown presents fine irregular subvertical striae, hardly perceptible on the anterior teeth but well developed on lateral and commissural ones.

The root is always strongly holaulacorhizid with a broad and deep median groove. Numerous lateral foramina are scattered on the outer face. The root lobes are generally subequal, although the mesial one is slightly more developed.

THE LOWER JAW

The anterior teeth of the lower jaw present a principal cusp, that is always suberect or slightly inclined toward the commissure.

The principal cusps of the antero-lateral ones are strongly inclined toward the commissure, which is accentuated by the longitudinally expanded appearance, characteristic of these teeth.

The parasymphysial and anterior teeth near the symphysis present the remains of one or two mesial secondary cusplets and two fair distal secondary cusplets. The latter ones are also present on the lateral and commissural teeth. The outer crown base also well overhangs the root and shows weak basal costules.

The crown base of the lateral and commissural teeth presents on the inner face one to seven strong costules, that are short and stout, situated mostly on the mesial part.

The roots are all holaulacorhizid. The deep median groove on lower anterior teeth is always narrower than on those of the upper ones. The mesial root lobe of the lateral and commissural teeth is more developed than the distal one. There are ten to twenty outer lateral foramina on lateral and commissural teeth.

There is a slight sexual dimorphism, in that only the lower anterior teeth of males appear to be slimmer than those of females.

Genus *Furgaleus* WHITLEY, 1951

This genus comprises two species: *Furgaleus ventrosa* WHITLEY, 1951 and *Furgaleus ventralis* WHITLEY, 1943. The type species of this genus is *Furgaleus ventrosa* WHITLEY, 1951 (Proc. R. zool. Soc. N.S. Wales, 1949-1950, pp. 61-68, fig. 8-10).

We restrict the description to the generic type, because its original description indicates that both species present a similar tooth morphology and the same dignathic heterodonty.

Furgaleus ventrosa WHITLEY, 1951
(Plate 8)

The dentition presents a fair dignathic heterodonty. The lower teeth are strictly monocuspid and their slim principal cusp is erect, i.e. mesially very long and distally presenting an extension of the cutting edge without any serration.

The anterior teeth of the upper jaw have a suberect principal cusp that is strongly inclined toward the commissure on the lateral and commissural teeth.

The mesial cutting edge of the upper anterior teeth near the symphysis shows remains of secondary cusplets, regularly inclining and smooth from the third or fourth anterior to the last commissural ones. The distal cutting edge presents one to five secondary cusplets.

The dimensions of all teeth are plurimillimetrical in range. On both, outer and inner faces the crowns are absolutely smooth. The constriction near the crown-root junction is strong and the crown base well overhangs the root, which is more expressed near the root lobes. This is caused by a median depression at the upper end of the median groove. This basal median depression is present on the roots of all teeth. The inner basal part of the crown presents small irregular folds. The median groove is particularly broad on the teeth of the lower jaw. On the teeth of the upper jaw it tends to become superficial, which could indicate a secondary anaularorhizid.

The root lobes are subequal in size.

The teeth in the upper jaw of *Furgaleus* and *Hemitriakis* show generally the same morphology, but the following details distinguish both genera:

- a. The striae on the outer crown base are better developed in *Hemitriakis* and effect the whole crown base and a part of the outer crown surface. In *Furgaleus* they are only present on the part of the outer crown base, that overhangs the root.
- b. One to five distal secondary cusplets more elevated in *Furgaleus* than in *Hemitriakis* with one to three cusplets.
- c. A persistent inner ornamentation on the crown in *Hemitriakis*: short, narrow, subvertical striae particularly on the mesial inner part.
- d. A fair outer median depression on the root in *Furgaleus*, which is practically absent in *Hemitriakis*.
- e. The outer crown base stronger overhangs the crown-root junction in *Furgaleus*.

The teeth in the lower jaw cannot be mistaken for those of the upper: they have a smooth, suberect principal crown without secondary cusplets on either mesial or distal cutting edge extensions and subequal root lobes in *Furgaleus*. A fair inner ornamentation, an inclined principal cusp flanked by secondary cusplets and unequal root lobes particularly on lateral and commissural teeth in *Hemitriakis*.

Genus *Mustelus* LINCK, 1790

This genus comprises the following 20 species (COMPAGNO, 1984):

<i>Mustelus antarcticus</i>	GUENTHER,	1870
<i>Mustelus asterias</i>	CLOQUET,	1821
<i>Mustelus californicus</i>	GILL,	1864
<i>Mustelus canis</i>	(MITCHILL,	1815)
<i>Mustelus dorsalis</i>	GILL,	1864
<i>Mustelus fasciatus</i>	GARMAN,	1913
<i>Mustelus griseus</i>	PIETSCHMANN,	1913
" <i>Mustelus</i> " <i>henlei</i>	(GILL,	1863)
<i>Mustelus higmani</i>	SPRINGER & LOWE,	1963
<i>Mustelus lenticulatus</i>	PHILIPPS,	1932
<i>Mustelus lunulatus</i>	JORDAN & GILBERT,	1882
<i>Mustelus manazo</i>	BLEEKER,	1854
<i>Mustelus mento</i>	COPE,	1827
<i>Mustelus mosis</i>	HEMPRICH & EHRENBERG,	1899
<i>Mustelus mustelus</i>	(LINNAEUS,	1758)
<i>Mustelus norrisi</i>	SPRINGER,	1939
<i>Mustelus palumbes</i>	SMITH,	1957
<i>Mustelus punctulatus</i>	RISSO,	1826
<i>Mustelus schmitti</i>	SPRINGER,	1939
<i>Mustelus whitneyi</i>	CHIRICHIGNO,	1973

Of these, we examined the latter 14 species and, with the exception of "*Mustelus*" *henlei*, found their tooth morphology corresponding to that of the type species *Mustelus mustelus* (LINNAEUS, 1758).

After COMPAGNO (1984), the tooth morphology of the other species listed also corresponds to that of *M. mustelus*, except for *M. whitneyi*. Unfortunately we were not able to examine the latter, and therefore we withhold further comment on this species.

Because of the significant differences in the tooth morphology of *M. mustelus* and "*M.*" *henlei*, we will describe and illustrate both species and comment on the latter one.

Mustelus mustelus (LINNAEUS, 1758)
(Plates 9, 10)

Squalus mustelus LINNAEUS, 1758, Syst. Nat., ed. 10, 1: 235.

This species presents a weak dignathic heterodonty. The dimensions of the numerous teeth are in millimetrical range. The monocuspid crown is low, with a strongly reduced principal cusp sometimes reduced to only an elevation, or totally absent.

In the latter case, the cutting edge is limited to a discrete longitudinal ridge. The inner face of the crown presents a large median protuberance. This well developed uvula rests on a homologous swelling of the root, without a perceptible constriction between root and crown.

This is in contrast to the uvula observed in the genera *Triakis* (*T. acutipinna* and *T. maculata*), *Scylliogaleus* and also in "*Mustelus*" *henlei*, in which the uvula is separated from the median root swelling by a fair constriction.

Because of the constriction of the crown-root junction the outer crown base well overhangs the root.

A pronounced inner ornamentation, covering the crown

base, consists of numerous short, primary costules, that are slim and sigmoid. The outer ornamentation consists of fewer primary costules, that are short and stout. A secondary ornamentation between the primary costules forms a fine reticulation, which is well developed on both inner and outer faces of the lateral teeth and the inner face of the anterior ones. The outer secondary ornamentation on the anterior teeth diminishes in the extreme mesial and distal regions.

On the outer face we found the discrete remains of an apron. This apron on the median basal part of the crown elevates little only, a phenomenon that is never observed in "*M.*" *henlei* nor in the genus *Scylliogaleus*.

The holaulacorhizid root has a broad and deep median groove. The root lobes are subequal, although the mesial one may be slightly more developed. Like for the inner lateral foramina, there are only a few outer ones, of which the two principal ones are seldom well developed (this in contrast to those observed in *Scylliogaleus*).

"*Mustelus*" *henlei* (GILL, 1863)
(Plate 11)

Rhinotriacis henlei GILL, 1863, Proc. Acad. nat. Sci. Philad., 1862, 14: 486.

The dentition of this species is very indistinctly dignathic heterodont, expressed by differences in the outer ornamentation and the degree of development of the secondary cusplets.

The dimensions of the teeth are millimetrical to plurimillimetrical in range.

The teeth of the upper jaw present a prominent, short, suberect principal cusp, flanked by one or two, poorly developed distal cusplets, and always one mesial cusplet. The outer ornamentation consists of fair, short costules, that reach on the lateral teeth the height of the secondary cusplets. A secondary, reticulated ornamentation exists, limited to the extreme mesial and distal regions of the crown base. An apron is absent, but the median basal area presents a mild depression.

The inner face presents a well perceptible though poorly developed uvula. This is situated on a very weak swelling of the root, from which it is separated by a nearly invisible constriction.

Like the whole inner crown base the uvula is ornamented by small, very fine costules. These are fairly well developed on the commissural teeth but nearly unperceptible on the antero-lateral teeth, where they are mostly replaced by very vague striae.

The inner secondary ornamentation, that is well developed in the other examined species of *Mustelus*, is absent, or very indistinct.

The root is holaulacorhizid with longitudinally expanded root lobes. The median groove is narrow but deep. The few outer lateral foramina are irregularly distributed and of the likewise few inner lateral foramina the two main ones are poorly distinguished from the other ones.

The mesial root lobe is slightly more developed than the distal one.

The lower teeth have a root of the same type and have also about the same dimensions. Their secondary cusplets are less developed. The mesial one is only perceptible on the very anterior teeth and the distal ones are poorly developed.

The outer ornamentation is vague and effects only the lower part of the crown base. The inner ornamentation presents only some weak, short striae.

The principal cusp inclines stronger toward the commissure than on the teeth of the upper jaw.

Conclusions on the genus *Mustelus*

It is very difficult to distinguish the various nominal species of *Mustelus* based on isolated teeth only.

Only the following differences can be stated in general :

- the variability of the principal ornamentation;
- the discrete differences in the secondary ornamentation;
- the number of primary costules and their degree of development;
- the size of the teeth;
- the perceptibility of remains of a principal cusp.

Most of these features also vary ontogenetically, which makes a reliable specific distinction, based on tooth morphology only, hardly possible.

As result of this study it must be considered possible, based on tooth morphology, that many of the nominal species of *Mustelus* present extremes only of a wide ranging morphological variability of a few true species, respectively.

On the other hand, compared with all the other species examined of *Mustelus*, "*Mustelus*" *henlei* differs significantly from all congeners with regards to its tooth morphology.

We noted the following remarkable features of "*M.*" *henlei* :

- a well developed principal cusp;
- partially persisting secondary cusplets, that are well developed on the upper teeth;
- a poorly developed inner uvula;
- a very poorly developed inner median swelling of the root;
- the nearly complete disappearance of ornamentation on the lower teeth;
- a poor outer median depression on the crown base;
- a fairly transversally expanded root.

COMPAGNO (1984) reassigned this species from the genus *Rhinotriacis* GILL, 1863 to *Mustelus* LINCK, 1790. Based on tooth morphology, it is very doubtful that this is correct. Referring to the conclusion on the genus *Triakis*, we were able to subdivide this genus into two groups : *T. scyllium* and *T. semifasciata* as one, and *T. acutipinna* and *T. maculata* as an other. Compared with these species, "*M.*" *henlei* presents odontological affinities particularly to the latter group. It is clearly distinguished odontologically from the subgenus *Triakis* (*T. scyllium* and *T. fasciata*) and from the remaining species of *Mustelus*.

But "*M.*" *henlei* can also be distinguished from *T. acutipinna* and *T. maculata* by the following features :

- the lesser reduction of the secondary cusplets;

- the lesser developed uvula and inner median root swelling;
- the different configurations of the principal cusp (non squatinoid);
- an apron is perceptible in *T. acutipinna* and *T. maculata* but unperceptible in "*M.*" *henlei*.

These observations indicate the diversity of triakid phylogenetic lineages in general, of which only the genus *Mustelus* ("*M.*" *henlei* and perhaps *M. whitneyi* excluded) appears to be monophyletic, while the other supraspecific taxa seem to be polyphyletic in originating from numerous different phylogenetic lineages.

Genus *Scylliogaleus* BOULENGER, 1902

This genus is monotypic with the only species *Scylliogaleus queckettii* BOULENGER, 1902 (Ann. Mag. nat. Hist. vol. 10, p. 51, pl. 4).

Scylliogaleus queckettii BOULENGER, 1902 (Plate 12)

The dentition of this genus is strictly monognathic heterodont.

The numerous teeth are very small, generally hemimillimetric. On the symphyseal, lateral or commissural teeth, a principal cusp of the crown is totally absent. A longitudinal, subrectilinear ridge divides the crown into an outer and inner face, which both are weakly swollen.

The outer surface of the crown is slightly depressed and presents a heavy ornamentation, that always diminishes at the extreme mesial and distal regions, in at most basal half of the crown's height. This principal ornamentation consists of numerous, small, irregular, slightly sigmoid ridges. The outer crown base overhangs fairly the root and shows a reticulated secondary ornamentation. However there is no trace of a pseudo-apron, in contrast to what we observed on *Mustelus* teeth.

The principal ornamentation is less strong, but its costules are fairly high. It reaches at the mesial and distal parts sometimes to the longitudinal ridge. The also reticulated inner secondary ornamentation is more regular than the outer one.

The lower outer crown base shows a simple weak bow in the occlusal view.

The inner face of the crown presents a very strong, thick uvula, that rests on a heavy median root swelling, formed by an intermediate, well pronounced constriction.

The root is holaulacorhizid or sometimes hemiaulacorhizid. The hemiaulacorhizy, consisting of an inner aperture of the median canal, is more frequent particularly on teeth of the lower jaw.

The few outer lateral foramina are subequal in size. The inner lateral foramina are variable in number. The two well distinguished principal ones flank the median root swelling.

The inner median foramina of the hemiaulacorhizid teeth are rather wide (as in Squatinoids).

The root lobes are subequal in size.

The following features separate the teeth of this genus from those of *Mustelus*, "*Mustelus*" *henlei* and the other Triakidae :

- a. Principal cusp totally absent.
- b. Apron or pseudo-apron totally absent.
- c. A characteristic ornamentation.
- d. A hemiaulacorhizid root.

Genus *Galeorhinus* BLAINVILLE, 1816

After the recentmost review (COMPAGNO, 1984), this genus is monotypic for *Galeorhinus galeus* (LINNAEUS, 1758), (Syst. Nat., ed. 10, 1 : 234).

Galeorhinus galeus (LINNAEUS, 1758)
(Plate 13)

The dentition of this species is very weakly dignathic heterodont in that the principal cusp of the upper teeth is somewhat more inclined.

The dimensions of the teeth are plurimillimetrical to subcentimetrical in range.

The upper and lower teeth present a principal cusp, that is suberect in those near the symphysis, and more or less strongly inclined in the lateral and commissural teeth. The mesial cutting edge is suberect, forming a weak bow toward the commissure, or is also sometimes sigmoid. This feature is independent of sex or age of a specimen. The lateral and commissural teeth present 2 to 8 very small distal secondary cusplets. Only the teeth near the symphysis bear 1 to 5 mesial secondary cusplets.

On the anterior teeth, the outer mesio-basal region of the crown always shows a weak serration, which is hardly visible on the mesial secondary cusplets.

The crown-root junction is a very weak constriction.

Except for 1 to 3 tiny mesial striae on the inner basal crown part, both outer and inner ornamentations as also an uvula are absent.

The root is fairly holaulacorhizid, with a narrow and deep median groove, but without an inner median depression. There are more than 20 outer lateral foramina, lined in a relatively regular way. The also numerous homologous inner ones are situated in small, narrow, subvertical depressions. It is impossible to distinguish any principal lateral foramina.

The root lobes are subequal in size and slightly inclined.

Genus *Hypogaleus* SMITH, 1957

The type species of this genus, by original designation *Hypogaleus zanzibarensis* SMITH, 1957 (Ann. Mag. nat. Hist., (12) : 10 p., fig. 2, pl. 19), was considered by COMPAGNO (1984) as a junior synonym of *Hypogaleus hyugaensis* (MIYOSI 1939). Hereby, the genus became monotypic.

Hypogaleus hyugaensis (MIYOSI, 1939)
(Plate 14)

Bull. biogeogr. Soc. Tokyo, 9 (5) : 91, fig. 1, as *Eugaleus hyugaensis*.

The dentition of this species presents a very weak dignathic heterodonty, in that the upper teeth are vertically longer than the lower ones.

The dimensions of all teeth are plurimillimetrical to hemicentimetrical in range.

The principal cusp of the teeth near the symphysis is suberect, while in the lateral teeth it is strongly inclined toward the commissure. The mesial cutting edge is relatively strongly sigmoid. The distal edge is strongly inclined mesially.

Extremely poorly developed mesial secondary cusplets are present on the lower parasymphysial teeth and occasionally also on the upper ones, on which they appear as simple ridges.

The distal secondary cusplets are very small and less numerous than in *Galeorhinus*. There are 4 to 5 cusplets on the anterior teeth, diminishing and disappearing toward the commissure.

The crown is not ornamented and an uvula is absent.

The constriction of the crown-root junction is very weak. The outer crown base is strongly curved in the same way as the root lobes do.

The root is holaulacorhizid, presenting a shallow inner median depression. The median groove is broad and deep. The outer lateral foramina are less numerous than in *Galeorhinus* (6 to 15 versus over 20), but their aperture is larger. The same differences hold true for the inner lateral foramina.

Furthermore, the following features separate *Hypogaleus* from *Galeorhinus* :

- a. The upper teeth are much longer than the lower ones.
- b. The distal secondary cusplets are less numerous.
- c. The mesial secondary cusplets are less developed.
- d. The mesial cutting edge of the principal cusp is stronger sigmoid.
- e. The root lobes are curved.
- f. Root foramina are less numerous.

The odontology of *Hypogaleus* presents very close affinities with *Galeorhinus*, *Hemitriakis* and *Furgaleus*, but differs greatly from the other Triakidae.

Genus *Gogolia* COMPAGNO, 1973

The type species of this monotypic genus is *Gogolia filewoodi* COMPAGNO, 1973 (Proc. Calif. Acad. Sci., 39 (19), p. 383). Known by the holotype female with an embryo only. We thank its author for having given us the possibility to obtain some teeth of this rare species.

Gogolia filewoodi COMPAGNO, 1973
(Plate 15)

The dentition presents a slight dignathic heterodonty. The teeth of the upper jaw differ from those of the lower by having an outer basal ornamentation on the crown.

The dimensions of the teeth are millimetrical to plurimillimetrical in range.

The principal cusp of the teeth near the symphysis is suberect and strongly inclined toward the commissure.

The mesial cutting edge, inclining toward the commissure, bears on anterior teeth a strong serration, that quickly diminishes and disappears toward the antero-lateral teeth. It is rather impossible that this serration could be the result of absorption of the mesial secondary cusplets. Except for the 2 to 4 parasymphysial teeth, the distal cusplets are fairly well developed.

The outer constriction near the crown-root junction is relatively deep, so that the crown base forms a pseudo-apron. The constriction is better pronounced on teeth of the lower jaw.

An uvula is absent.

An outer ornamentation on the crown base of the upper teeth consists of tiny, irregular and sigmoidal costules, that rise subvertically and then incline sigmoid-like toward the commissure.

This phenomenon is particularly pronounced on the distal part of the crown.

The crown surfaces of the lower teeth are strictly smooth. The root is in general holaulacorhizid. A sporadic hemiaulacorhizy cannot be excluded, but the samples were effected by cleaning with too strong enzymetic solutions.

The suspected hemiaulacorhizy is based on a deep median groove, that is very narrow on the inner and wide on the outer part.

The inner median depression is poorly developed as are also the few lateral foramina.

Based on only one specimen, we cannot comment on a possible intraspecific variability.

Genus *Iago* COMPAGNO & SPRINGER, 1971

This genus is represented by 2 species: *Iago garricki* FOURMANOIR & RIVATON, 1979 and the type species *Iago omanensis* (NORMAN, 1939). COMPAGNO & SPRINGER, 1971: Fishery Bull. Fish Wild. Serv. U.S., 69 (3), p. 615.

Iago omanensis (NORMAN, 1939) (Plate 16, 17)

Eugaleus omanensis NORMAN, 1939, John Murray Exped. Sci. Rep., 7 (1): 11.

This species presents hardly any dignathic heterodonty; only the outer ornamentation of the upper teeth is more pronounced.

The dimensions of the teeth are hemimillimetrical to millimetrical in range.

Except for the parasymphysial teeth of the upper jaw, the principal cusp of which sometimes is flanked by a mesial and distal cusplet, all teeth are monocuspid. The slender cusp inclines more and more toward the commissure. The mesial cutting edge is suberect and slightly sigmoid. The distal cutting edge is sharply angled.

The outer crown base of the upper teeth presents some small subvertical costules, that incline rapidly toward the commissure and join in an irregular, sigmoidal ridge along the lower part of the crown base.

The extreme mesial and distal regions of the crown base present a fine, reticulated, secondary ornamentation.

The inner crown surface of upper and lower teeth is strictly smooth.

The outer crown surface of the lower teeth near the symphysis is also smooth. The anterior to extreme lateral lower teeth present a slender sigmoid ridge running subparallel to the outer crown base and arising half way the mesial region.

The extreme lateral to commissural lower teeth present some outer mesio-basal costules and the same distal sigmoid ridge.

The reticulated secondary ornamentation is also present. The constriction near the crown-root junction is pronounced in the teeth of both upper and lower jaws.

The pseudo-apron of the outer crown base tends to develop costules.

An uvula and inner median depression of the root are absent.

The root is always holaulacorhizid, with a broad, deep median groove.

About 3 to 9 lateral foramina are scattered on the outer face and show apertures of different size, as well as the extremely irregularly scattered inner, secondary lateral foramina.

The mesial root lobe of the teeth is better developed than the distal one, except for the upper teeth near the symphysis. The root lobes are subequal in size, but the mesial one is slightly less voluminous than the distal one. With the exception of the commissural teeth, the root base is more or less flat.

Key to the genera based on odontological characters:

1. *Principal cusp hardly perceptible or even absent*:
 - a – Apron or pseudo-apron absent
 - Root type hemiaulacorhizid
 - *Scylliogaleus*
 - b – Discrete remains of a pseudo-apron present
 - A poorly developed set of principal lateral foramina
 - *Mustelus*
(with exception of "*M.*" *henlei* and *M. whitneyi*)
2. *Principal cusp well developed, mesial or distal cusplets and apron present*:
 - *Gogolia*
3. *Principal cusp well developed, mesial or distal cusplets present but apron absent*:
 - a. – Poorly developed uvula present:
 - Outer ornamentation on the crown base well developed
 - Principal cusp short and suberect
 - *Rhinotriacis henlei*
 - b – Uvula absent and ornamentation on the crown absent:
 - Mesial cutting edge strongly sigmoidal
 - Up to 5 distal cusplets
 - *Hypogaleus*

- Mesial cutting edge suberect
 - Up to 8 distal cusplets
 *Gaelorhinus*
 - c - Uvula absent and ornamentation on the crown present :
 - Mesial cusplets present
 - One or two distal cusplets present
 *Triakis (Triakis)*
 - Mesial cutting edge smooth
 - Root type holaulacorhizid to anaulacorhizid
 - Up to 3 distal cusplets
 *Furgaleus*
 (upper teeth only)
 - Mesial cutting edge smooth
 - Root type holaulacorhizid
 - Up to 5 distal cusplets
 *Hemitriakis*
4. *Principal cusp well developed but mesial and distal cusplets absent :*
- a - Uvula present
 - Inner and outer ornamentation consisting of numerous small longitudinal costules
 *Triakis (Cazon)*

- b - Uvula absent
 - Inner and outer ornamentation present
 *Furgaleus*
 (lower teeth only)
 - Inner and outer ornamentation absent
 - Distal cutting edge sharply angled
 *Iago*

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The S.E.M. photographs were taken by Mr. P. Grootaert, Institut Royal des Sciences naturelles de Belgique, Brussels and printed by Mr. H. Stout, Brussels.

Erratum

Unlike mentioned in the general introduction (1987) of this series, the figured teeth will be deposited at Brussels, Belgium, Institut Royal des Sciences Naturelles de Belgique (I.R.S.N.B.), or with the specimen in its original collection.

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Glossary

(also applying to first issue of this series : Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supra specific taxa of Chondrichthyan fishes. Part A : Selachii No. 1 : Order : Hexanchiformes - Family : Hexanchidae. Commissural teeth. Herman J., Hovestadt-Euler M., Hovestadt D.C., Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie, 57 : 43-56, 1987)

Anaulacorhizid

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 end of jaw.

Dignathic

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

Distal

Toward end of jaw.

File

Tooth row from symphysis toward end of jaw (longitudinally).

Heterodonty

Different tooth morphology within a set of teeth.

Inner face

View from inside the mouth.

Lateral

Tooth positions half way along the jaw.

Median keel

Tranverse ridge dividing crown into inner and outer face.

Mesial

Toward junction (symphysis) of left and right jaw part.

Monognathic

Heterodont by having different tooth morphology within one jaw only.

Outer face

View from outside the mouth.

Posterior

Tooth positions toward the end of jaw.

Row

Tooth row from inner face to outer face of jaw (transversally).

Symphysial

Teeth at junction of both halves of a jaw.

Uvula

Lobate extension of the inner crown base.

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Plate 1. – *Triakis (Triakis) scyllium* MUELLER & HENLE, 1839, male 62 cm (t.l.), Japan. Upper anterior (1), upper lateral (2), upper lateral, more posterior (3), lower anterior (4) and lower posterior (5) teeth; outer (a) and inner (b) views.

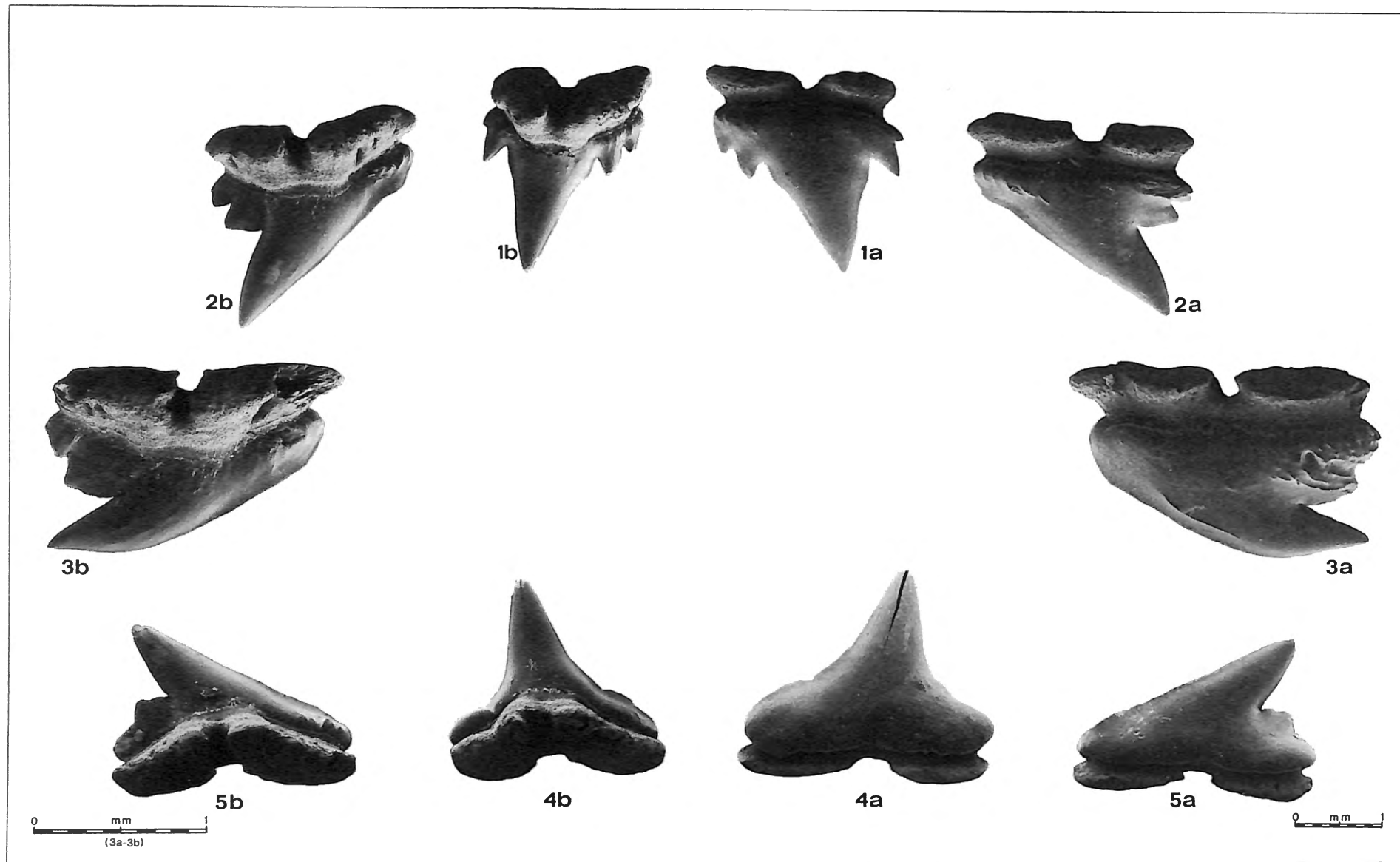


Plate 2. – *Triakis (Triakis) semifasciata* GIRARD, 1854, female 148 cm (t.l.), California. Upper anterior (1), upper lateral (2), upper commissural (3), lower anterior (4) and lower posterior (5) teeth; outer (a) and inner (b) views.

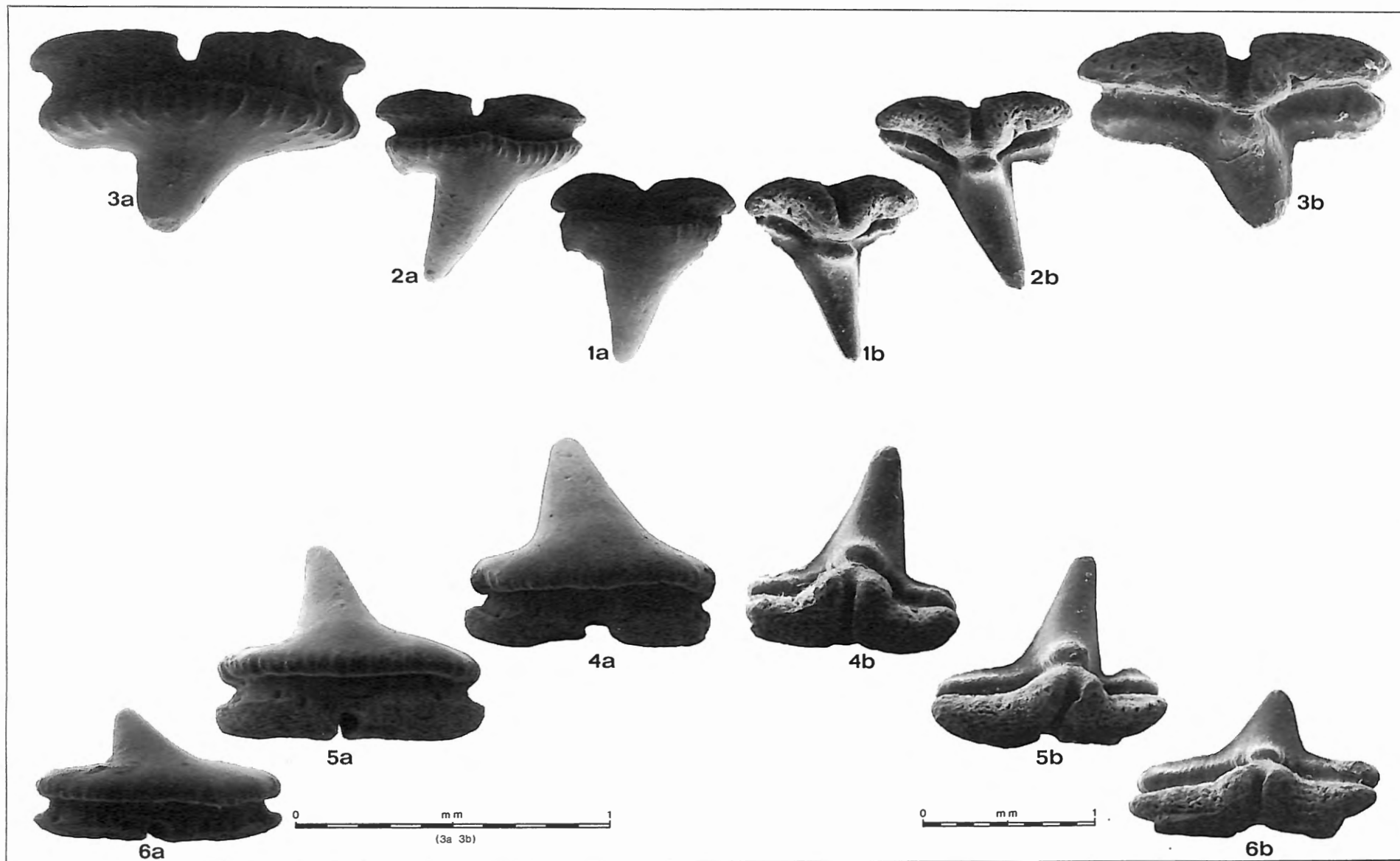


Plate 3. — *Triakis (Cazon) acutipinna* Kato, 1968, male 89 cm (t.l.), Ecuador. Upper anterior (1), upper lateral (2), upper posterior (3), lower anterior (4) and lower lateral (5) and lower lateral near the commissure (6); outer (a) and inner (b) views.

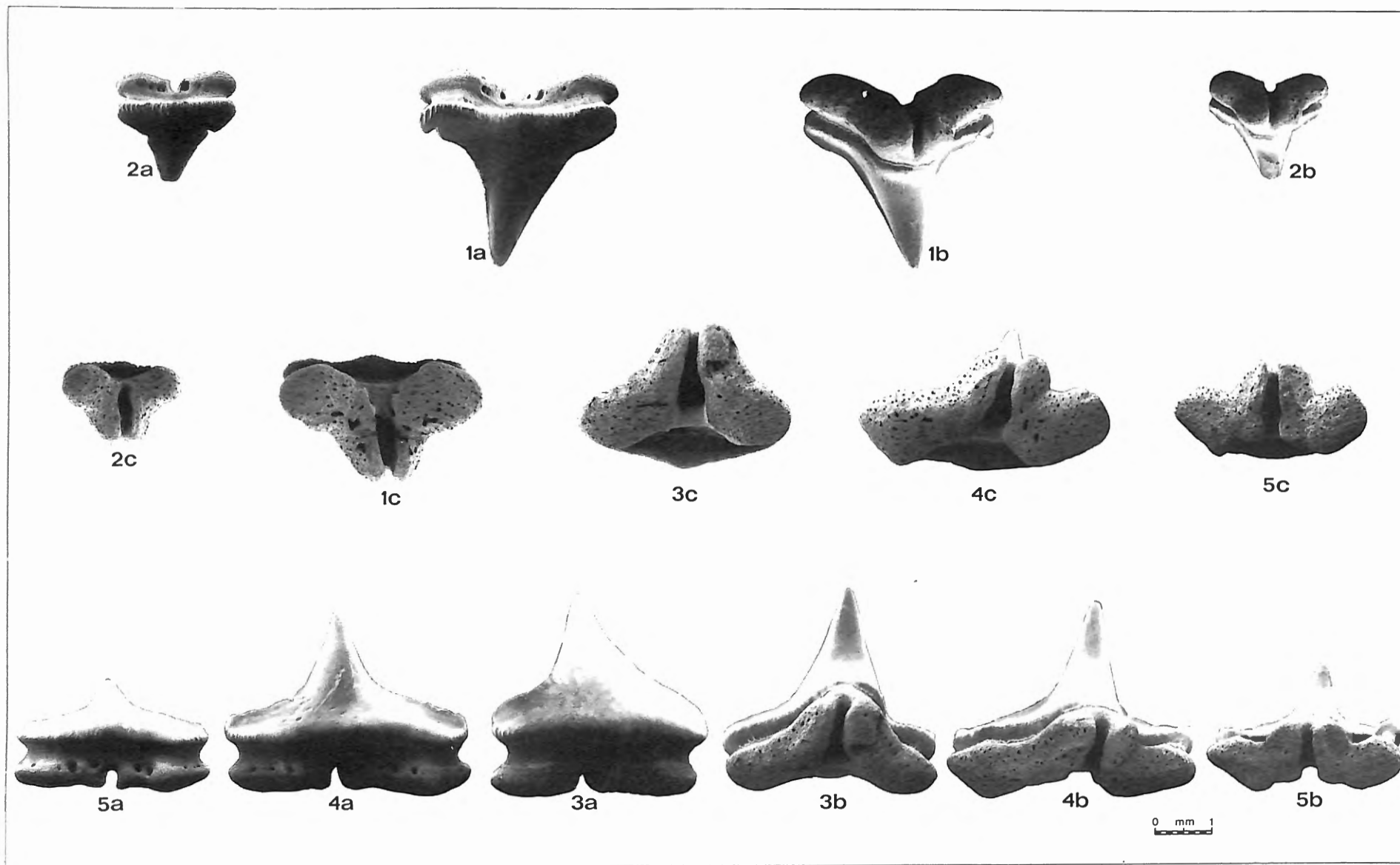


Plate 4. – *Triakis (Cazon) maculata* KNER & STEINDACHNER, 1867, female 149 cm (t.l.), Peru. Upper anterior (1), upper lateral (2), lower anterior (3), lower antero-lateral (4) and lower lateral (5) teeth; outer (a), inner (b) and radicular (c) views.

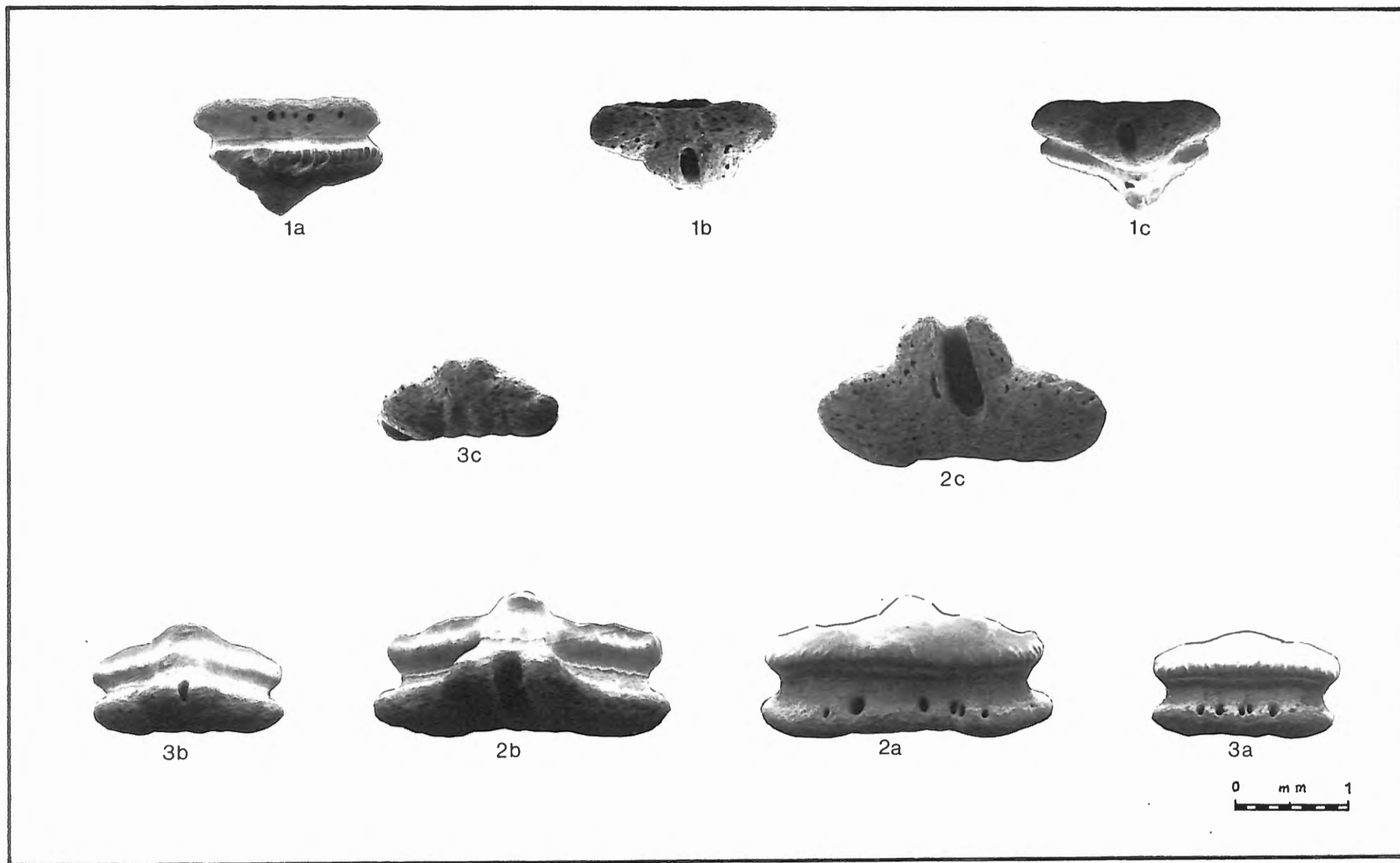


Plate 5. – *Triakis (Cazon) maculata* KNER & STEINDACHNER, 1867, female 149 cm (t.l.), Peru. Upper commissural (1), lower postero-lateral (2) and lower commissural (3) teeth; outer (a), inner (b) and radicular (c) views.

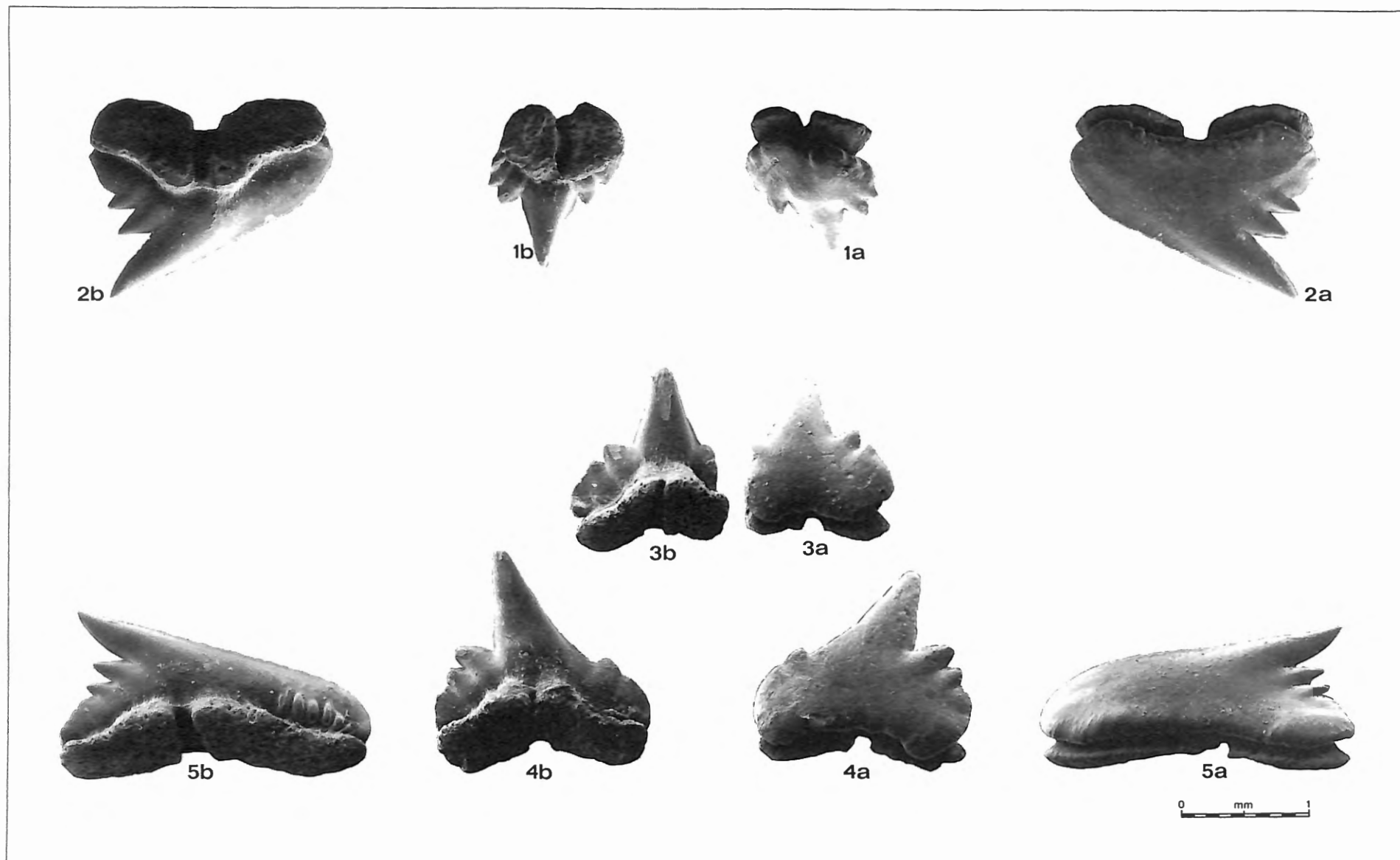


Plate 6. – *Hemitriakis japonica* (MUELLER & HENLE, 1839), male 88 cm (t.l.), China Sea. Upper parasymphysial (1), upper anterior (2), lower parasymphysial (3), lower anterior (4) and lower antero-lateral (5) teeth; outer (a) and inner (b) views.



Plate 7. – *Hemitriakis japonica* (MUELLER & HENLE, 1839), male 88 cm (t.l.), China Sea. Upper lateral (1), upper postero-lateral (2), lower lateral (3), lower postero-lateral (4) teeth; outer (a) and inner (b) views.

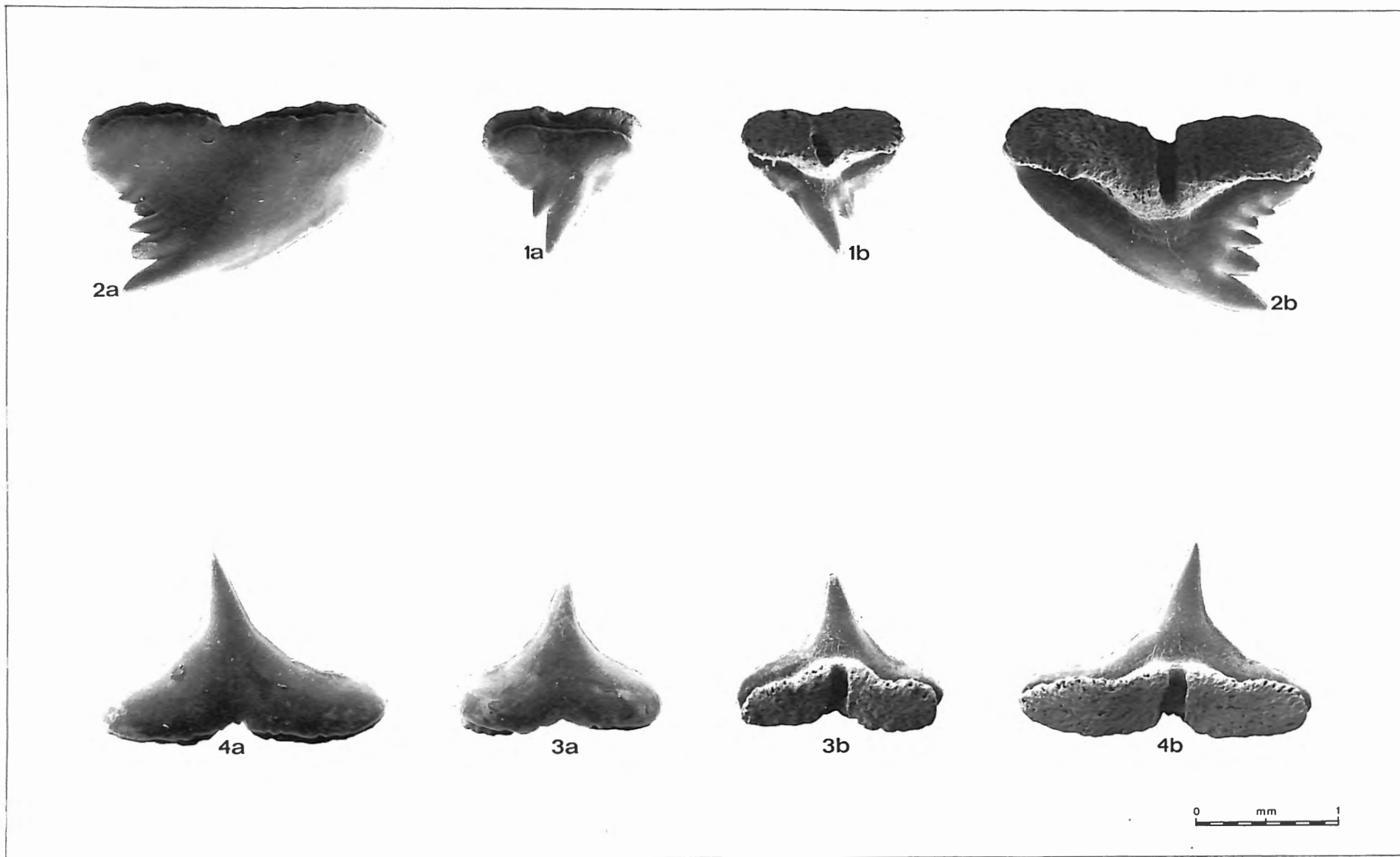


Plate 8. — *Furgaleus ventrosa* WHITLEY, 1951, male 98 cm (t.l.), North Australia. Upper parasymphysial (1), upper antero-lateral (2), lower anterior (3) and lower lateral (4) teeth; outer (a) and inner (b) views.

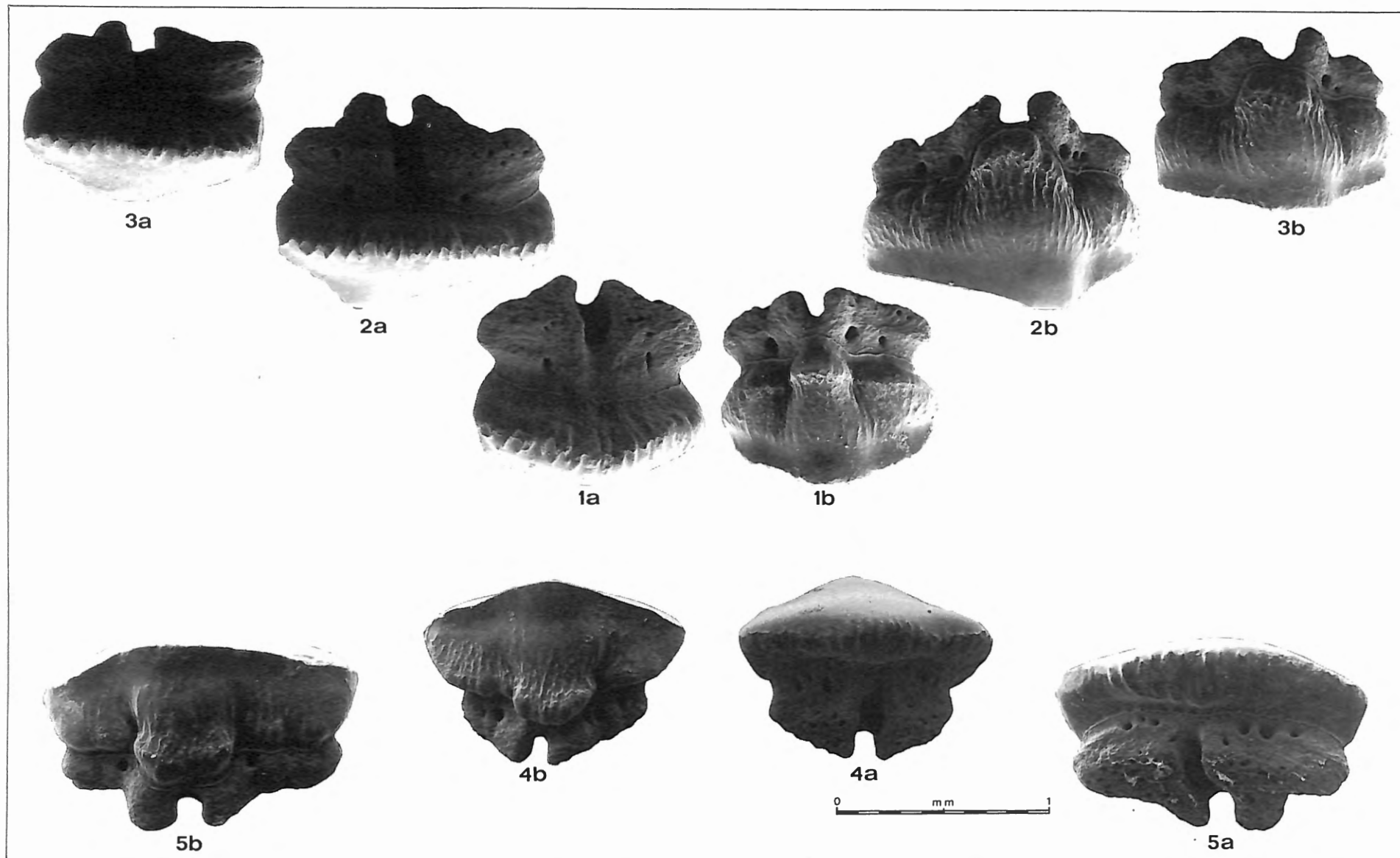


Plate 9. – *Mustelus mustelus* (LINNAEUS, 1758), female 89 cm (t.l.), Senegal. Upper parasymphysial (1), upper anterior (2), upper lateral (3), lower parasymphysial (4) and lower antero-lateral (5) teeth; outer (a) and inner (b) views.

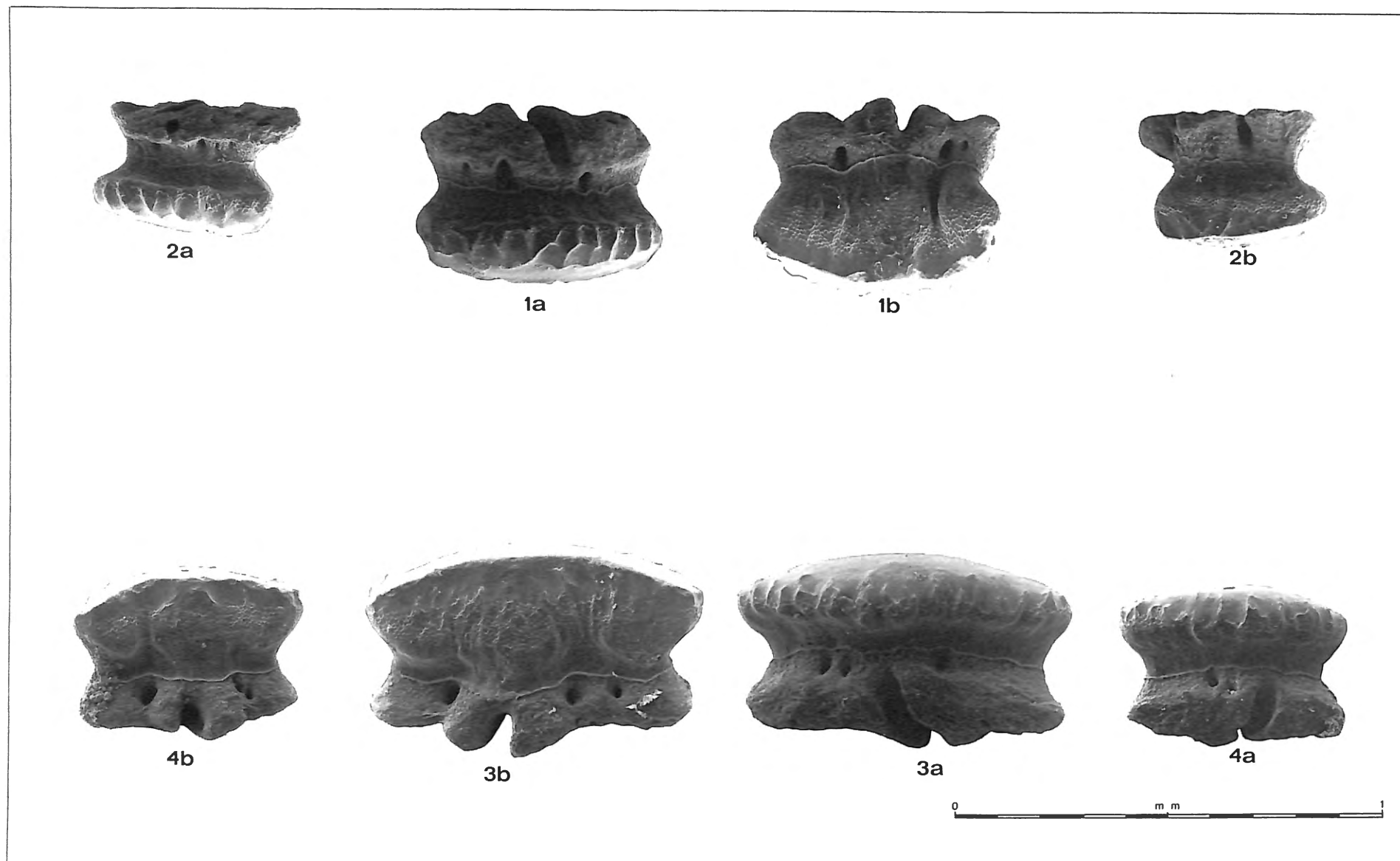


Plate 10. – *Mustelus mustelus* (LINNAEUS, 1758), female 89 cm (t.l.), Senegal. Upper postero-lateral (1), upper commissural (2), lower lateral (3) and lower postero-lateral (4) teeth; outer (a) and inner (b) views.

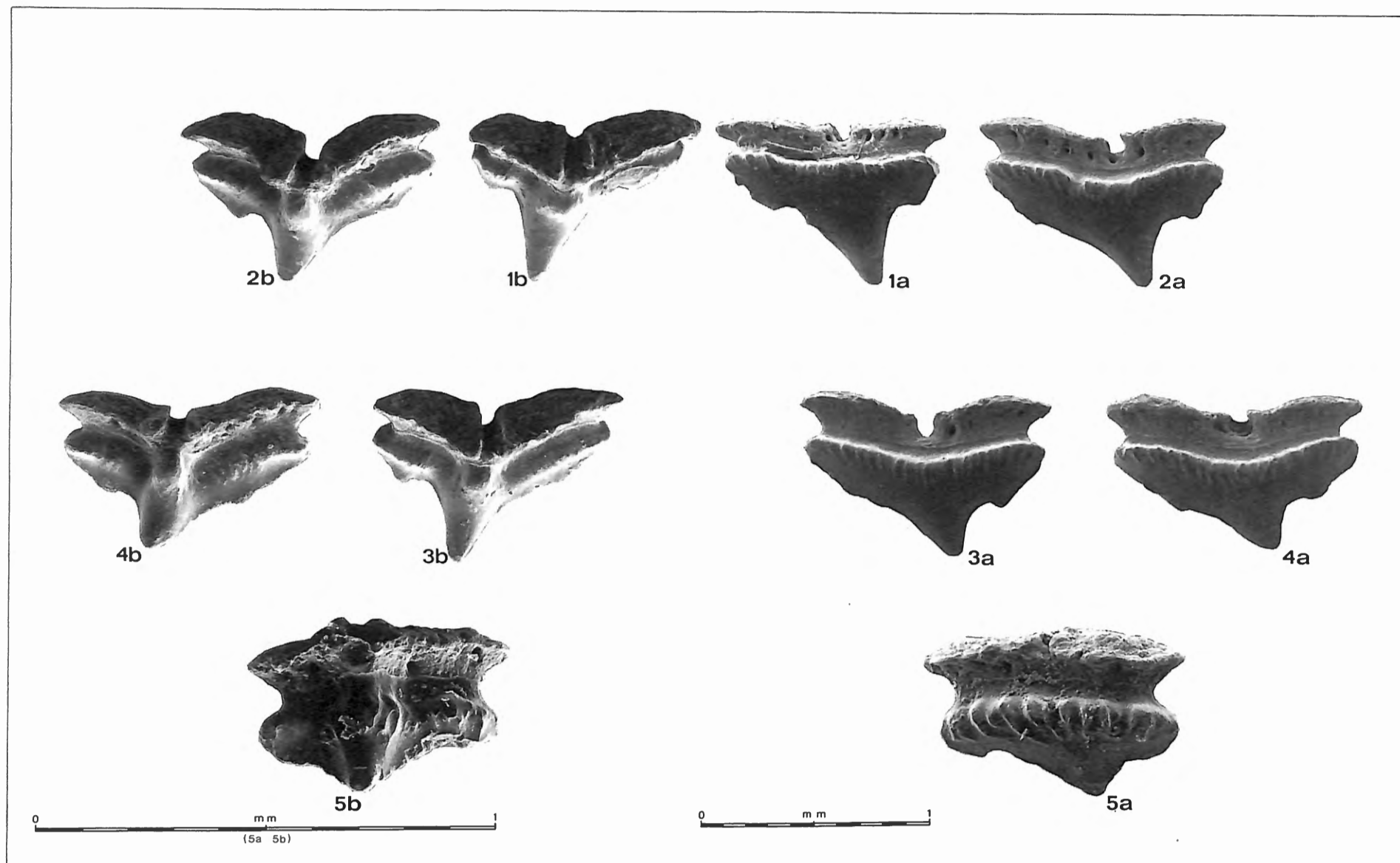


Plate 11. – *Rhinotriacis henlei* GILL, 1862, male 81 cm (t.l.), California. Upper parasymphysial (1), upper anterior (2), upper lateral (3), upper postero-lateral (4) and commissural (5) teeth; outer (a) and inner (b) views.

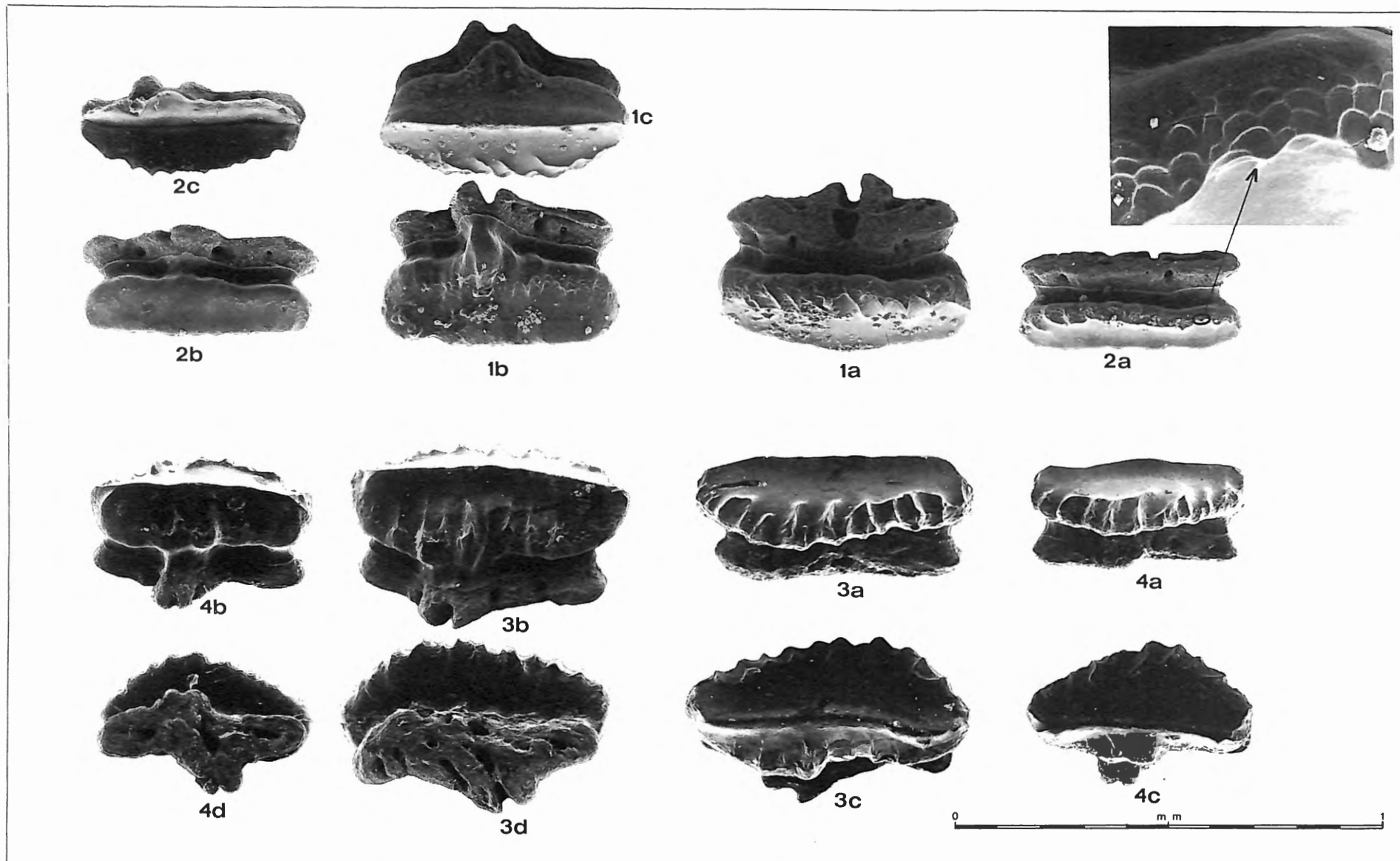


Plate 12. — *Scylliogaleus queckettii* BOULENGER, 1902, male 33 cm (t.l.), South Africa. Upper anterior (1), upper lateral (2), lower antero-lateral (3) and lower postero-lateral (4) teeth; outer (a), inner (b), occlusal (c) and radicular (d) views. Magnification of detail of 2a : 650 times.

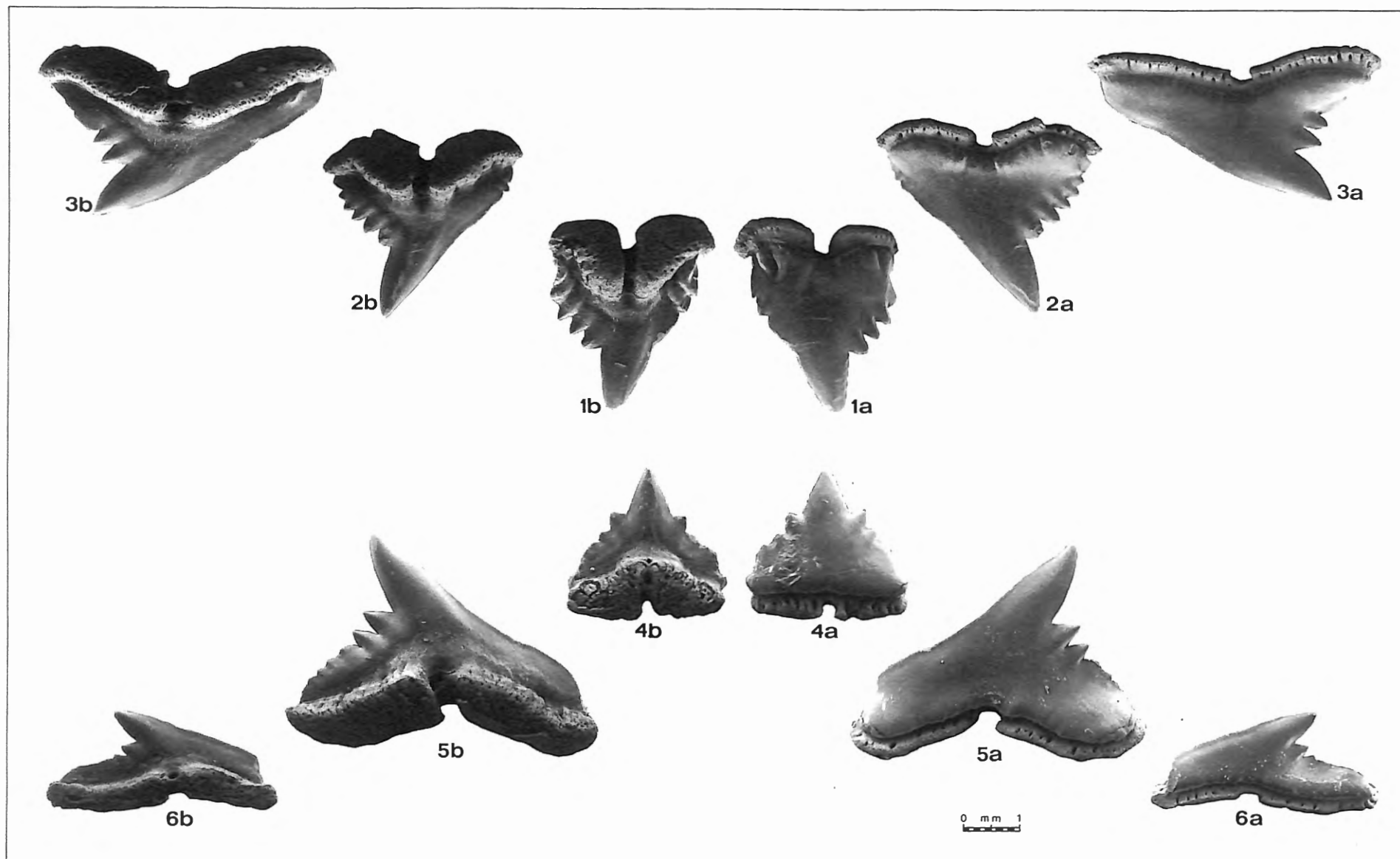


Plate 13. – *Galeorhinus galeus* (LINNAEUS, 1758), male 143 cm (t.l.), North Hebrides, North Atlantic. Upper parasymphysial (1), upper anterior (2), upper lateral (3), lower pseudosymphysial (4), lower lateral (5) and last lateral (6) teeth; outer (a) and inner (b) views.

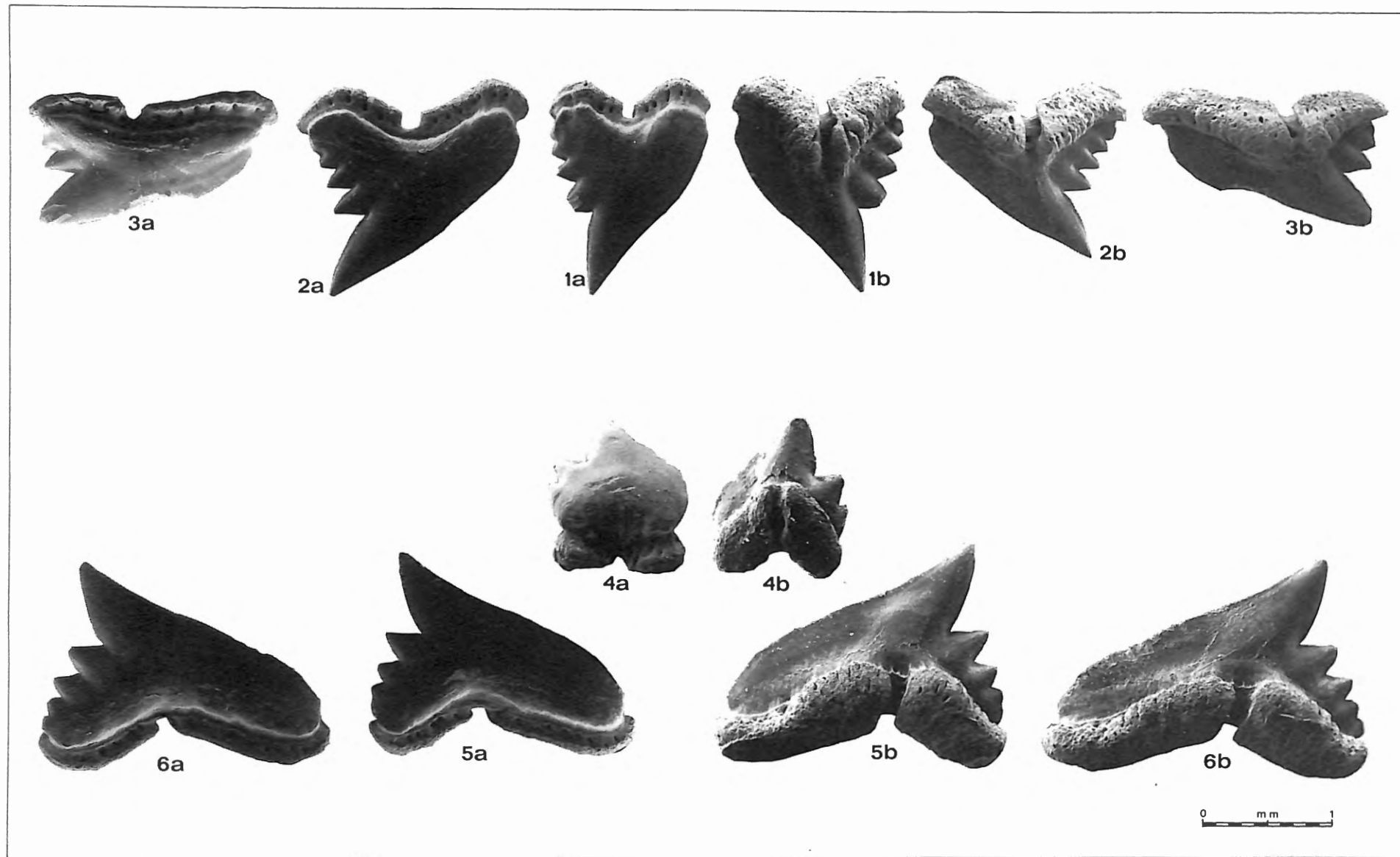


Plate 14. – *Hypogaleus hyugaensis* (Miyosi, 1939), male 127 cm (t.l.), Indian Ocean. Upper parasymphysial (1), upper anterior (2), upper postero-lateral (3), lower parasymphysial (4), lower anterior (5) and lower lateral (6) teeth; outer (a) and inner (b) views.



Plate 15. – *Gogolia filewoodi* COMPAGNO, 1973, female 74 cm (t.l.), North New Guinea. Upper anterior (1), upper lateral (2), upper postero-lateral (3), lower pseudosymphysial (4), lower anterior (5) and lower lateral (6) teeth; outer views only.

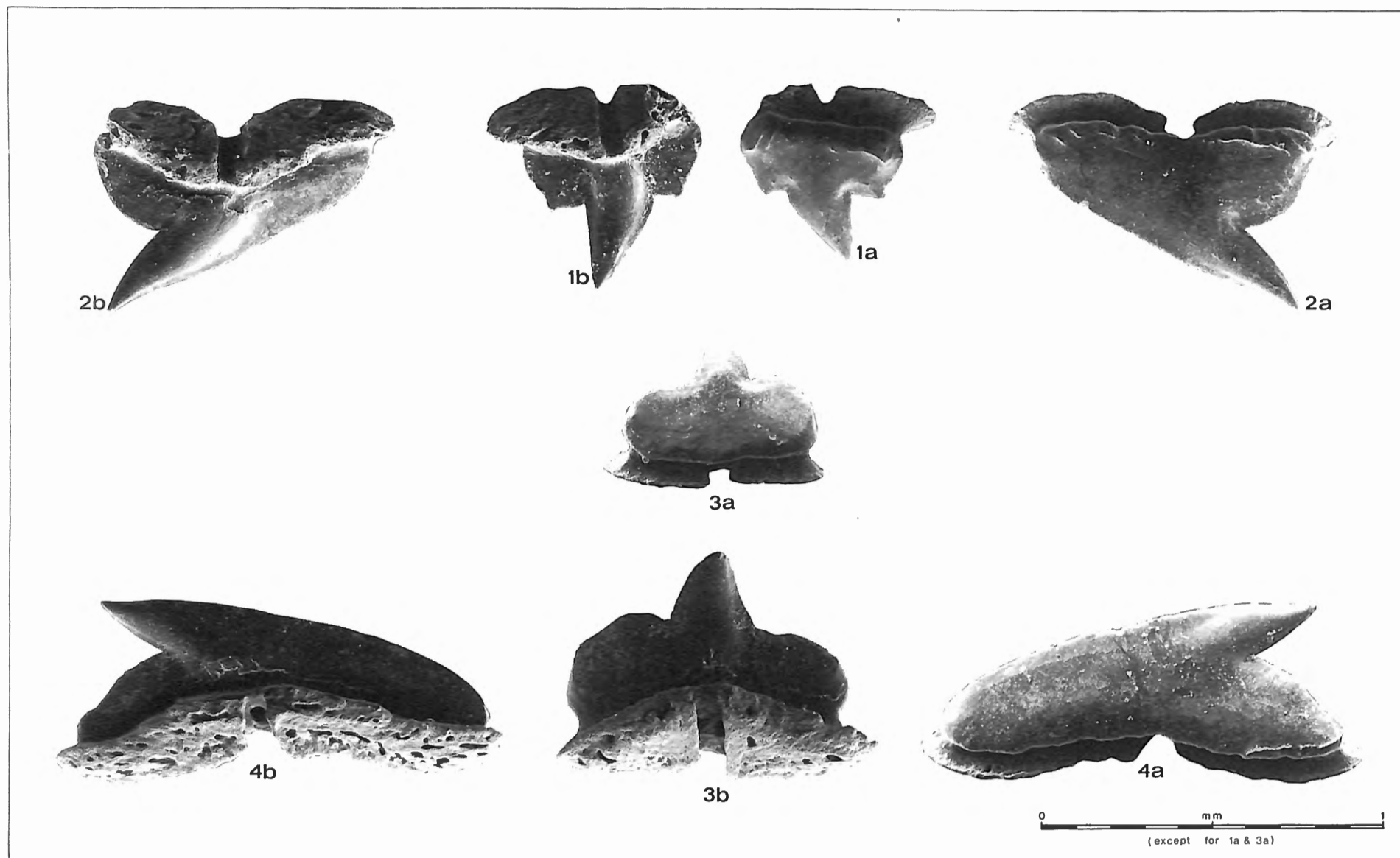


Plate 16. — *Iago omanensis* (NORMAN, 1939), female 31 cm (t.l.), Persian Gulf. Upper parasymphysial (1), upper anterior (2), lower pseudosymphysial (3), lower lateral (4) teeth; outer (a) and inner (b) views.

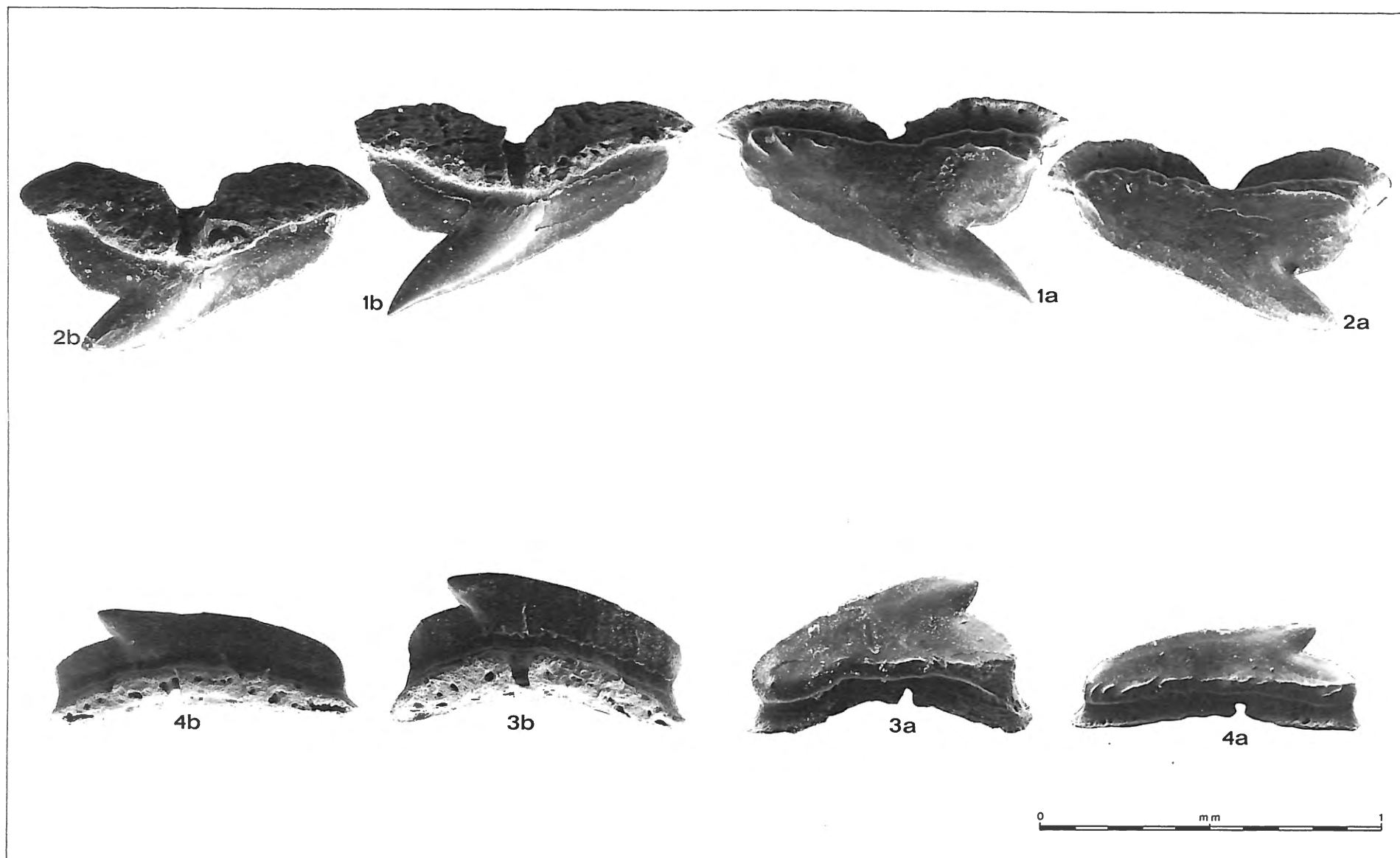


Plate 17. — *Iago omanensis* (NORMAN, 1939), female 31 cm (t.l.), Persian Gulf. Upper lateral (1), upper postero-lateral (2) and lower postero-lateral (3 and 4) teeth; outer (a) and inner (b) views.