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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. 2c : Order : Carcharhiniformes Families : Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae and Carcharhinidae

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Abstract

The description of micro-teeth within the Carcharhiniformes is hereby completed by presentation of generic representatives for the remaining families Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae and Carcharhinidae. Detailed descriptions of the tooth morphology are given, as well as SEM-photographs. The tooth morphology of the genera herein concerned is compared with those published of the other carcharhiniform families in two previous issues of this series, in order to elucidate the interrelationships within this shark order also from an odontological point of view. The dental histology for the carcharhiniform genera is commented on, and their dental vascular types are re-examined. The results are summarized in a differential diagnosis for all carcharhiniform genera and families. Dental morphology, histology and vascularisation results allow to provide an odontological key to all supraspecific taxa of this order and to suggest a number of systematical adjustments. The glossary for the series, as published so far, has been complemented and updated.
Key-words : Elasmobranchii, Selachii, Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae, Carcharhinidae, Odontology.

Résumé

La description de la morphologie dentaire des genres appartenant aux Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae et Carcharhinidae complète l'étude odontologique des Carcharhiniformes à laquelle deux fascicules précédemment publiés (Triakidae et Scyliorhinidae) ont été consacrés.
Lorsque leurs dimensions l'autorisèrent, ces dents ont été figurées à l'aide de clichés M.E.B.
L'histologie dentaire des Carcharhiniformes est commentée et leurs modes de vascularisation dentaire sont réexaminés.
Les données que fournissent conjointement morphologie, histologie et vascularisation dentaires permettent d'établir une clef odontologique pour l'ensemble des taxons supraspécifiques de cet ordre, et de formuler un certain nombre de propositions de réajustements systématiques. Le glossaire qui intéresse l'ensemble de cette série de publications a été revu et sensiblement augmenté.
Mots-clés : Elasmobranchii, Selachii, Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae, Carcharhinidae, Odontologie.

Kurzfassung

Die Beschreibung der Mikrozähne innerhalb der Carcharhiniformes wird hiermit vervollständigt durch die Behandlung von Gattungsvertretern der restlichen Familien Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae und Carcharhinidae. Deren Zahnmorphologie wird im einzelnen beschrieben, begleitet von REM-Photos. Die Zahnmorphologie der hier behandelten Gattungen wird verglichen mit denjenigen der anderen carcharhiniformen Familienvertreter, die bereits in zwei vorhergehenden Beiträgen dieser Serie behandelt wurden, um die Verwandtschaftsbeziehungen innerhalb dieser Haiordnung auch unter odontologischen Gesichtspunkten zu erhellen. Die Zahnhistologie der carcharhiniformen Gattungen wird kommentiert, und die verschiedenen Formen des Zahngefäßsystemes sind erneut untersucht worden. Alle Ergebnisse sind in einer Differentialdiagnose für alle Gattungen und Familien der Carcharhiniformes zusammengefaßt. Die somit vollständigen Ergebnisse zur Zahnmorphologie, -histologie und -gefäßversorgung ermöglichten die Aufstellung eines zahnmorphologischen Bestimmungsschlüssel für alle supraspezifischen Taxa dieser Haiordnung und Vorschläge für eine Reihe von möglichen Änderungen der Klassifikation. Das Glossar für bisher veröffentlichte Beiträge der Serie wurde vervollständigt und auf den aktuellen Stand gebracht.
Schlüsselwörter : Elasmobranchii, Selachii, Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae, Carcharhinidae, Odontologie.

Introduction

To complete Part 2 on Carcharhiniformes of this series, this fascicle will deal with the following families : Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae and Carcharhinidae. The tooth morphology of their supraspecific taxa is described and eventually illustrated by SEM-photographs. For Triakidae and Scyliorhinidae, see Part 2a (HERMAN *et al.*, 1988) and 2b (HERMAN *et al.*, 1991) respectively. The dimensions of teeth of the following genera were too large to produce SEM-

photographs, and consequently their illustration is thus beyond the scope of this series. However, their morphology is well known and illustrated in previous works, such as BASS, D'AUBREY & KISTNASAMY (1973, 1975), BIGELOW & SCHROEDER (1948), CADENAT & BLACHE (1981) and COMPAGNO (1984, 1988) as is shown in the table below :

	BIGELOW & SCHROEDER	BASS & al.		CADENAT & BLACHE	COMPAGNO	
Genus	1948	1973	1975	1981	1984	1988
Hemipristis			pl. 5			f. 3.1
Isogomphodon	f. 73				p. 511	pl. 19
Carcharhinus		pl. 10			p. 488	
Glyphis					p. 509	f. 3.1
Lamiopsis					p. 512	pl. 19
Nasolamia					p. 516	
Negaprion			pl. 4		p. 518	
Prionace	f. 47, 48		pl. 6	f. 167	p. 522	
Galeocerdo	f. 44		pl. 7	f. 164	p. 504	pl. 19
Sphyrna	f. 85, 86		pl. 12		p. 554	
Eusphyra					p. 540	

Teeth of a subadult specimen of *Isogomphodon* are illustrated additionally.

The systematic arrangement of the order Carcharhiniformes following below is based on tooth morphology. A key and a systematic diagram are provided to assist other investigators and promote further considerations.

A major revision of Carcharhiniformes was recently presented by COMPAGNO (1988), and the nomenclature of all the taxa mentioned in the present paper is according to this work.

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 : CARCHARHINIFORMES
sensu COMPAGNO (1988)

The order comprises eight families : Triakidae, Scyliorhinidae, Proscylliidae, Leptochariidae, Pseudotriakidae, Hemigaleidae, Sphyrnidae and Carcharhinidae.

The tooth morphology descriptions and illustrations, as well as separate systematic evaluations on the Triakidae and Scyliorhinidae were published in previous fascicles of this series (Part A : 2a and 2b).

The teeth of the following 113 specimens of 36 species were examined :

Carcharhinus albimarginatus
1 sex unknown
Carcharhinus amboinensis
1 sex unknown
Carcharhinus brachyurus
1 sex unknown
Carcharhinus brevipinna
1 sex unknown 1 female
Carcharhinus falciformis
1 sex unknown 1 female 2 males
Carcharhinus galapagensis
1 sex unknown
Carcharhinus leucas
1 sex unknown
Carcharhinus limbatus
4 sex unknown 1 male
Carcharhinus longimanus
1 sex unknown
Carcharhinus melanopterus 1 female
Carcharhinus plumbeus
1 sex unknown

Carcharhinus sealei		1 male
Carcharhinus signatus	1 female	
Carcharhinus sorrah		3 males
Chaenogaleus macrostoma	2 females	
Ctenacis fehlmanni (holotype)	1 female	
Eridacnis barbouri	1 female	1 male
Eridacnis radcliffei		1 male
Eridacnis sinuans		1 male
Gollum attenuatus		1 male
Hemigaleus microstoma		1 male
Leptocharias smithii	4 females	3 males
Loxodon macrorhinus	3 females	1 male
Negaprion acutidens 1 sex unknown		
Paragaleus pectoralis	2 females	2 males
Prionace glauca	8 females	6 males
Proscyllium habereri	1 female	1 male
Pseudotriakis acrales (holotype)		1 male
Pseudotriakis microdon	4 females	6 males
Rhizoprionodon acutus	5 females	5 males
Scoliodon terranovae	1 female	1 male
Sphyrna lewini 2 sex unknown	1 female	2 males
Sphyrna mokarran 2 sex unknown		
Sphyrna tudes		1 male
Sphyrna zygaena	10 females	7 males
Triaenodon obesus	1 female	

The revision of COMPAGNO (1988) resulted in the following arrangement of families and subfamilies :

Family : SCYLIORHINIDAE
Subfamily : *Atelomycterinae*
Schroederichthyinae
Scyliorhininae
Pentanchinae : Tribe : *Galeini*
Pentanchini

Family : PROSCYLLIIDAE
Subfamily : *Proscylliinae*
Golluminae

Family : PSEUDOTRIAKIDAE

Family : LEPTOCHARIIDAE

Family : TRIAKIDAE
Subfamily : *Triakinae*
Galeorhininae : Tribe : *Iagini*
Galeorhinini

Family : HEMIGALEIDAE
Subfamily : *Hemigaleinae*
Hemipristinae

Family : CARCHARHINIDAE
Subfamily: *Galeocerdinae*
Scoliodontinae
Carcharhininae: Tribe: *Rhizoprionodontini*
Isogomphodontini
Carcharhinini
Triaenodontini

Family : SPHYRNIDAE

REMARK

Odontological features also allow grouping into families and subfamilies. However, this scheme differs rather widely from that of COMPAGNO (1988).
The authors will here not draw any nomenclatorially valid conclusions from their odontological results. Being aware of dealing with one complex of characters only, they will present their odontological results and leave it to following revising authors to incorporate also odontological points of view in a full systematic review with possible taxonomic and nomenclatorial changes.

Description of the odontological morphotypes

Family : Proscylliidae FOWLER, 1941

This family, after COMPAGNO (1988), includes the two subfamilies :

Proscylliinae

Genus *Proscyllium* HILGENDORF, 1904, type species *Proscyllium habereri.*
Genus *Eridacnis* SMITH, 1913, type species *Eridacnis radcliffei.*
Genus *Ctenacis* COMPAGNO, 1973, type species *Ctenacis fehlmanni.*

Golluminae

Genus *Gollum* COMPAGNO, 1973, type species *Gollum attenuatus.*

The teeth of species of the family Proscylliidae in general have a well developed principal cusp flanked by up to three cusplets.
The root is mostly secondarily anaulacorhizid, often secondarily hemiaulacorhizid and rarely holaulacorhizid.

HETERODONTY

A weak dignathic heterodonty can be present by relatively higher cusplets and a shorter principal cusp in lower teeth. A weak sexual heterodonty is sometimes present by a slightly higher principal cusp and more cusplets in females. A gradient monognathic heterodonty is always present by little broader lateral teeth with a more inclined or oblique principal cusp. The lateral teeth and those toward the commissure are mostly smaller than the anterior ones.

Genus : *Ctenacis* COMPAGNO, 1973

The type species of this monotypic genus is *Ctenacis fehlmanni* (SPRINGER, 1968). Two upper teeth of the holotype were available for examination.

Ctenacis fehlmanni (SPRINGER, 1968)
(Plate 1)

Proceedings of the Biological Society of Washington, 81 : 613-624.
The teeth of this species have a broad based, relatively short principal cusp. The principal cusp is oriented more or less obliquely toward the commissure, and one also short and broad based, distal cusplet is present.
The root varies between holaulacorhizid and secondarily anaulacorhizid and has two lobes, that are relatively long and narrow and form an angle at the root base. The dimensions of the teeth are plurimillimetrical in range.
The outer face of the principal cusp and cusplet is weakly convex, presenting well developed striae, that run from crown base toward apex of the principal cusp and cusplet. A reticulated ornamentation is present between the striae on the crown base.
The inner face of the principal cusp and cusplet is strongly convex, also presenting striae, that run from crown base toward apex of the principal cusp and cusplet.
The outer face of the root is rather high, presenting an irregular series of about five well developed but small foramina.
The inner face shows a ridge, having about the same shape as the angle of the root lobes. It divides the inner face of the root into two sections, and its central part is more or less protuberant. A foramen is present in the centre of the ridge.

Genus : *Eridacnis* SMITH, 1913

This genus comprises three species : *Eridacnis barbouri* (BIGELOW & SCHROEDER, 1944), *Eridacnis sinuans* (SMITH, 1957) and the type species *Eridacnis radcliffei* SMITH, 1913.

Eridacnis radcliffei SMITH, 1913
(Plates 2, 3)

Proceedings of the United States National Museum, 45 (200) : 599-600.
The teeth of this species have a broad based, relatively short principal cusp. The principal cusp is oriented sometimes a little obliquely toward the commissure, and one also short and broad based distal and mesial cusplet is present in anterior upper teeth. Cusplets are absent on upper anterior, lower anterior and latero-anterior teeth. The posterior teeth have up to three mesial cusplets and sometimes another distal one.
The root is secondarily anaulacorhizid, showing two relatively long and narrow lobes forming an angle at the root base. The dimensions of the teeth are plurimillimetrical in range.
The outer face of the principal cusp is weakly convex, presenting a few well developed striae, which run from crown base halfway to the apex of the principal cusp. A reticulated ornamentation is present between the striae on the crown base. The inner face of the principal cusp and cusplet is strongly convex, also presenting striae, which run from crown base toward apex of the principal cusp.
The outer face of the root is rather low, presenting an irregular series of about five well developed but small foramina.
The inner face shows a ridge, which has about the same shape as the angle of the root lobes. It divides the inner face of the root into two sections, and its central part is more or less protuberant. A foramen is present in the centre of the ridge.

Genus : *Proscyllium* HILGENDORF, 1904

This genus is monotypic with the type species *Proscyllium habereri* Hilgendorf, 1904.

Proscyllium habereri HILGENDORF, 1904
(Plates 4, 5)

Sitzungsberichte der Gesellschaft für Naturforschende Freunde Berlin, Jahrgang 1904 (2) : 39-41.
The teeth of this species have a broad based, relatively short principal cusp. The principal cusp is oriented more or less obliquely toward the commissure, and two or sometimes three also short and broad based distal cusplets are present.
The root is secondarily hemiaulacorhizid, showing two relatively long and narrow lobes forming an obtuse angle at the root base. The dimensions of the teeth are plurimillimetrical in range.
The outer face of the principal cusp and cusplet is weakly convex, presenting well developed striae, which run from crown base toward apex of the principal cusp and cusplet. A reticulated ornamentation is present between the striae on the crown base of the posterior teeth.
The inner face of the principal cusp and cusplet is strongly convex, also presenting striae, which run from crown base toward apex of the principal cusp and cusplet.
The outer face of the root is rather high, presenting an irregular series of about five well developed foramina.
The inner face shows a ridge, which has about the same shape as the angle of the root lobes. It divides the inner face of the root into two sections and its central part is more or less protuberant. A foramen is present in the centre of the ridge and root base.

Genus : *Gollum* COMPAGNO, 1973

The type species of this monotypic genus is *Gollum attenuatus* (GARRICK, 1954).

Gollum attenuatus (GARRICK, 1954)
(Plates 6, 7)

Transactions of the Royal Society of New Zealand, 82 (3) : 695-702.
The teeth of this species have a broad based, relatively short principal cusp. The principal cusp is oriented more or less obliquely toward the commissure and flanked by a well developed mesial and distal cusplet on anterior teeth, sometimes a poorly developed second mesial cusplet on lateral teeth along with loss of distal cusplets. But up to six or seven distal cusplets exist on posterior and commissural teeth.
The root is secondarily hemiaulacorhizid, showing two relatively long and narrow lobes forming an angle. The dimensions of the teeth are plurimillimetrical in range.
The outer face of the principal cusp and cusplet is weakly convex, presenting well developed, but fine striae, which run from crown base toward apex of the principal cusp and cusplet. A reticulated ornamentation is present between the striae on the crown base. The crown base overhangs a rather high basal depression below its entire length.
The inner face of the principal cusp and cusplet is strongly convex, also presenting well developed, fine striae, which run from crown base toward apex of the principal cusp and cusplet. The outer face of the root is rather high, presenting an irregular series of about five well developed foramina.
The inner face shows a ridge, that has about the same shape as the angle of the root lobes. It divides the inner face or the root into two sections and its central part is more or less protuberant. A foramen is present in the centre of the ridge.

Family : Pseudotriakidae GILL, 1893

This family is monotypic with the genus *Pseudotriakis*. The teeth in the family Pseudotriakidae in general have a well developed principal cusp flanked by up to three cusplets on each side.
The root is holaulacorhizid to secondarily anaulacorhizid.

HETERODONTY

A weak dignathic heterodonty may be shown by relatively higher cusplets and a shorter principal cusp in lower teeth. No sexual heterodonty has been observed. A gradient monognathic heterodonty is always present by little broader lateral teeth. The lateral teeth and those toward the commissure are mostly smaller than the anterior ones and can have up to seven cusplets.

Genus : *Pseudotriakis* BRITO CAPELLO, 1867

The genus is, after COMPAGNO (1988), monotypic with the type species *Pseudotriakis microdon* BRITO CAPELLO, 1867. *Pseudotriakis acrales* JORDAN & SNYDER, 1904 has been synonymised with *Pseudotriakis microdon*. In spite of this fact the teeth of the holotype of *Pseudotriakis acrales* will be illustrated (Plate 10).

Pseudotriakis microdon BRITO CAPELLO, 1867
(Plates 8, 9)

Jornal de Sciencias mathematicas, physicas e naturales, Lisboa, 1 (4) : 316 + 321.
The teeth of this species have a broad based, relatively short principal cusp, which is more distinct in the lower jaw. The principal cusp points more or less obliquely toward the commissure and is commonly flanked by one, also short and broad based cusplet. Next to each cusplet, on the extreme edges, a poorly developed second cusplet is present, which is more distinct on upper lateral teeth.
The root varies between holaulacorhizid and secondarily anaulacorhizid and shows two relatively long and narrow lobes forming a sharp angle at the root base. The dimensions of the teeth are plurimillimetrical in range.
The outer face of the principal cusp and cusplet is weakly convex, presenting well developed, short basal costules. The crown more or less overhangs the root. Striae on principal cusp and cusplets and a reticulated ornamentation are absent. The inner face of the principal cusp and cusplet is strongly convex, also presenting well developed, fine striae running from crown base toward apex of the principal cusp and cusplets. Their density is rather high with about eleven to seventeen striae on the principal cusp and five to seven on the cusplets. A basal ornamentation is absent.
The outer face of the root is rather high, presenting a series of about three to five well developed foramina, of which those in the centre are often merged.
The inner face shows a ridge having about the same shape as the angle of the root lobes. It divides the inner face of the root into two sections, and its central part is strongly protuberant. On each root lobe, two to three foramina are present on the root part toward the crown on the mesial and distal part. Foramina are absent near the crown-root junction. A central foramen is often present in the centre of the ridge, which is sometimes more or less elongated toward the root base, forming partly a groove or sometimes even a complete median groove. On the basal part, usually some randomly scattered foramina are present.

Family : Leptochariidae GRAY, 1851

This family is monotypic with the genus *Leptocharias* SMITH, 1838.

HETERODONTY

A slight dignathic heterodonty is shown by a relatively higher principal cusp in lower teeth. Sexual heterodonty is presented by anterior teeth with a longer principal cusp and a sigmoidal mesial cutting edge in males. Except for the parasymphysial rows, a disjunct monognathic heterodonty is presented by anterior teeth, with a high principal cusp strongly oriented obliquely toward the commissure and much smaller lateral and posterior teeth with a slightly oblique principal cusp.

Genus : *Leptocharias* SMITH, 1838

This genus is monotypic with the type species *Leptocharias smithii* (MÜLLER & HENLE, 1839).

Leptocharias smithii (MÜLLER & HENLE, 1839)
(Plates 11, 12)

Systematische Beschreibung der Plagiostomen : 56.
The disjunct monognathic heterodonty requires to describe anterior and lateral teeth separately.

ANTERIOR TEETH

The crown has a very high principal cusp, which is strongly inclined toward the commissure. The mesial cutting edge is slightly sigmoidal in males and straight in females. A poorly developed mesial and distal cusplet is present in upper teeth, but mostly absent in lower teeth.
The root varies between secondarily hemiaulacorhizid and secondarily anaulacorhizid and shows two lobes, which are relatively short but broad and sharply angled at the base.
The dimensions of the teeth are plurimillimetrical in range.
The outer face of the principal cusp and eventual cusplets is rather convex. It presents poorly (on anteriors) or well developed (on laterals to commissurals) striae running from crown base toward apex in upper teeth, are quite absent in lower teeth. A reticulated ornamention is absent.
The inner face of the principal cusp is strongly convex, presenting short, well developed basal costules. A basal ornamentation is absent.
The outer face of the root is rather low. Foramina are absent.
The inner face shows a ridge of about the same shape as the angle of the root lobes. It divides the inner face of the root into two sections. Its central part is more or less protuberant. Foramina are absent near the crown-root junction. A foramen is sometimes present in the centre of the ridge, which is sometimes more or less elongated toward the root base. An additional central foramen is often present at the basal part.

LATERAL TEETH

The crown has a high principal cusp, which is inclined toward the commissure. The mesial cutting edge is sometimes weakly sigmoidal in males and straight in females. A well developed mesial and distal cusplet is present in both upper and lower teeth, with sometimes a poorly developed second cusplet at the extreme mesial part.
The root is secondarily anaulacorhizid and shows two long and broad lobes, which are angled at the base.
The dimensions of the teeth are plurimillimetrical in range.
The outer face of the principal cusp and cusplets is rather convex. It presents strongly developed striae running from crown base toward apex. A reticulated ornamentation is absent.
The inner face of the principal cusp is strongly convex, presenting short, poorly developed basal costules. A basal ornamentation is absent.
The outer face of the root is rather low, with a central foramen.
The inner face shows a ridge of about the same shape as the angle of the root lobes. It divides the inner face of the root into two sections. Its central part is more or less protuberant. Foramina are absent near the crown-root junction. A foramen is sometimes present in the centre of the ridge. Numerous foramina are scattered over the root lobes.

Family : Hemigaleidae HASSE, 1879

This family includes, after COMPAGNO (1988), two subfamilies :

Hemigaleinae

Genus *Hemigaleus* BLEEKER, 1852, type species *Hemigaleus microstoma.*
Genus *Chaenogaleus* GILL, 1862, type species *Chaenogaleus macrostoma.*
Genus *Paragaleus* BUDKER, 1935, type species *Paragaleus pectoralis.*

Hemipristinae

Genus *Hemipristis* AGASSIZ, 1843, type species *Hemipristis serra.*

The teeth of species of the family Hemigaleidae in general have, except for the parasymphysial rows, a broad

based principal cusp with sometimes 7 or more distal cusplets in upper teeth and a rather slender principal cusp in lower teeth.
The root is always strictly holaulacorhizid.

HETERODONTY

A strong dignathic heterodonty is present in all genera. Sexual heterodonty, as well as ontogenetic heterodonty has not been observed. Except for the parasymphysial rows, the monognathic heterodonty is gradient in both upper and lower jaws in Hemigaleinae, and gradient in upper but disjunct in lower jaws in Hemipristinae.

Genus : *Hemigaleus* BLEEKER, 1852

This genus is monotypic with the type species *Hemigaleus microstoma* BLEEKER, 1852.

Hemigaleus microstoma BLEEKER, 1852
(Plates 13, 14)

Verhandelingen Bataviaans Genootschap voor Kunst en Wetenschap, 24 : 46.
The dentition presents a fair dignathic heterodonty. The teeth of the upper jaw have a rather broad based crown, which is strongly inclined toward the commissure in anterior teeth, even stronger inclined in lateral teeth and finally loosing distal cutting edge by extreme inclination in posterior teeth.
The teeth of the lower jaw have a principal cusp, which is always suberect and never inclines toward commissure. The principal cusp of posterior teeth is low.
The root of both upper and lower teeth is strictly holaulacorhizid. The dimensions of the teeth are plurimillimetrical in range.

UPPER TEETH

The upper teeth have the principal cusp strongly inclined toward the commissure. The long and smooth mesial cutting edge is weakly sigmoidal. The distal cutting edge is very short and toward the crown base replaced by a series of six or seven cusplets gradually reduced in height. The root is broad and rather low. The outer face of the principal cusp and cusplets is rather flat and smooth. Striae, costules or ornamentation are absent.
The inner face of the principal cusp and cusplets is weakly convex and smooth. Striae, costules or ornamentation are absent.
The outer face of the root is moderately high, and the root lobes present a series of numerous foramina. At the central root base, the basal part of the inner median groove is visible.
The inner part of the root presents a distinct median groove, which is broad and rather deep, running from crown-root junction toward the root base. It divides the root into two obtusely angled root lobes. A blunt ridge is present on the lobes near the crown-root junction, dividing the lobes into an upper and lower part. Foramina are present within the median groove and on the root lobes near the crown-root junction.

LOWER TEETH

The lower teeth have a suberect principal cusp. The smooth mesial and distal cutting edges are arched. Cusplets are absent. The crown becomes more asymmetrical and shorter toward the commissural teeth.
The outer face of the principal cusp is smooth and slightly convex. Striae, costules or ornamentation are absent. The inner crown base is arched or somewhat angled.
The inner face of the principal cusp is fairly convex. Striae, costules or ornamention are absent.
The outer face of the root is low and shows a series of ten or more foramina. The inner median groove is visible at the central root base.
The inner face of the root presents a broad and rather deep median groove, which divides the root into two angled lobes.
A blunt ridge is present on the lobes near the crown-root junction. It divides the lobes into upper and lower parts.
Some foramina are present within the median groove.

Genus : *Chaenogaleus* GILL, 1862

The genus is monotypic with the type species *Chaenogaleus macrostoma* (BLEEKER, 1852).

Chaenogaleus macrostoma (BLEEKER, 1852)
(Plates 15, 16)

Verhandelingen Bataviaans Genootschap voor Kunst en Wetenschap, 24 : 46.
The dentition is dignathic heterodont. The teeth of the upper jaw have a rather broad based crown, which is strongly inclined toward the commissure in anterior teeth, even stronger inclined in lateral teeth.
The teeth of the lower jaw have a principal cusp, which is always suberect in anterior teeth, slightly inclined toward the commissure in lateral teeth, and again suberect but lower in posterior teeth.
The root of both upper and lower teeth is strictly holaulacorhizid. The dimensions of the teeth are plurimillimetrical in range.

UPPER TEETH

The upper teeth have a principal cusp, which is strongly inclined toward the commissure. The mesial cutting edge is long, smooth and weakly sigmoidal. The distal cutting edge is very short and toward the crown base

replaced by a series of five or six cusplets gradually reduced in height. The root is broad and rather low.
The outer face of the principal cusp and cusplets is rather flat and smooth. Striae, costules or ornamentation are absent.
The inner face of the principal cusp and cusplets is weakly convex and smooth. Striae, costules or ornamentation are absent. The outer face of the root is moderately high. At the central root base, the basal part of the inner median groove is visible.
The inner part of the root presents a distinct median groove, which is broad and rather deep, running from crown-root junction toward the root base. It divides the root into two obtusely angled lobes. A blunt ridge is present on the lobes near the crown-root junction, dividing the lobes into upper and lower parts. Foramina are present within the median groove and on the root lobes near the crown-root junction.

LOWER TEETH

The lower teeth have a suberect, high principal cusp. The smooth mesial and distal cutting edges are strongly arched at the base, forming mesial and distal extensions of the cutting edges. Cusplets are absent. The crown becomes more asymmetrical and shorter toward the commissural teeth.
The outer face of the principal cusp is smooth and slightly convex. Striae, costules or ornamentation are absent. The inner crown-base is more or less arched.
The inner face of the principal cusp is fairly convex. Striae, costules or ornamentation are absent.
The outer face of the root is low and shows a series of ten or more foramina. The inner median groove is visible at the central root base.
The inner face of the root presents a broad and rather deep median groove, which divides the root into two angled, rather narrow lobes.
A blunt ridge is present on the lobes near the crown-root junction, which is protuberant in the centre of the root. It divides the lobes into upper and lower parts.
Some foramina are present within the median groove.

Genus : *Paragaleus* BUDKER, 1935

The genus comprises, after COMPAGNO (1988), three species : *Paragaleus tengi* (CHEN, 1963), *Paragaleus leucolomatus* COMPAGNO & SMALE, 1985 and the type species *Paragaleus gruveli* BUDKER, 1935 (= *Paragaleus pectoralis* (GARMAN, 1906)).

Paragaleus pectoralis (GARMAN, 1906)
(Plates 17, 18)

Bulletin of the Museum of Comparative Zoology, Harvard College, 46 (11) : 203.

The dentition presents a fair dignathic heterodonty. The teeth of the upper jaw have a rather broad based crown, which is strongly inclined toward the commissure in anterior teeth, even stronger inclined in lateral teeth, and loosing the distal cutting edge by extreme inclination in posterior teeth.
The teeth of the lower jaw have a principal cusp, which is always suberect but becoming lower toward the commissure.
The root of both upper and lower teeth is strictly holaulacorhizid. The dimensions of the teeth are plurimillimetrical in range.

UPPER TEETH

Except for the parasymphysial row, the upper teeth have a principal cusp strongly inclined toward the commissure. The mesial cutting edge is long, normally smooth and weakly sigmoidal (sometimes a cusplet-like irregularity may be present at the base). The distal cutting edge is very short and toward the crown base replaced by a series of four to seven cusplets gradually reduced in height.
The root is broad and rather low.
The outer face of the principal cusp and cusplets is rather flat and smooth. Striae, costules or ornamentation are absent.
The inner face of the principal cusp and cusplets is weakly convex and smooth. Striae, costules or ornamentaton are absent.
The outer face of the root is moderately high. At the central root base, the basal part of the inner median groove is visible.
The inner part of the root presents a distinct median groove, which is broad and rather deep, running from crown-root junction toward the root base. It divides the root into two obtusely angled lobes. A blunt ridge is present on the lobes near the crown-root junction, which is protuberant in the centre of the root. It divides the lobes into upper and lower parts. Foramina are present within the median groove and on the root lobes near the crown-root junction.

LOWER TEETH

The lower teeth have a suberect, high principal cusp. The mesial and distal cutting edges are strongly arched at the base, forming mesial and distal extensions of the cutting edges. Distal cusplets are present in very lateral teeth. The crown becomes more asymmetrical and shorter toward the commissural teeth.
The outer face of the principal cusp is smooth and slightly convex. Striae, costules or ornamentation are absent. The inner crown base is almost straight.
The inner face of the principal cusp is fairly convex. Striae, costules or ornamentation are absent.
The outer face of the root is low and shows a series of

ten or more foramina. The inner median groove is visible at the central root base.
The inner face of the root presents a broad and rather deep median groove, which divides the root into two weakly angled, rather narrow lobes.
A blunt ridge is present on the lobes near the crown-root junction, which is protuberant in the centre of the root. It divides the lobes into upper and lower parts.
Some foramina are present within the median groove.

Family : Carcharhinidae JORDAN & EVERMANN, 1896

This family comprises, after COMPAGNO (1988), the subfamilies Galeocerdinae, Scoliodontinae and Carcharhininae.
Galeocerdinae do not have microteeth and are therefore neither described nor illustrated here.

Subfamily : *Carcharhininae* JORDAN & EVERMANN, 1896

This subfamily comprises four tribes, of which only Rhizoprionodontini and Triaenodontini are described and illustrated below, because microteeth are missing in taxa of the other two tribes.

Tribe : *Triaenodontini* BONAPARTE, 1838

This tribe comprises the single genus *Triaenodon*.

Genus : *Triaenodon* MÜLLER & HENLE, 1837

This genus is monotypic with the type species *Triaenodon obesus* (RÜPPELL, 1837), sensu COMPAGNO (1988).

HETERODONTY

This genus has weakly dignathic heterodont teeth. Sexual or ontogenetical heterodonty has not been observed. Except for the symphysial and first anterior rows, a gradient monognathic heterodonty is present by slightly broader and oblique lateral teeth. Teeth in rows toward the commissure are lower and rather strongly inclined.

Triaenodon obesus (RÜPPELL, 1837)
(Plates 19, 20)

In : Fische des Rothen Meeres, Neue Wirbeltiere zu der Fauna von Abyssinien gehörig, 11 : 64.
Both upper and lower anterior teeth have a high, suberect but broad principal cusp, which becomes more oblique in lateral teeth and more inclined in posterior teeth. A firm mesial and distal cusplet is always present at the basal part of each cutting edge. Both mesial and distal cutting edges are smooth.
The root is neo-holaulacorhizid, with two angled lobes. The dimensions of the teeth are plurimillimetrical in range.
The outer face of principal cusp and cusplets is flat. Striae, costules and ornamentation are absent.
The inner face of principal cusp and cusplets is rather convex. Striae, costules and ornamentation are absent.
The outer face of the root presents a series of numerous foramina. At the central basal part, the inner median groove is visible.
The inner part of the root presents a shallow median groove, which runs from just below the crown-root junction toward the root base. The upper central part of the root is slightly protuberant. One or two foramina are present within the median groove.

Tribe : *Rhizoprionodontini* COMPAGNO, 1988

This tribe comprises, after COMPAGNO (1988), the genera *Loxodon* and *Rhizoprionodon*.

Genus : *Loxodon* MÜLLER & HENLE, 1838

This genus is monotypic, with the type species *Loxodon macrorhinus* MÜLLER & HENLE, 1839.

HETERODONTY

Teeth are weakly dignathic heterodont. Sexual heterodonty is present by a more sigmoidal mesial cutting edge in males. Ontogenetic heterodonty has not been observed. Except for the symphysial upper rows, a gradient monognathic heterodonty is present by slightly broader and more inclined lateral teeth. The teeth toward the commissure are lower and rather strongly inclined.

Loxodon macrorhinus MÜLLER & HENLE, 1839
(Plates 21, 22)

Systematische Beschreibung der Plagiostomen. 61.
Both upper and lower anterior teeth have a rather inclined principal cusp, which becomes more inclined in lateral and posterior teeth. Cusplets are absent, and a distal blade is always present, which joins the distal cutting edge in a notch. Both mesial and distal cutting edges are smooth. The root is neo-holaulacorhizid, with two obtusely angled lobes. The dimensions of the teeth are plurimillimetrical in range.
The outer face of principal cusp is flat. Numerous short costules are present on the crown base, but striae and ornamentation are absent.
The inner face of principal cusp and cusplets is slightly convex. Striae, costules and ornamentation are absent.
The outer face of the root presents a series of numerous foramina. At the central basal part, the inner median groove is visible.
The inner part of the root presents a relatively broad and deep median groove running from crown-root junction toward the root base. The root lobes are rather flat.

One rather large foramen is present within the median groove.

Genus : *Rhizoprionodon* WHITLEY, 1929

This genus comprises 7 species : *Rhizoprionodon acutus* (RÜPPELL, 1835), *Rhizoprionodon lalandei* (VALENCIENNES, 1839), *Rhizoprionodon longurio* (JORDAN & GILBERT, 1882), *Rhizoprionodon oligolinx* SPRINGER, 1964, *Rhizoprionodon porosus* (POEY, 1861), *Rhizoprionodon taylori* (OGILBY, 1915) and *Rhizoprionodon terranovae* (RICHARDSON, 1836).

HETERODONTY

Teeth are weakly dignathic heterodont. Sexual heterodonty is present by a more sigmoidal mesial cutting edge in males. Ontogenetic heterodonty has not been observed. Except for the symphysial upper rows, a gradient monognatic heterodonty is present by slightly broader and more inclined lateral teeth. The teeth toward the commissure are lower and rather strongly inclined.

Rhizoprionodon acutus (RÜPPELL, 1837)
(Plates 23 to 26)

In : Fische des Rothen Meeres, Neue Wirbeltiere zu der Fauna von Abyssienien gehörig, 11 : 65.
Both upper and lower anterior teeth have a rather inclined, but more or less suberect principal cusp, becoming more inclined in lateral and posterior teeth. A mesial cusplet is absent, but a poorly developed cusplet arising from a distal blade is always present. Both mesial and distal cutting edges, as well as the distal cusplet are weakly serrated. The root is neo-holaulacorhizid, with two obtusely angled lobes.
The teeth are plurimillimetical in size.
The outer face of principal cusp is flat. Numerous short, very fine costules are present on the crown base, but striae and ornamentation are absent.
The inner face of principal cusp and cusplets is slightly convex. Striae, costules and ornamentation are absent.
The outer face of the root presents a series of numerous foramina. At the central basal part, the inner median groove is visible.
The inner part of the root presents a relatively broad and shallow median groove running from crown-root junction toward the root base. The root lobes are rather flat. One rather large foramen is present within the median groove.

Subfamily : *Scoliodontinae* WHITLEY, 1934

This subfamily comprises the single genus *Scoliodon*.

Genus : *Scoliodon* MÜLLER & HENLE, 1837

This genus is monotypic with the type species *Scoliodon laticaudus* MÜLLER & HENLE, 1838.

HETERODONTY

Teeth are strongly dignathic heterodont in males and weakly heterodont in females. Sexual heterodonty is presented by a more sigmoidal suberect principal cusp, which is twisted in its vertical axis in anterior lower teeth of males only. Ontogenetic heterodonty has not been observed. Except for anterior lower rows in males and the symphysial upper rows and parasymphysial rows in both sexes, a gradient monognatic heterodonty is present by slightly broader and more inclined lateral teeth. The teeth toward the commissure are lower and rather strongly inclined.

Scoliodon laticaudus MÜLLER & HENLE, 1838
(Plates 27, 28)

Systematische Beschreibung der Plagiostomen. 27.
Both upper and lower anterior teeth have a rather inclined principal cusp in males, which becomes more inclined in lateral and posterior teeth. Cusplets are absent, and a distal blade is always present. Both mesial and distal cutting edges as well as distal blade are smooth.
The root is neo-holaulacorhizid with two obtusely angled, or, in lower anteriors of males, subquadrangularly shaped lobes. The dimensions of the teeth are plurimillimetrical in size.
The outer face of principal cusp is weakly convex. Striae, costules and ornamentation are absent.
The inner face of principal cusp and cusplets is slightly convex. Striae, costules and ornamentation are absent.
The outer face of the root presents a series of numerous foramina. At the central basal part, the inner median groove is visible.
The inner part of the root presents a relatively broad, shallow median groove running from crown-root junction toward the root base. The root lobes are rather flat.
One rather large foramen is present within the median groove.

LATERAL LOWER TEETH OF MALES

The principal cusp is twisted in its vertical axis, and mesial and distal cutting edges are sigmoidal but smooth. Cusplets, as well as distal blade are absent.
The root is neo-holaulacorhizid. The root lobes are subquadrangularly shaped.
The outer face of the principal cusp is strongly convex. Striae, costules and ornamentation are absent.
The inner face of the principal cusp is strongly convex. Striae, costules and ornamentation are absent.
The outer face of the root has a weak central depression.

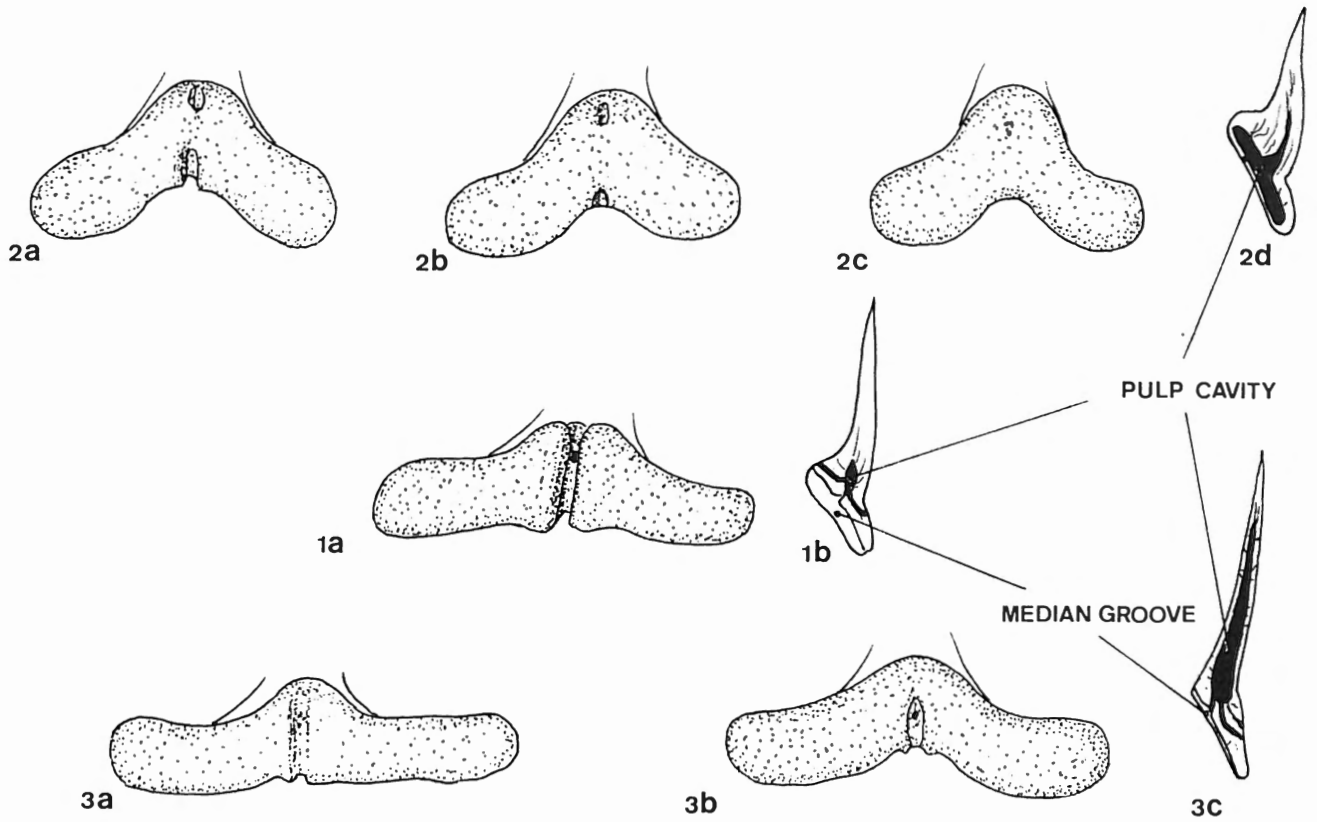

Fig. 1. – *Vascularisation types of carcharhiniform teeth (for explanation, see text).*

The basal part of the median groove is visible.
The inner face of the root is strongly protuberant. The median groove is rather deep and narrow, running from crown-root junction toward the root base, but does not reach the base.

Differential diagnosis for all supraspecific taxa of Carcharhiniformes

Carcharhiniform teeth have derived from the holaulacorhizid root type. This type of root (see fig. 1 : 1a, 1b) is still existing in some families (Triakidae and Hemigaleidae), but ongoing development of vascularisation has led to two further different concepts of root type :
1. – A closed median groove by merging of the inner surfaces of both root lobes. This results in secondarily hemiaulacorhizy and secondarily anaulacorhizy (Scyliorhinidae and Leptochariidae). Internally, the pulp cavity is merged with the former median groove (see fig. 1 : 2a, 2b, 2c and 2d).
2. – A shallower median groove by flattening of the inner root surface and/or rising of its bottom (Carcharinidae). Internally, the pulp cavity is greatly expanded, extremely so in upper teeth (see fig. 1 : 3a, 3b and 3c). Root lobes are more flattened and very obtusely angled. The authors introduce the term *neo-holaulacorhizy* for this phenomenon.

There are some intermediate forms between holaulacorhizy and neo-holaulacorhizy, which are demonstrated in several taxa of Triakidae, Sphyrnidae and Carcharhinidae.
Within the Triakidae, *Iago, Galeorhinus, Hemitriakis, Gogolia* and *Paragaleus* tend to develop neo-holaulacorhizy, in that root lobes are rather flattened and sometimes a rather shallow median groove is present. However, their root is still strictly holaulacorhizid.
Although they already have a neo-holaulacorhizid type of root, the Sphyrnidae, as well as the carcharhinid genera *Loxodon, Rhizoprionodon* and *Scoliodon* sometimes have a deep, though broad, median groove.
The following remarkable features were noted during our examinations :
— The intergeneric morphological differences in teeth of Proscylliidae and Scyliorhinidae are minimal and cannot support maintaining two separate families.
— There are no morphological differences between teeth of *Pseudotriakis microdon* and *Pseudotriakis acrales,* which supports their synonymy. However, the tooth morphology of *Pseudotriakis* has all basic characters of the Scyliorhinidae : a secondarily-anaulacorhizy via secondarily-hemiaulacorhizy, multi-cuspidity, striae on both inner and outer faces of the crown, and a weak dignathic heterodonty.
— The strong dignathic heterodonty of *Furgaleus* is absent in all further genera of the Triakidae. However,

the presence of this feature and all other tooth morphological characters of *Furgaleus* are typical for the Hemigaleidae.

— There is hardly any morphological difference between teeth of the genera *Galeorhinus* and *Hypogaleus* and thus there is hardly any justification to maintain two separate genera.

— The tooth morphological differences between the subgenera *Triakis* and *Cazon* are very extreme : cusplets present, uvula absent in *Triakis (Triakis)*, cusplets absent and uvula present in *Triakis (Cazon)*.

— Although the multicuspid crown suggests a triakid condition, the genus *Triaenodon* has a neo-holaulacorhizid type of root.

— The genera of the Sphyrnidae have a rather uniform tooth morphology, and a second genus cannot be supported.

— COMPAGNO (1973d, 1984, 1988), followed by CAPPETTA (1987), described the histotype of the genus *Hemipristis* as osteodont, which thus differs from all other carcharhinoids having an orthodont histotype of teeth. However, the teeth of the fossil ancestors of this genus were orthodont (see COMPAGNO, 1973d : 25 and plate 1 and 1988 : 270, 271 and figs. 3, 6 A, B, C and D). The living *Hemipristis* have a pulp cavity, which has been intruded by the osteodentine of the root. This in fact, has led to another kind of histotype than the osteodont one but does not coincide with orthodonty. It indicates a further evolutionary stage of the neo-holaulacorhizid type of root. The authors introduce the term *pseudo-osteodonty* for this phenomenon.

— The genus *Galeocerdo* has a root type atypical for the Carcharhinidae described above. The root has an anaulacorhizid appearance, due to the absence of a median groove.

The type of root vascularisation and the degree of dignathic heterodonty allows grouping the carcharhiniform families in three main groups. Further morphological tooth characters support the grouping of the genera in eighteen subfamilies of which one comprises two tribes : (see also Parts 2a and 2b of this series).

Differential odontological characterization of carcharhiniform subgenera

— Root usually holaulacorhizid
  Weak dignathic heterodonty
  Triakidae :
    Median groove narrow and deep
      Principal cusp suberect
        Cusplets present
          T. (Triakis)
        Cusplets absent
          T. (Cazon)
      Principal cusp poorly developed or absent
        Rhinotriacis
        Mustelus
        Scylliogaleus
    Median groove rather shallow
      Principal cusp strongly inclined
        Distal blade present
          Iago
        Distal cusplets present
          Galeorhinus
          Hypogaleus
          Hemitriakis
          Gogolia
  Strong dignathic heterodonty
  Hemigaleidae :
    Mesial cutting edge smooth in upper teeth
    Distal cusplets present
    Lower teeth suberect
      Hemigaleus
      Paragaleus
      Chaenogaleus
      Furgaleus
— Root varies between holaulacorhizid, secondarily hemiaulacorhizid and secondarily anaulacorhizid :
  Leptochariidae :
    Leptocharias
  Scyliorhinidae :
    Root lobes short, broad and subquadrangulary shaped
      Atelomycterus
      Aulohalaelurus
    Principal cusp short and massive, with convex inner face
      Scyliorhinus
      Poroderma
      Cephaloscyllium
    Principal cusp massive, multicuspid
    Root lobes sharply angled
      Pseudotriakis
    Principal cusp inclining toward commissure, or becoming oblique
    Root lobes rather short
    Cusplets present
      Apristurus
      Galeus
      Holohalaelurus
      Bythaelurus
      Haploblepharus
      Parmaturus
      Asymbolus
      Gollum
      Eridacnis
    Principal cusp high, oblique toward commissure
    Only one distal cusplet present
      Ctenacis
    Principal cusp triangular
    Cusplets poorly developed

Lateral teeth with extended root lobes, principal cusp short
Schroederichthys
Halaelurus
Proscyllium
Basal face of root concave
Cephalurus

— Root neo-holaulacorhizid with a broad, deep median groove; root lobes expanded and generally obtusely angled :
Sphyrnidae :
Sphyrna
Carcharhinidae :
Weak dignathic heterodonty
Mesial cutting edge smooth and inclined
Distal blade present
Loxodon
Scoliodon
Distal cusplets present
Rhizoprionodon

— Root neo-holaulacorhizid with a broad shallow median groove : root lobes expanded and generally obtusely angled :
Weak dignathic heterodonty
Principal cusp high and slender but mesially and distally expanded, sometimes weakly serrated
Isogomphodon (Plate 29)
Cutting edges smooth
Cusplets present
Triaenodon
Strong dignathic heterodonty
Principal cusp of upper teeth with serrated mesial and distal cutting edges; cusplets absent
Principal cusp of lower teeth slender
Carcharhinus
Nasolamia
Lamiopsis
Prionace
Glyphis
Negaprion
Root type pseudo-osteodont
Hemipristis

CONCLUSIONS

Except for the genus *Galeocerdo,* the carcharhiniform families can be distinguished by three root types : holaulacorhizid, secondarily anaulacorhizid (with secondarily hemiaulacorhizy as intermediate stage) and neo-holaulacorhizid. These root types represent the evolutionary development of vascularisation. (See differential diagnosis above).

Regarding tooth morphology, the Proscylliidae reveal close similarity with the Scyliorhinidae, so that separate families cannot be supported. However, the proscylliid genus *Ctenacis* might be placed in a separate subfamily because of its generally more differentiated tooth morphology.

Due to its close odontological similarity with the family Scyliorhinidae, *Pseudotriakis* could well be ranked as scyliorhinid subfamily only.

The strong dignathic heterodonty of the triakid genus *Furgaleus,* reflecting a long evolutionary development from dignathic homodonty, is unlike Triakidae. However, this feature and all other tooth characters are similar to the Hemigaleidae.

The distinction by odontology between *Galeorhinus* and *Hypogaleus* is of minor importance, and therefore both may be congeneric.

The tooth morphological differences between *Triakis (Triakis)* and *Triakis (Cazon)* are so extreme, that each of them could represent a separate generic taxon.

Scylliogaleus quecketti is the only triakid genus with a secondarily hemiaulacorhizid type of root. This indicates a development within the Triakidae to a possible secondarily anaulacorhizy as in Scyliorhinidae and Leptocharriidae. However, this development is much more gradual in Triakidae. The rather poorly developed principal cusp and cusplets and the presence of an uvula in *Rhinotriacis* still present some characteristic remains of *Mustelus.* Both *Scylliogaleus* and *Rhinotriacis* could well be separate derivations from the *Mustelus*-group.

Triaenodon has often been placed in the Triakidae. However, this is very unlikely due to its neo-holaulacorhizid root type, which could well support a suprageneric rank within the Carcharhinidae.

Odontological results do not support subdivision of Sphyrnidae into several genera and subgenera.

Considering the pseudo-osteodont histotype of teeth in *Hemipristis* as a further evolutionary developmental stage of the neo-holaulacorhizid root type, this genus cannot be related with the Hemigaleidae, which always have strictly holaulacorhizid roots. *Hemipristis,* on the other hand, has all morphological tooth characters of the Carcharhinidae.

Odontological differences between the genera *Loxodon* and *Rhizoprionodon* are of minor importance and overlapping in several cases. A distinction on generic level appears therefore unjustified. The lateral and posterior teeth in the genus *Scoliodon* are similar to those in *Loxodon* and *Rhizoprionodon,* which indicates an intrageneric relationship of these three taxa.

The root type and general morphology in the genus *Galeocerdo* are rather unique among all carcharhiniform species. Its present assignment to the Carcharhiniformes is therefore rather doubtful.

Odontological key to the carcharhiniform genera

1a Principal cusp poorly developed or even absent . . 2

2a Apron or pseudo-apron absent.
Root type hemiaulacorhizid . . . . . *Scylliogaleus*

2b Remains of pseudo-apron present.
Several poorly developed lateral foramina present . . . . . *Mustelus*
(with the exception of *"M." henlei* and *"M." whitneyi*)

1b Principal cusp well developed 3

3a Root holaulacorhizid including the variations from a straight deep median groove to a syncreted median groove 4

4a Root strictly holaulacorhizid with a deep median groove 5

5a Distal cusplet present 6

6a Mesial cusplets present 7

7a Apron present . . . . . *Gogolia*

7b Apron absent 8

8a Uvula poorly developed.
Outer ornamentation on crown base well developed.
Principal cusp short and suberect . . . *Rhinotriacis*

8b Uvula absent.
One or two distal cusplets present.
Ornamentation on crown absent . . *Triakis (Triakis)*

6b Mesial cusplets absent 9

9a Ornamentation on crown absent 10

10a Distal cutting edge length about 1/3 of the mesial one 11

11a Mesial cutting edge strongly sigmoidal 12

12a More than 5 distal cusplets 13

13a Up to 6 distal cusplets . . . . . *Chaenogaleus*
(upper teeth only)

13b Up to 7 distal cusplets . . . . . *Paragaleus*
(upper teeth only)

12b 5 or less distal cusplets . . . . . *Hypogaleus*

11b Mesial cutting edge suberect.
Up to 8 distal cusplets . . . . . *Galeorhinus*

10b Distal cutting edge length about 1/5 of the mesial one.
Up to 7 distal cusplets . . . . . *Hemigaleus*
(upper teeth only)

9b Ornamentation on crown present 14

14a Up to 3 distal cusplets present . . . . . *Furgaleus*
(upper teeth only)

14b Up to 5 distal cusplets present . . . . *Hemitriakis*

5b Distal cusplets absent 15

15a Uvula present.
Inner and outer ornamentation consisting of numerous longitudinal costules . . . . . *Triakis (Cazon)*

15b Uvula absent 16

16a Mesial blade present . . . . . *Iago*

16b Mesial blade absent 17

17a Principal cusp low, almost triangular . . *Furgaleus*
(lower teeth only)

17b Principal cusp moderately high 18

18a Principal cusp broad based . . . . . *Paragaleus*
(lower teeth only)

18b Principal cusp narrow based 19

19a Principal cusp moderately high . . . . *Hemigaleus*
(lower teeth only)

19b Principal cusp high . . . . . *Chaenogaleus*
(lower teeth only)

4b Root varies from irregularly holaulacorhizid to secondarily anaulacorhizid by syncretion of the median groove 20

20a Root lobes in basal view relatively short and subquadrate, forming a straight line at root base 21

21a Principal cusp elongated but broad based flanked by one cusplet at each side.
Outer and inner striae well developed . *Atelomycterus*

21b Principal cusp elongate and slender.
Poorly developed second cusplets present.
Outer and inner striae poorly developed or absent . . . . . *Aulohalaelurus*

20b Root lobes in basal view long 22

22a Root lobes narrow 23

23a Outer view : root very low.
Basal view : root lobes merged and concave . . . 24

24a Principal cusp slender and elongate.
Cusplets poorly developed, flanking the principal cusp . . . . . *Cephalurus*

24b Principal cusp low, inclined toward the commissure.
Up to 3 mesial and one distal cusplets . *Cephalurus-like*
(SE-Pacific specimen)

23b Root lobes rather plain in basal view 25

25a Root lobes very long and narrow, forming an obtuse angle 26

26a Principal cusp massive, triangular, and its outer face strongly convex 27

27a Outer face of root very high . . . . . *Poroderma*

27b Outer face of root low 28

28a Cusplet poorly developed . . . . . *Scyliorhinus*

28b Cusplets well developed.
Outer basal costules on crown well developed . . . . . *Cephaloscyllium*

26b Principal cusp slender.
Outer face weakly convex 29

29a Principal cusp inclining toward commissure (better visible in lateral teeth) 30

30a Principal cusp strongly inclined toward the commissure.
2 or 3 narrowly elongated mesial cusplets present . . . . . *Apristurus*

30b Principal cusp weakly inclined toward the commissure 31

31a Mesial and distal cusplets poorly developed . . . . . *Eridacnis*

31b Mesial cusplets well developed 32

32a 1 or 2 narrowly elongated mesial cusplets present (second one less developed) . . . . . *Galeus*

32b 2 or 3 short mesial cusplets present . . *Holohalaelurus*

29b Principal cusp erect or slightly oblique only . . . 33

33a High outer depression at crown base present . . . 34

34a Outer striae absent.
Outer basal costules on crown present . . *Bythaelurus*

34b Striae on inner face of crown coarse and well developed.
Outer basal costules on crown absent . . *Parmaturus*

33b High outer depression at crown base absent . . . 35

35a Mesial cusplets present 36

36a Secondary cusplets poorly developed or absent . . . . . *Asymbolus*

36b Secondary cusplets well developed 37

37a Outer basal costules coarse . . . . . *Haploblepharus*

37b Outer basal costules fine . . . . . *Gollum*

35b Mesial cusplets absent . . . . . *Ctenacis*

25b Root lobes in basal view very long and narrow, sometimes forming a straight line instead of a very obtuse angle 38

38a Cusplets well developed.
Crown low, more or less triangular . . *Proscyllium*

38b Cusplets poorly developed 39

39a Principal cusp poorly developed with expanded mesial and distal cutting edges.
Crown low, triangular in anterior teeth . . . *Halaelurus*

39b Crown low, more or less triangular.
Lower teeth : strong outer costulation, striae absent . . . . . *Schroederichthys*

22b Root lobes long and broad 40

40a Root lobes sharply angled.
Principal cusp short and massive . . . *Pseudotriakis*

40b Root lobes obtusely angled 41

41a Principal cusp rather high and slightly oblique . . . . . *Leptocharias*
(lateral and posterior teeth)

41b Principal cusp elongated and extremely oblique . . . . . *Leptocharias*
(Anterior teeth)

3b Root neo-holaulacorhizid 42

42a Median groove rather deep 43

43a Principal cusp weakly convex in both inner and outer faces 44

44a Smooth distal blade present 45

45a Principal cusp broad based and as high as the total length of the root.
Dimensions of teeth at least 8 mm . . . . . *Sphyrna*

45b Mesial cutting edge more or less sigmoidal.
Principal cusp about half as high as the total length of the root.
Dimensions of teeth up to 4 mm . . . . . *Loxodon*
. . . . . *Scoliodon*
(lateral and posterior teeth)

44b Distal blade presenting cuspidity.
Cutting edges serrated . . . . . *Rhizoprionodon*

43b Elongated principal cusp strongly convex in inner and outer faces, strongly orientated distally and twisted in its vertical axis.
Distal blade and cusplets absent . . . . . *Scoliodon*
(anterior teeth)

42b Root strictly neo-holaulacorhizid with a shallow median groove 46

46a Mesial and distal cusplets present 47

47a Principal cusp rather broad. Cusplets well developed . . . . . *Triaenodon*

47b Principal cusp elongated. Cusplets poorly developed . . . . . *Hemipristis* (lower anterior teeth)

46b Mesial and distal cusplets absent 48

48a Principal cusp elongated 49

49a Principal cusp slender 50

50a Inner central part of root protuberant . . . *Prionace* (lower teeth)

50b Inner part of root flattened 51

51a Serration on mesial and distal cutting edges present . . . . . *Glyphis* (lower anterior teeth)

51b Mesial and distal cutting edges smooth 52

52a Mesial and distal extensions of cutting edges as long as the principal cusp . . . . . *Nasolamia* (lower teeth)

52b Principal cusp longer than both mesial and distal cutting edges . . . . . *Isogomphodon* (lower teeth and upper anterior teeth)

49b Principal cusp broad based 53

53a Mesial and distal cutting edges expanded 54

54a Cutting edges smooth 55

55a Mesial and distal cutting edges strongly expanded . . . . . *Negaprion*

55b Mesial and distal cutting edges weakly expanded . . . . . *Lamiopsis* (lower teeth)

54b Cutting edges serrated 56

56a Cutting edges finely serrated 57

57a Principal cusp shorter than root length . *Carcharhinus* (lower teeth)

57b Principal cusp longer than root length . *Isogomphodon* (upper lateral and posterior teeth)

56b Cutting edges coarsely serrated . . . *Carcharhinus* (upper teeth)

53b Only distal cutting edge extended . . . . *Nasolamia* (upper teeth)

48b Principal cusp triangular 58

58a Principal cusp erect, or weakly inclined 59

59a Cutting edges finely serrated . . . . . *Lamiopsis* (upper teeth)

59b Cutting edges coarsely serrated . . . . . *Glyphis*

58b Principal cusp strongly inclined toward commissure 60

60a Cutting edges finely serrated . . . . . *Hemipristis* (upper and lower lateral teeth)

60b Cutting edges coarsely serrated . . . . . *Prionace* (upper teeth)

Acknowledgements

We would like to thank Dr. J.L.V. COMPAGNO, formerly San Francisco State University, California, and Dr. J.P. GOSSE, Institut Royal des Sciences naturelles de Belgique, Brussels, for permission to examine specimens at their disposal.
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Glossary

(also applying to previous issues of this series and complementing the previous glossaries).

CONCERNING THE JAW

Anterior
: Tooth position close to the junction of left and right jaw parts.

Commissural
: Tooth position near the end of jaw.

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

File
: Tooth row from symphysis toward end of jaw.

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

Homodonty
: Equal tooth morphology within a tooth file.

Lateral
: Tooth positions half way along the jaw.

Longitudinal
: Symphysial/commissural direction of a file.

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

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

Posterior
: Tooth positions toward the angle of jaw.

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

Row
: Tooth row from inner face to outer face of jaw.

Symphysial
: Teeth at junction of both halves of a jaw.

Transversal
: Outer/inner direction of a row.

CONCERNING THE TOOTH

An-, Hemi-, Hol- and Polyaulacorhizid
: Concerning their vascularisation, E. Casier (1947) recognized and described 4 phylogenetically significant root types within the orthodont histotypes of elasmobranch teeth.

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

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

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

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

Apron
: Expansion of the central part of the outer crown base.

Basal
: Bottom face concerned.

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

Crown
: Enamelated tooth part.

Distal
: Tooth edge or part toward angle of jaws.

Histotype
: Type of internal tooth vascularisation.

Inner face
: Directed toward the jaw cartilage.

Longitudinally
: Apico-basally directed structuring on a tooth.

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

Median keel
: Transverse ridge dividing the crown into inner and outer face.

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

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

Orthodont
: Histotype of vascularisation, by which a tooth is supplied primarily by an internal pulp cavity radiating into numerous tiny canals penetrating the orthodentine layer.

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

Outer face
: Directed outward the jaw cartilage.

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

Pseudo-osteodont
: The former pulp cavity of an originally orthodont histotype type of tooth being filled secondarily with osteodontine.

Pulp cavity
: Cavity inside the tooth from which the vascularisation is spread via canaculi.

Root
: Non-enamelated tooth part, which forms the junction with the jaw and provides vascularisation of the tooth.

Striae
: Vertical ridges running from crown base toward apex.

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

Secondarily hemiaulacorhizid
: Median groove of holaulacorhizid type of root overgrown to various extent, but terminally groove or pores still open.

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

Transversal
: Mesio-distally directed.

Uvula
: Lobate extension of the inner crown base.

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Composition of the plates

As far as possible, at least one plate with SEM-photographs of isolated teeth is presented for each of the genera. The plates have a constant composition : the upper part always shows upper teeth and the lower part lower teeth.
The choice of left or right jaw halves depends on the preservation quality of the specimen's tooth files only. Photographs of posterior and commissural teeth are mostly more enlarged than those of other teeth.

Legend

ps = pseudo- or parasymphysial position
a = anterior position
al = antero-lateral position
l = lateral position
lp = latero-posterior position
p = posterior position
c = commissural position

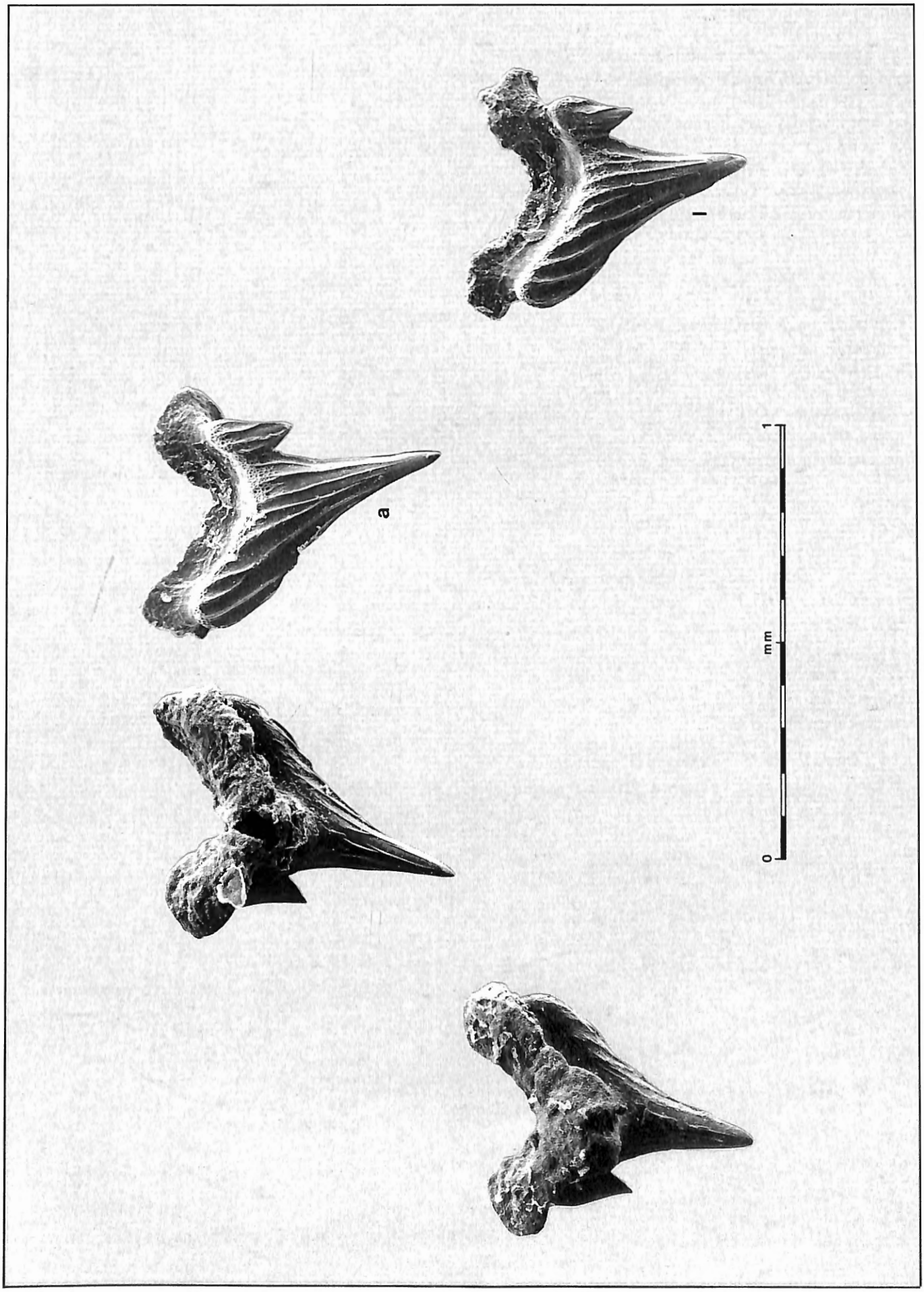

Plate 1. – Ctenacis fehlmanni (*Springer, 1968*), *female 46 cm (t.l.), holotype, Somalia.*

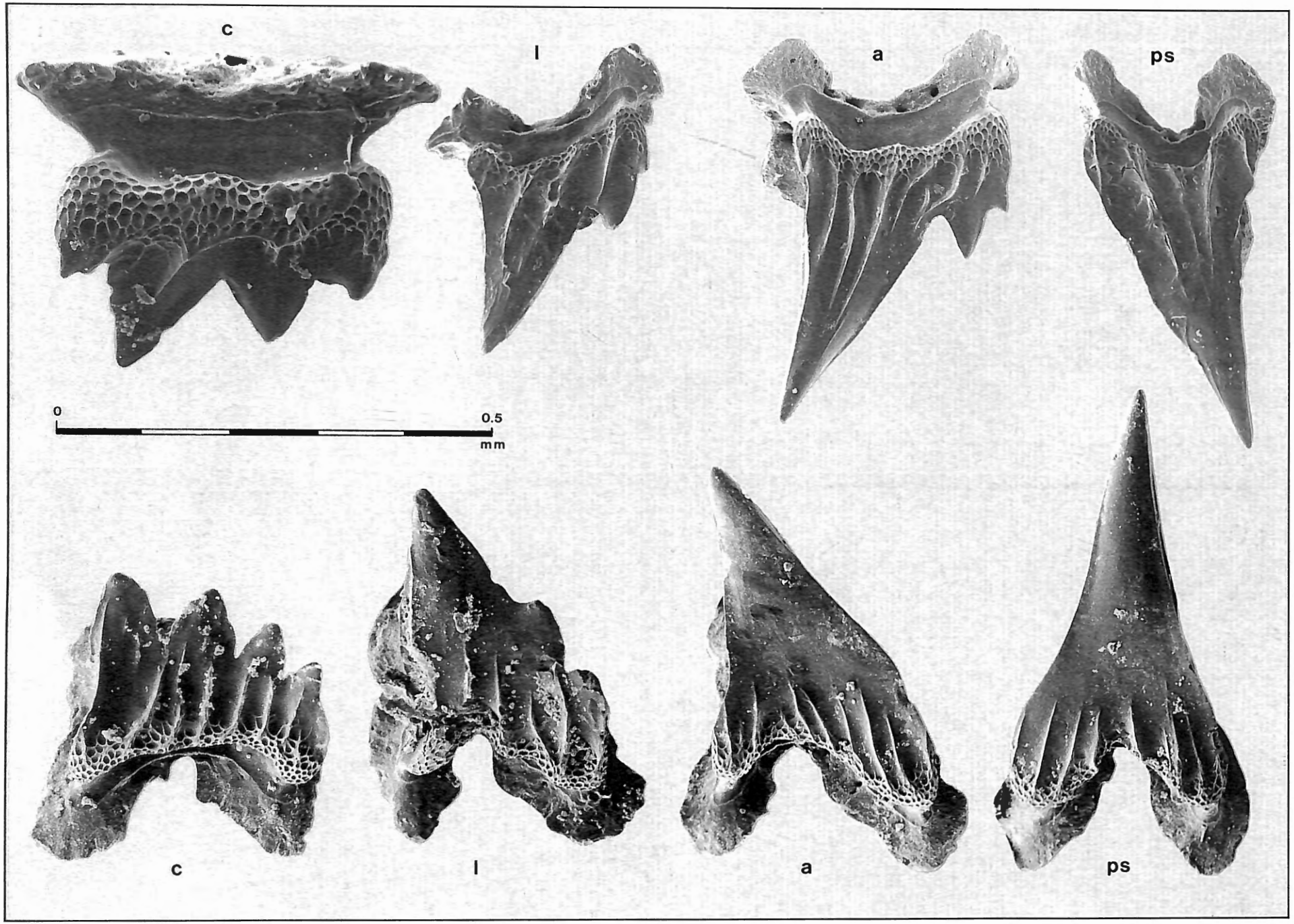

Plate 2. – Eridacnis radcliffei *Smith, 1913, male 21 cm (t.l.), Balayan Bay, Philippines. Upper commissural tooth is 2 times more enlarged than the other teeth.*

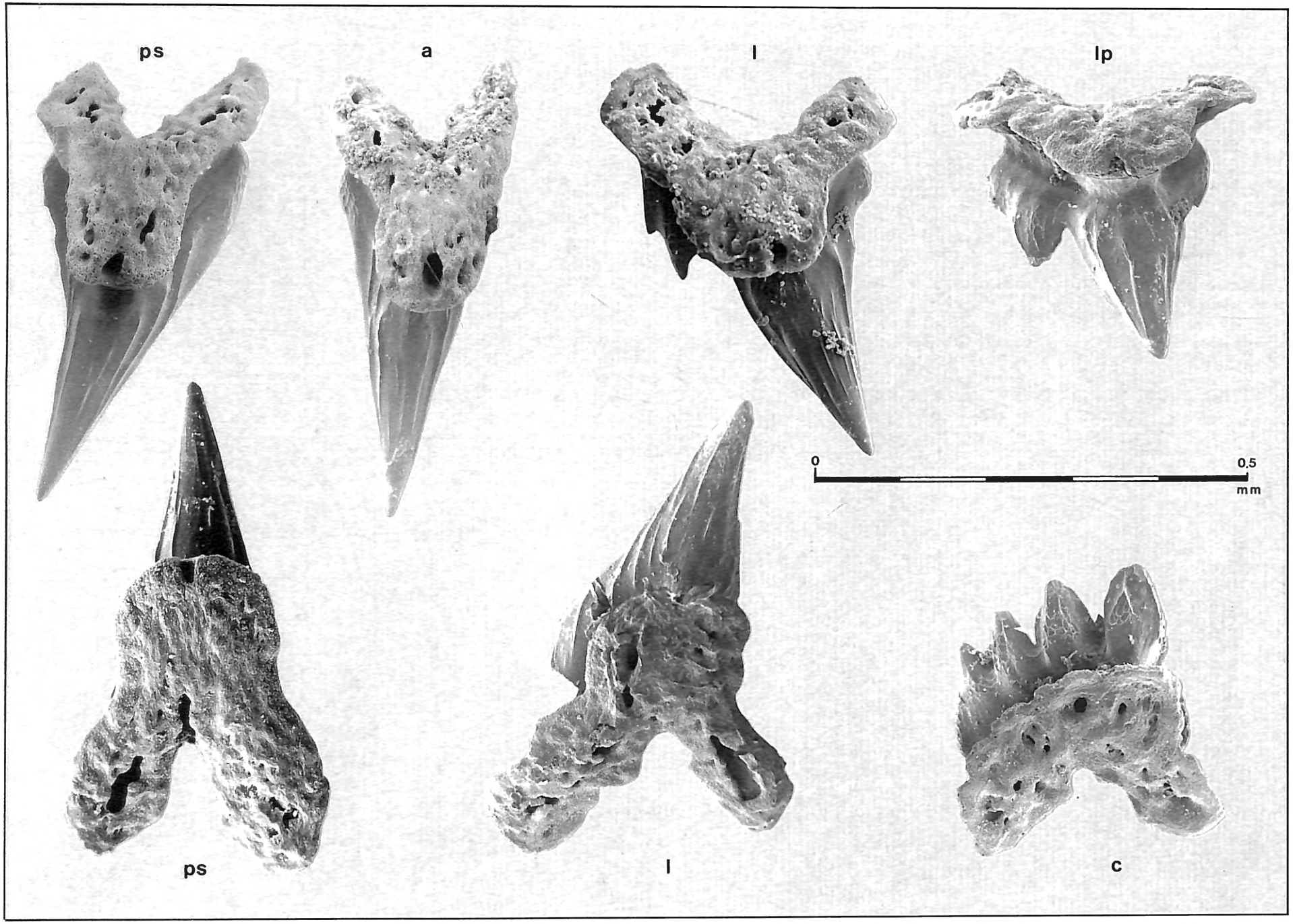

Plate 3. – Eridacnis radcliffei *Smith, 1913, male 21 cm (t.l.), Balayan Bay, Philippines.*

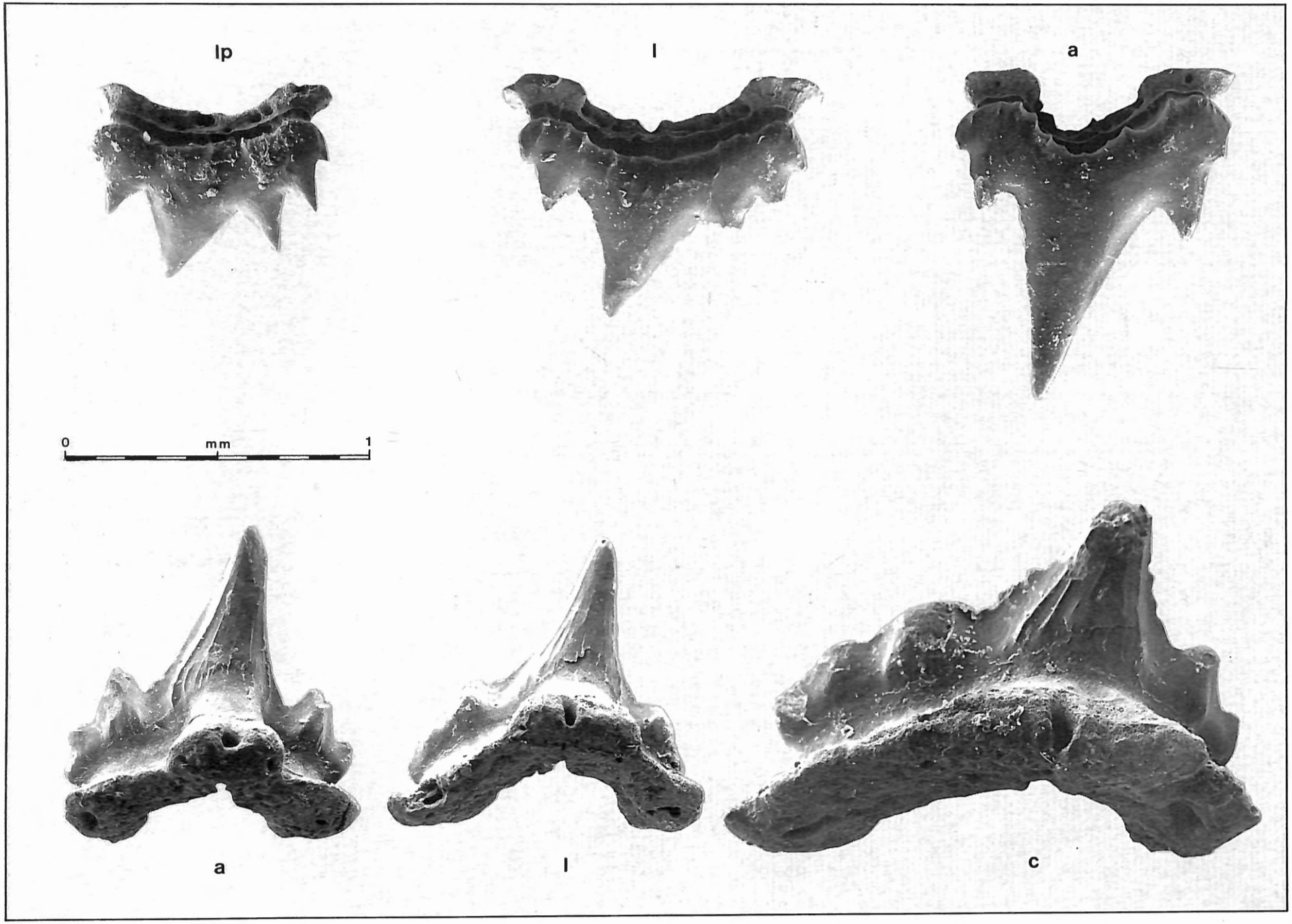

Plate 4. – Proscyllium habereri *Hilgendorf, 1904, male 48 cm (t.l.), Taiwan. Lower commisural tooth is 2 times more enlarged than the other teeth.*

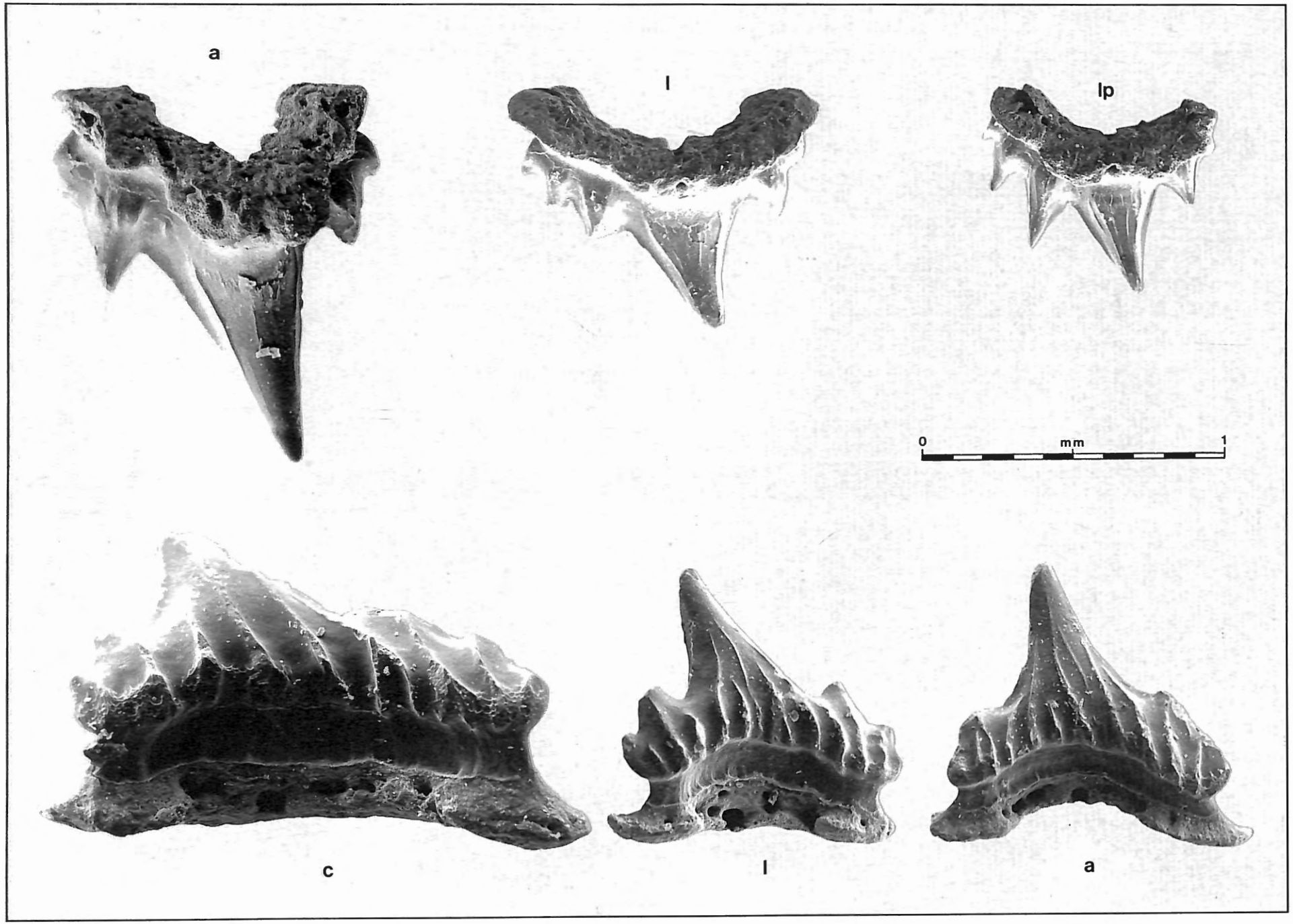

Plate 5. – Proscyllium habereri *HILGENDORF, 1904, male 48 cm (t.l.), Taiwan. Lower commisural tooth is 2 times more enlarged than the other teeth.*

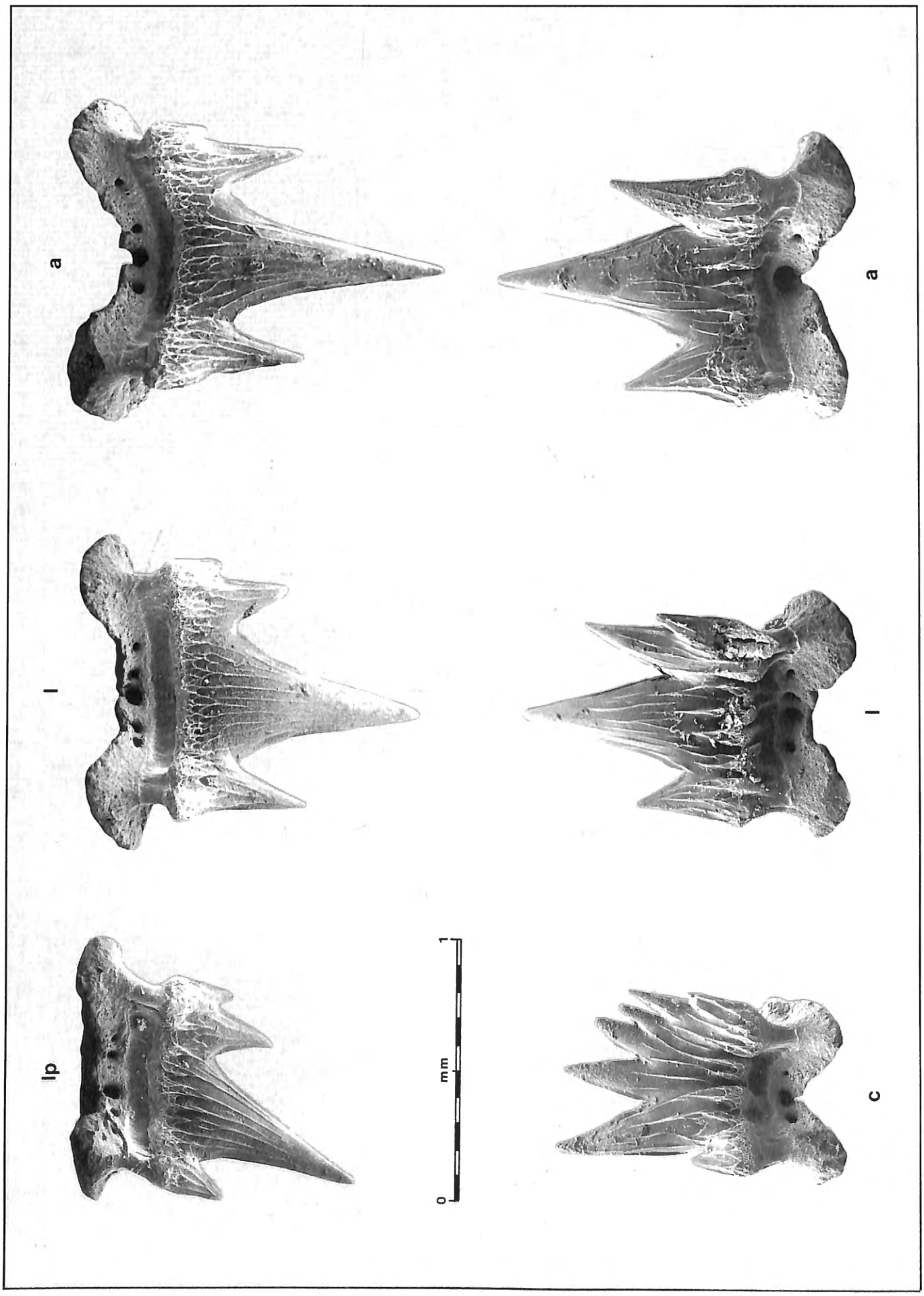

Plate 6. – Gollum attenuatus *(Garrick, 1954), male 95 cm (t.l.), Auckland, New Zealand.*

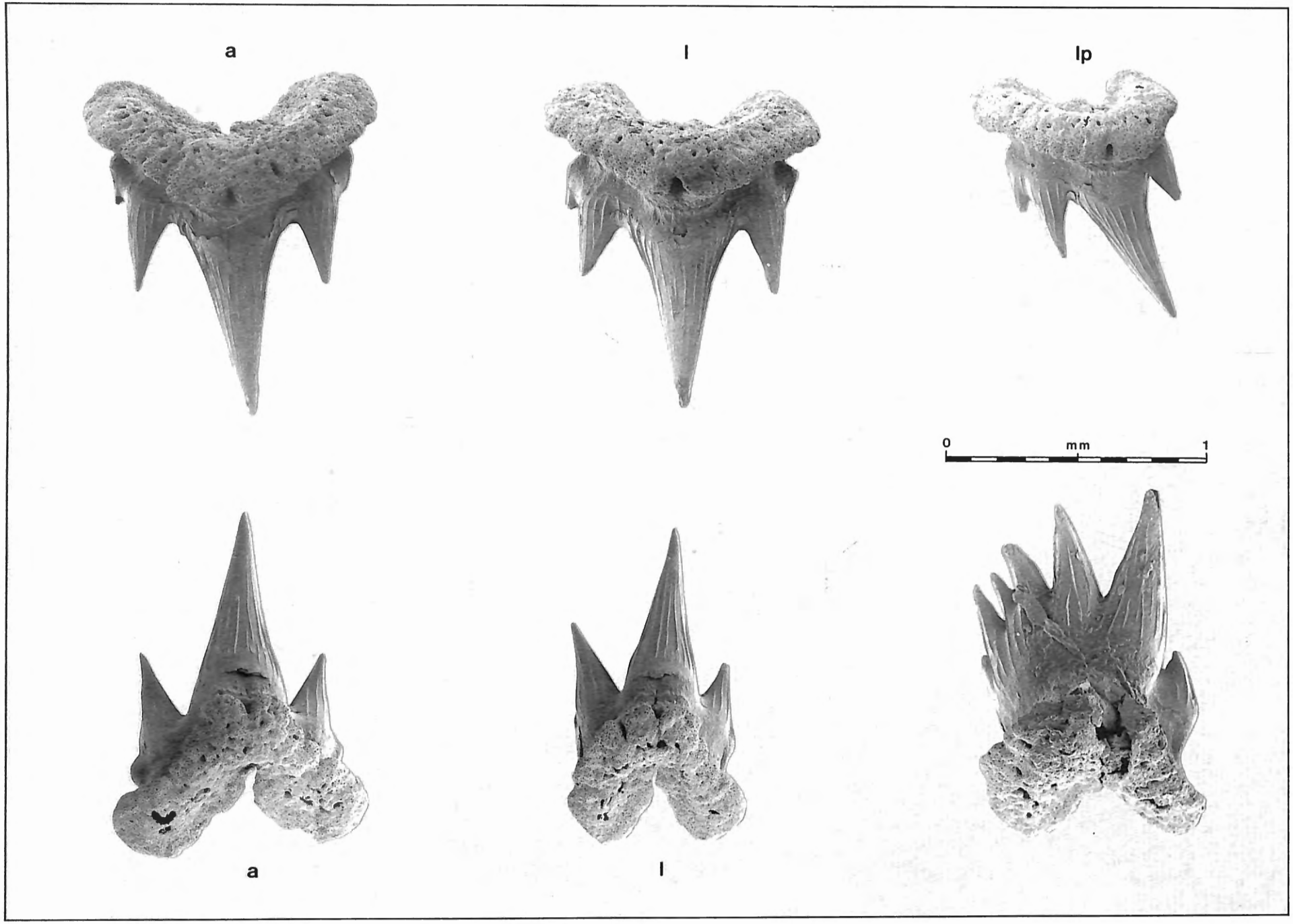

Plate 7. – Gollum attenuatus *(Garrick, 1954), male 95 cm (t.l.), Auckland, New Zealand. Lower commissural tooth is 1.5 times more enlarged than the other teeth.*

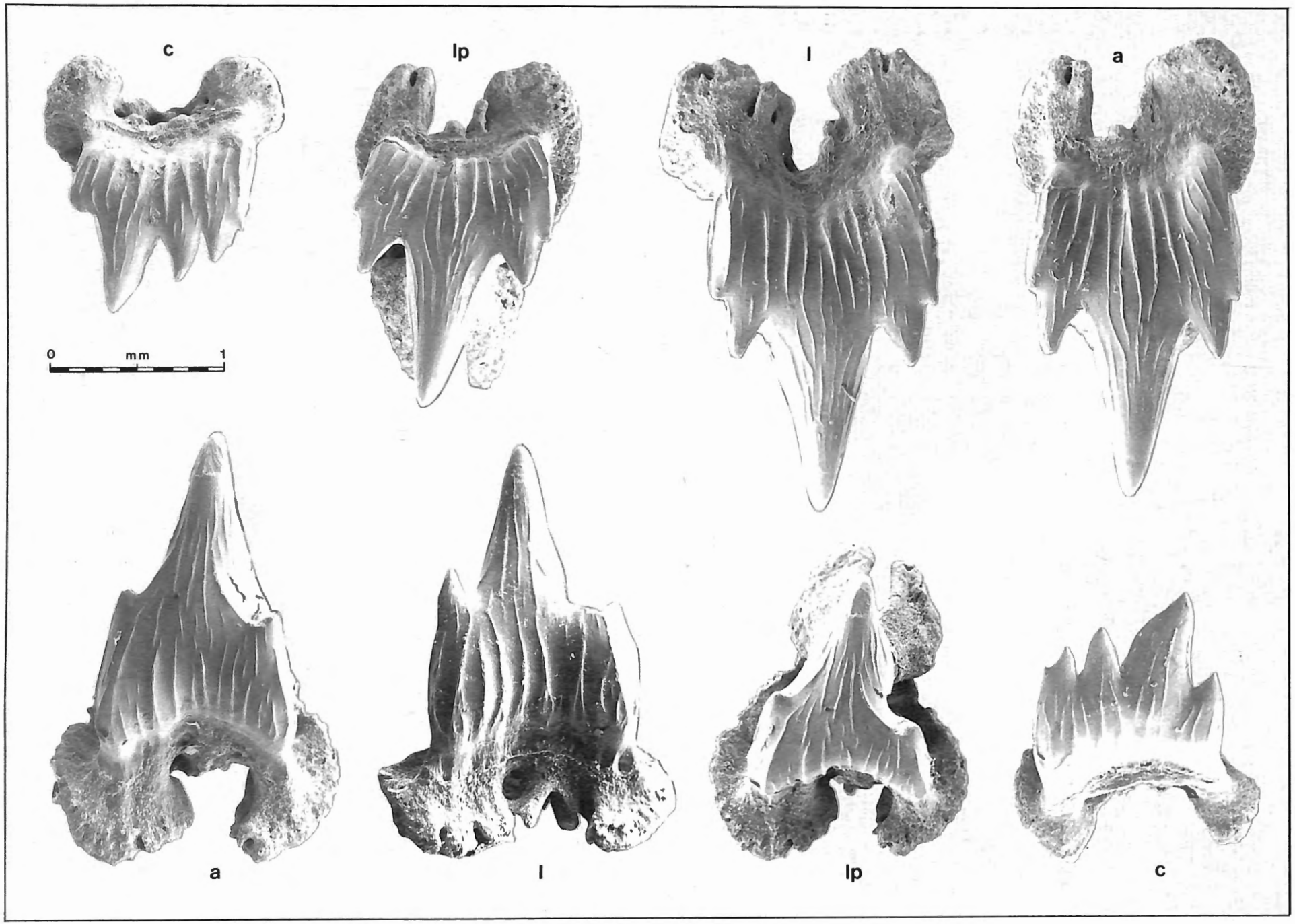

Plate 8. – Pseudotriakis microdon *Brito Capello, 1867, female 240 cm (t.l.), Gulf of Gascogne, France.*

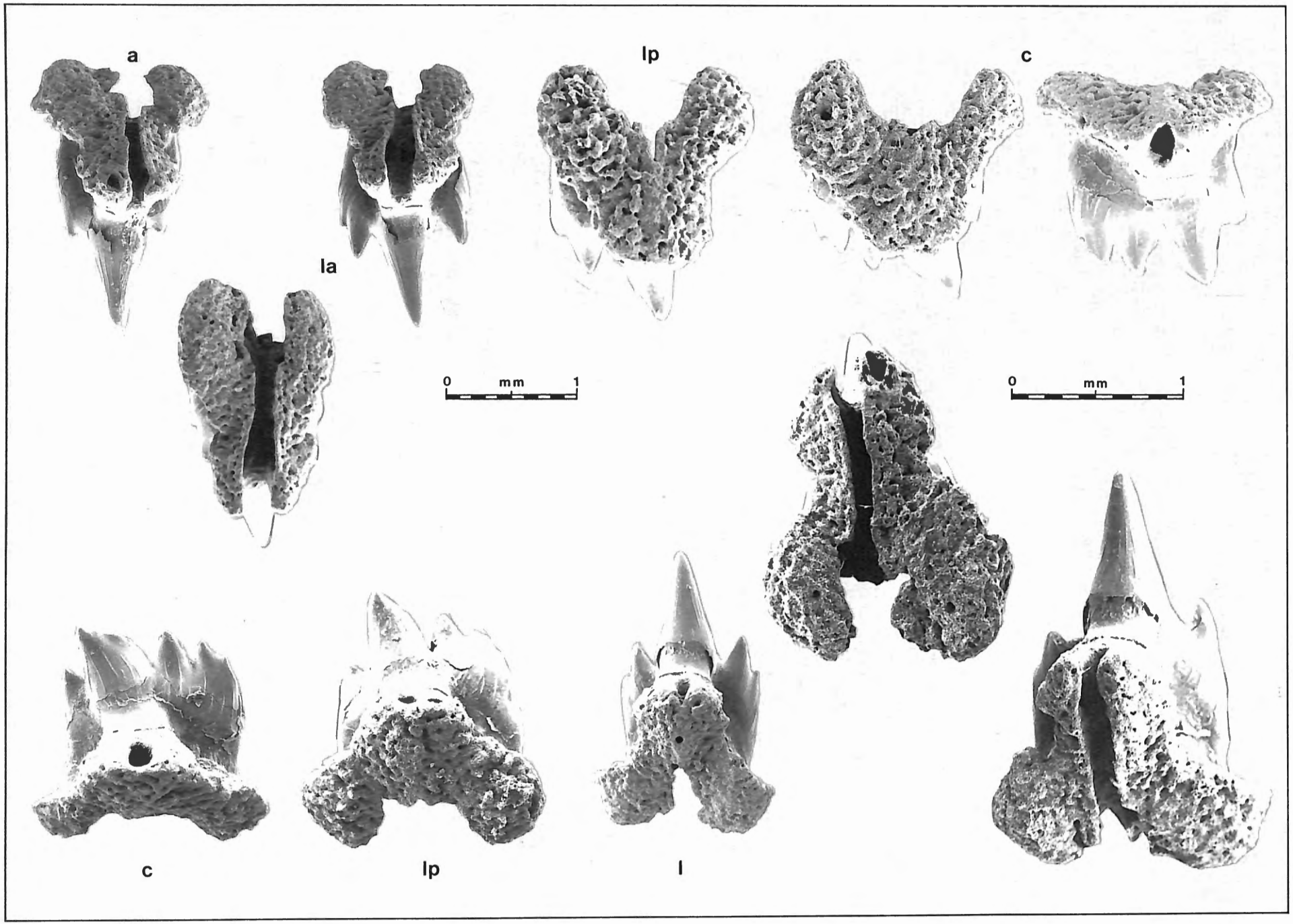

Plate 9. – Pseudotriakis microdon *Brito Capello, 1867, female 240 cm (t.l.), Gulf of Gascogne, France.*

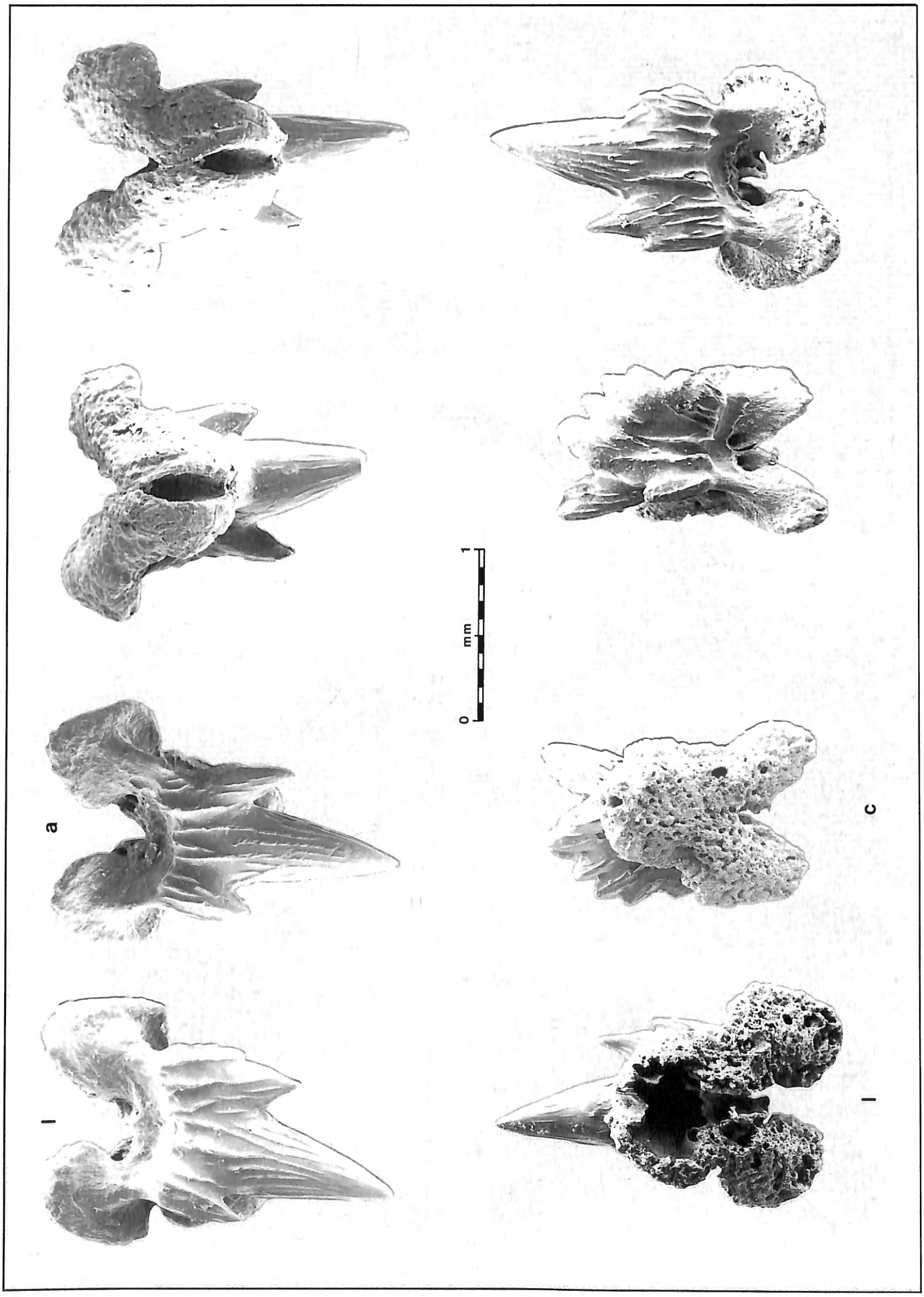

Plate 10. – Pseudotriakis acrales JORDAN & SNYDER, 1904, *female 197 cm (t.l.), holotype, Suruga Bay, Japan.*

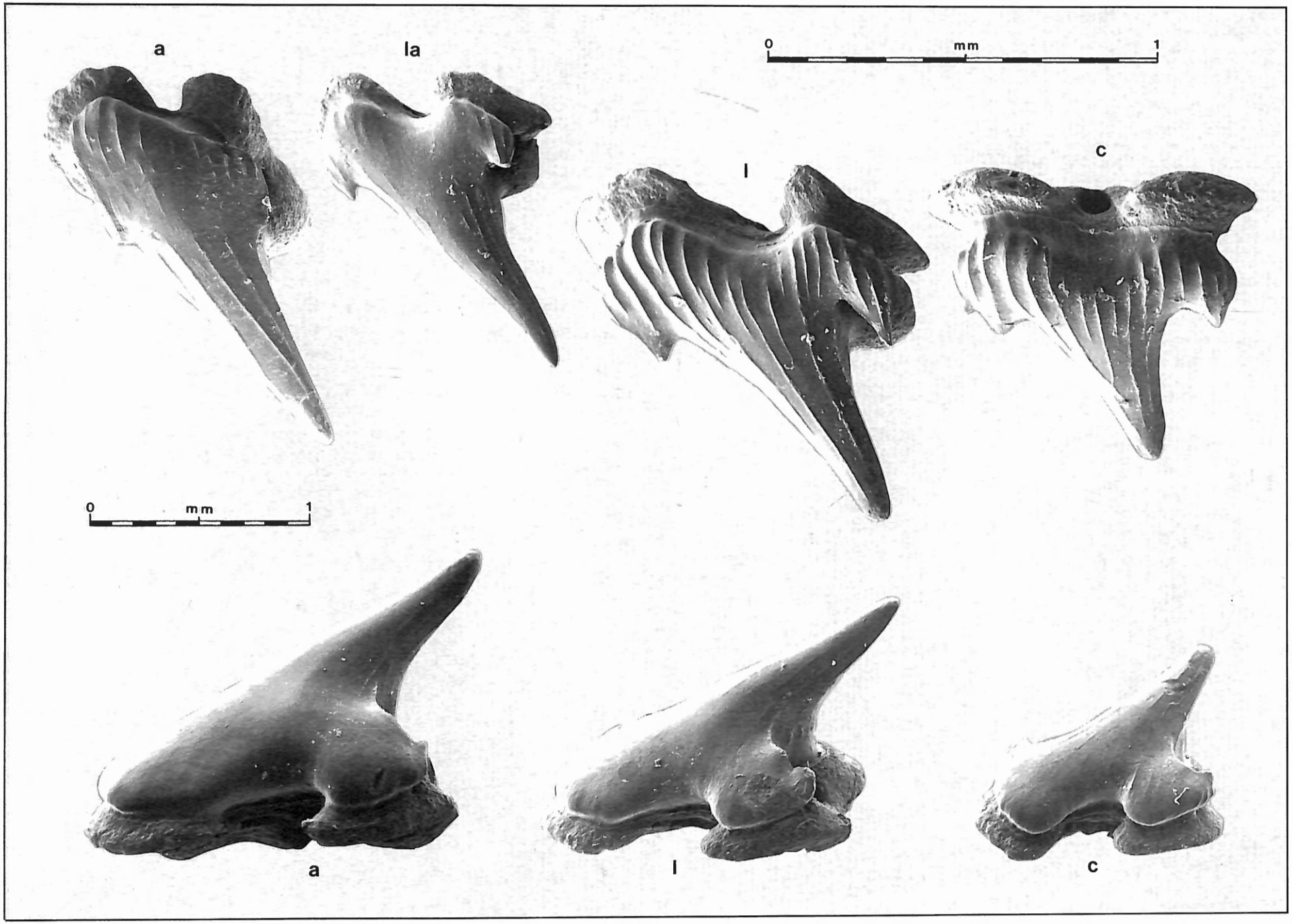

Plate 11. – Leptocharias smithii *Müller & Henle, 1839, male 65 cm (t.l.), Angola.*

Plate 12. – Leptocharias smithii *Müller & Henle, 1839, male 65 cm (t.l.), Angola.*

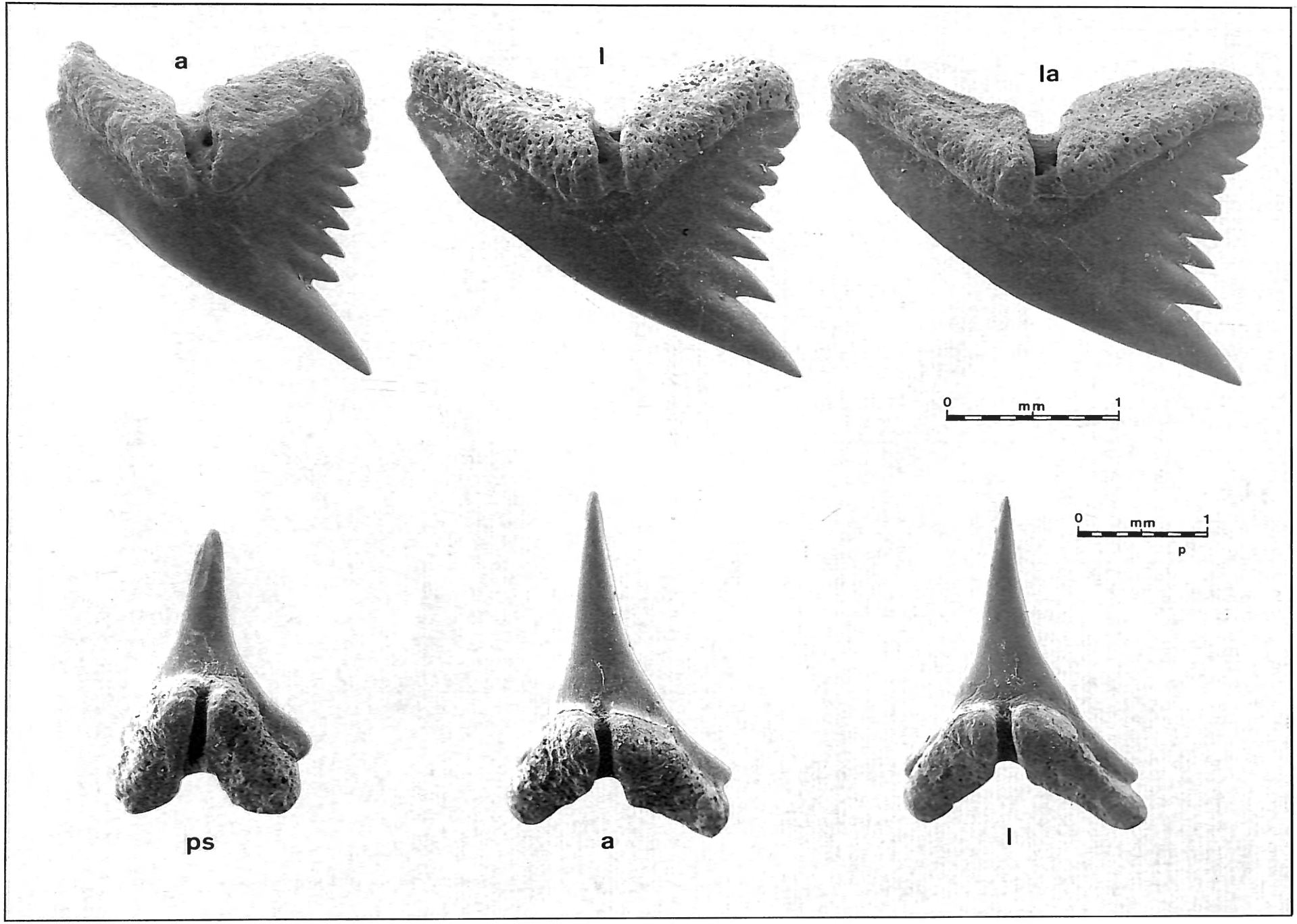

Plate 13. – Hemigaleus microstoma *Bleeker, 1852, male 71 cm (t.l.), South of Celebes Island, Indonesia.*

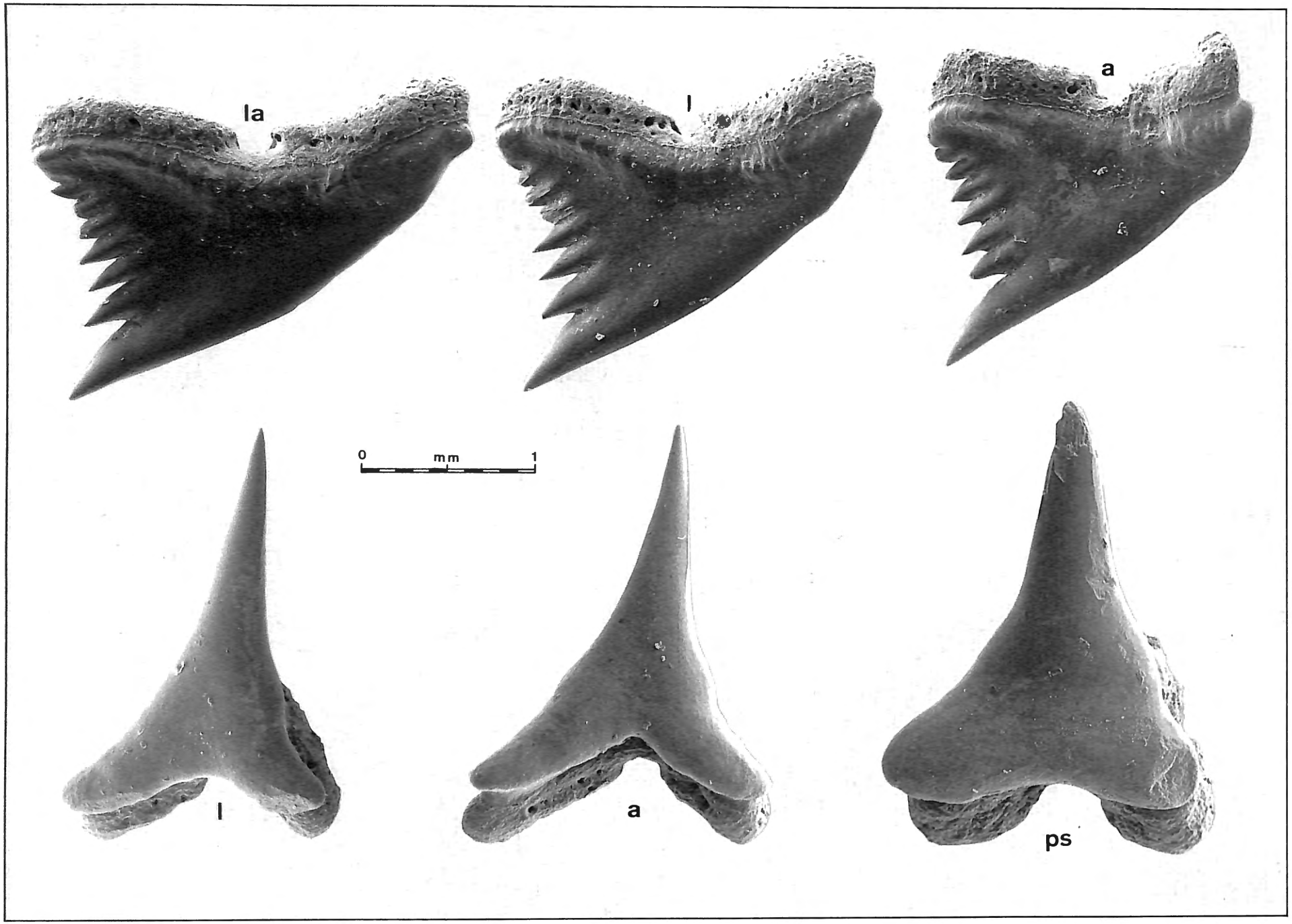

Plate 14. – Hemigaleus microstoma *Bleeker, 1852, male 71 cm (t.l.), South of Celebes Island, Indonesia.*

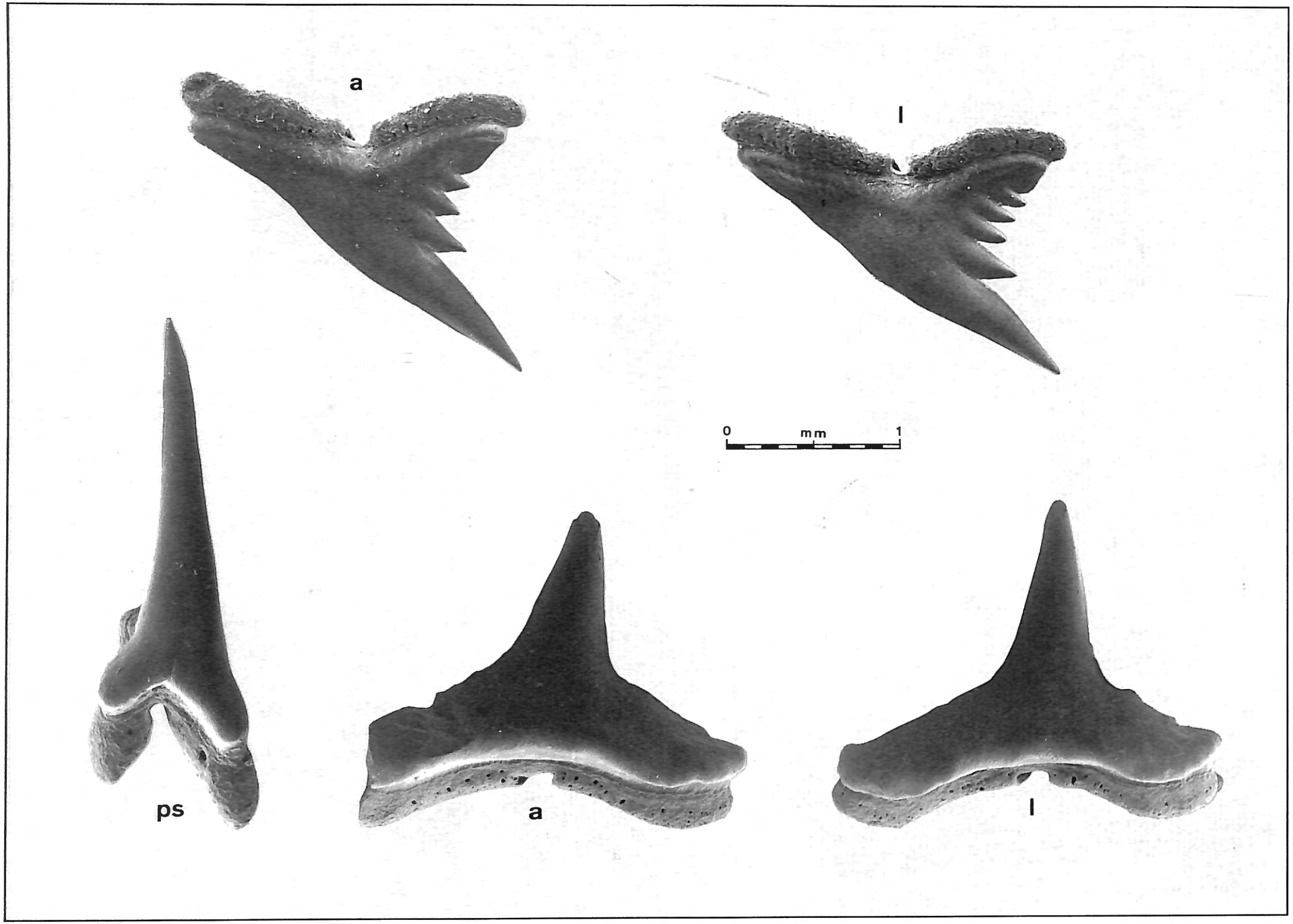

Plate 15. – Chaenogaleus macrostoma *(Bleeker, 1852), female 60 cm (t.l.), Palau Island, Philippines.*

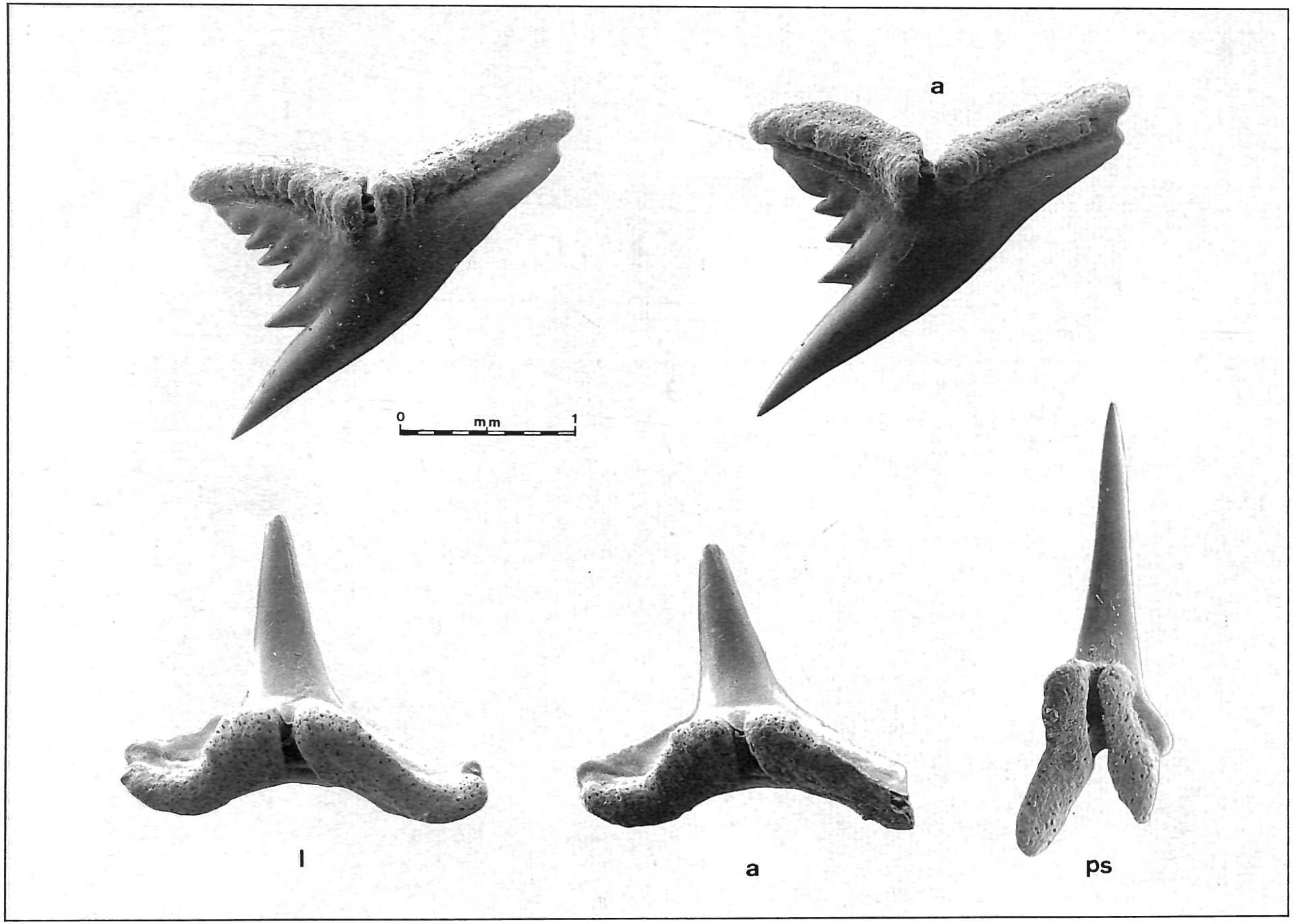

Plate 16. – Chaenogaleus macrostoma *(Bleeker, 1852), female 60 cm (t.l.), Palau Island, Philippines.*

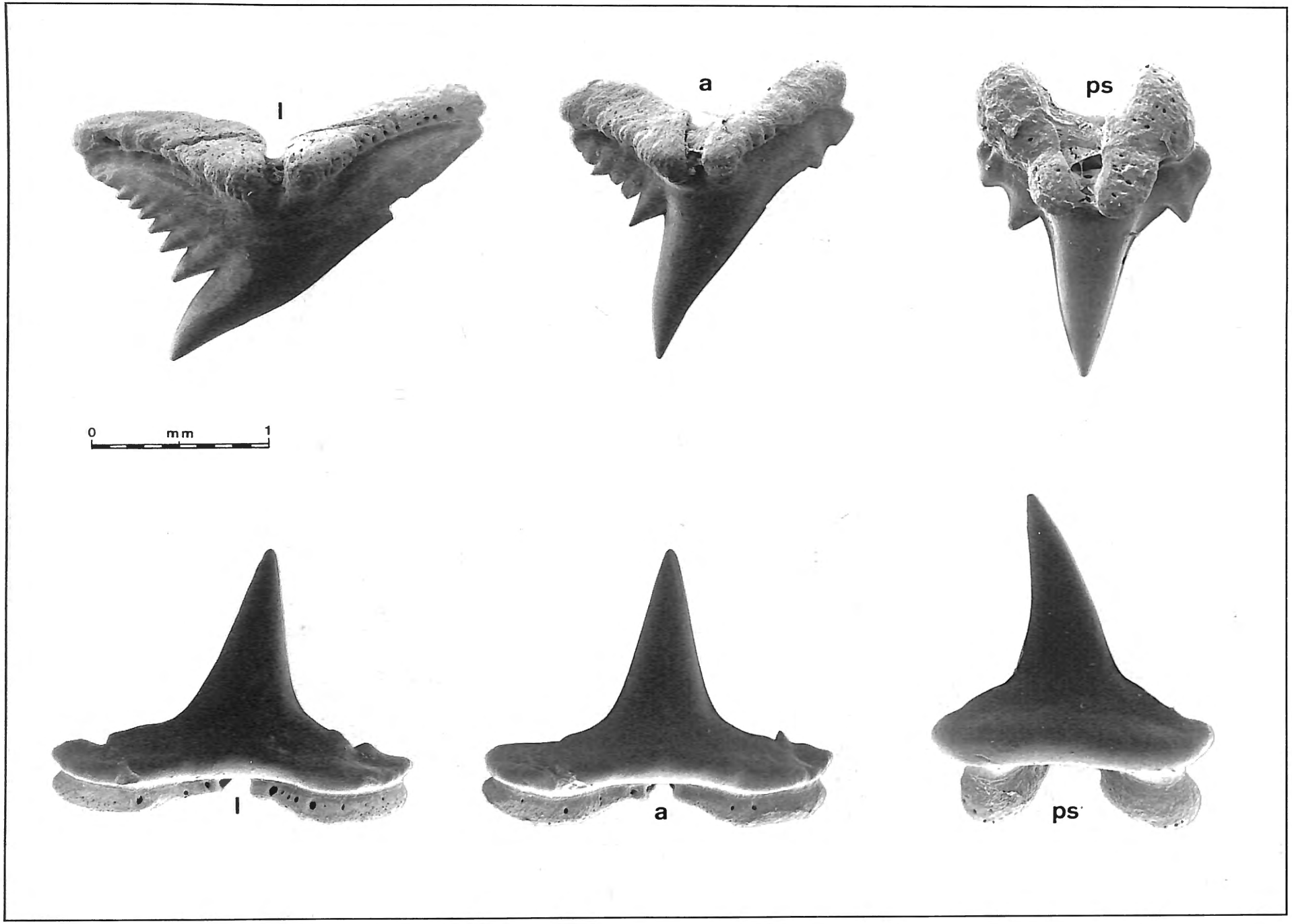

Plate 17. – Paragaleus pectoralis *(Garman, 1906), male 86 cm (t.l.), Atlantic coast of South Africa.*

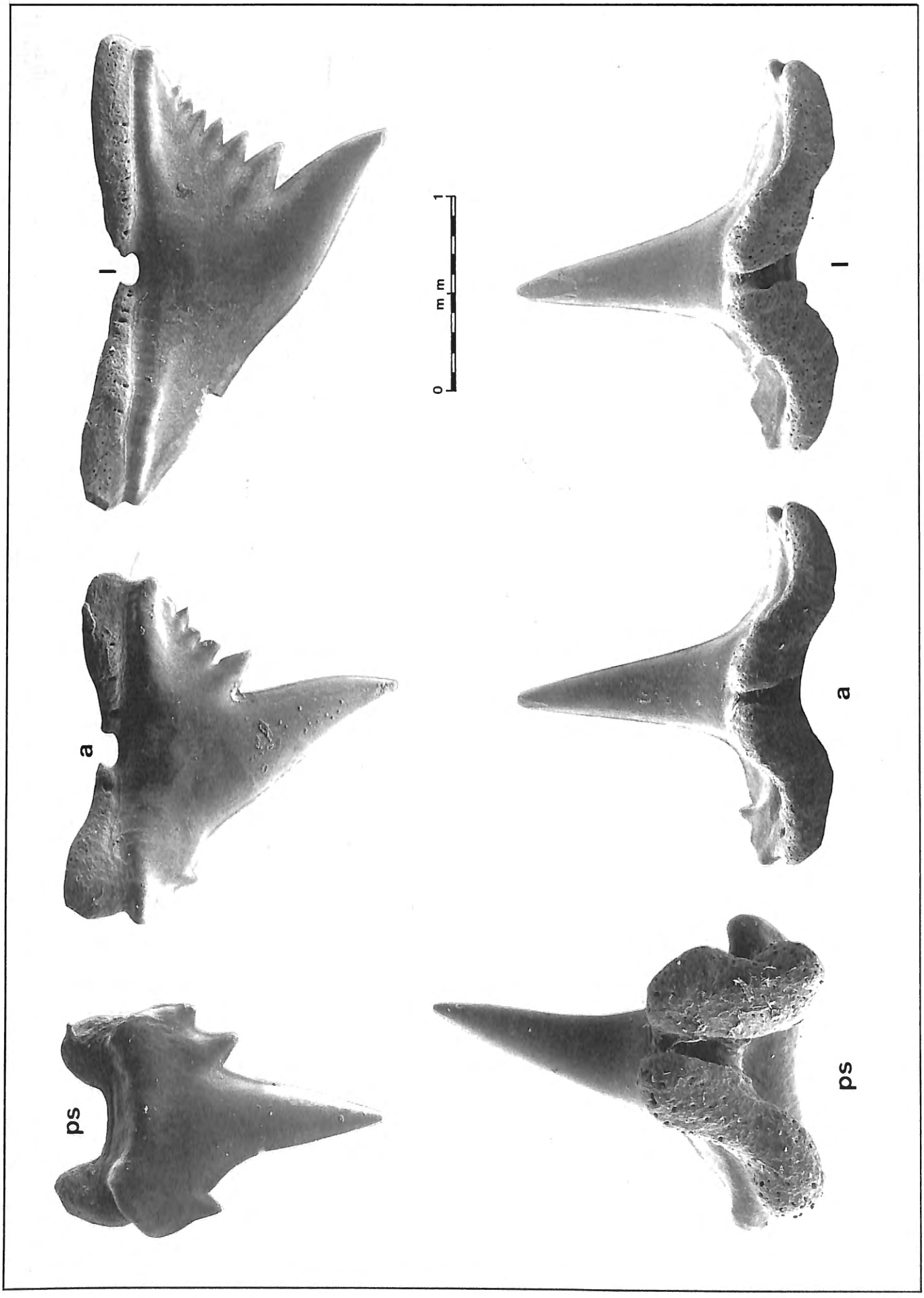

Plate 18. – Paragaleus pectoralis (Garman, 1906), male 86 cm (t.l.), Atlantic coast of South Africa.

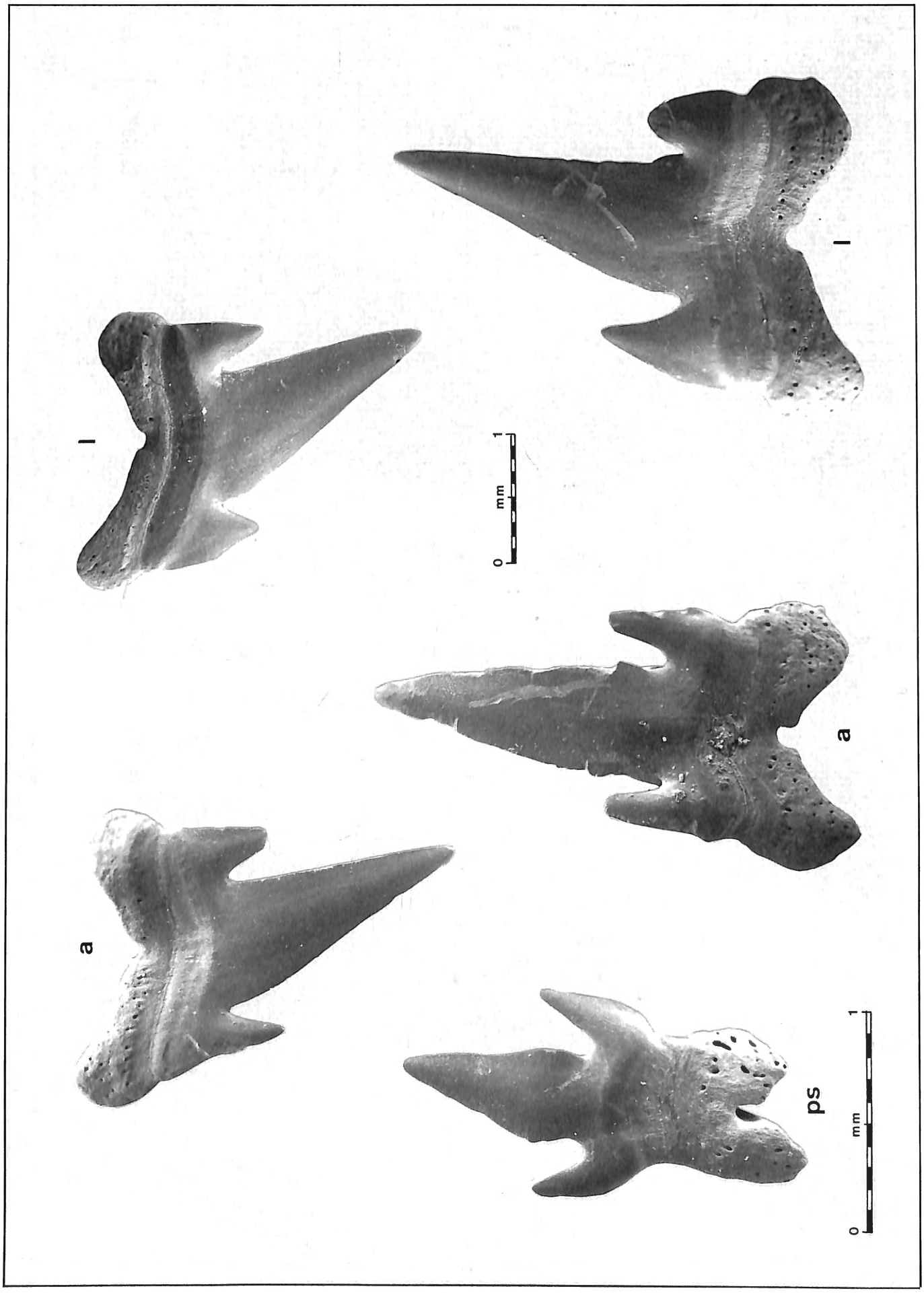

Plate 19. – Triaenodon obesus *RÜPPELL, 1837, female 88 cm (t.l.), Indonesia.*

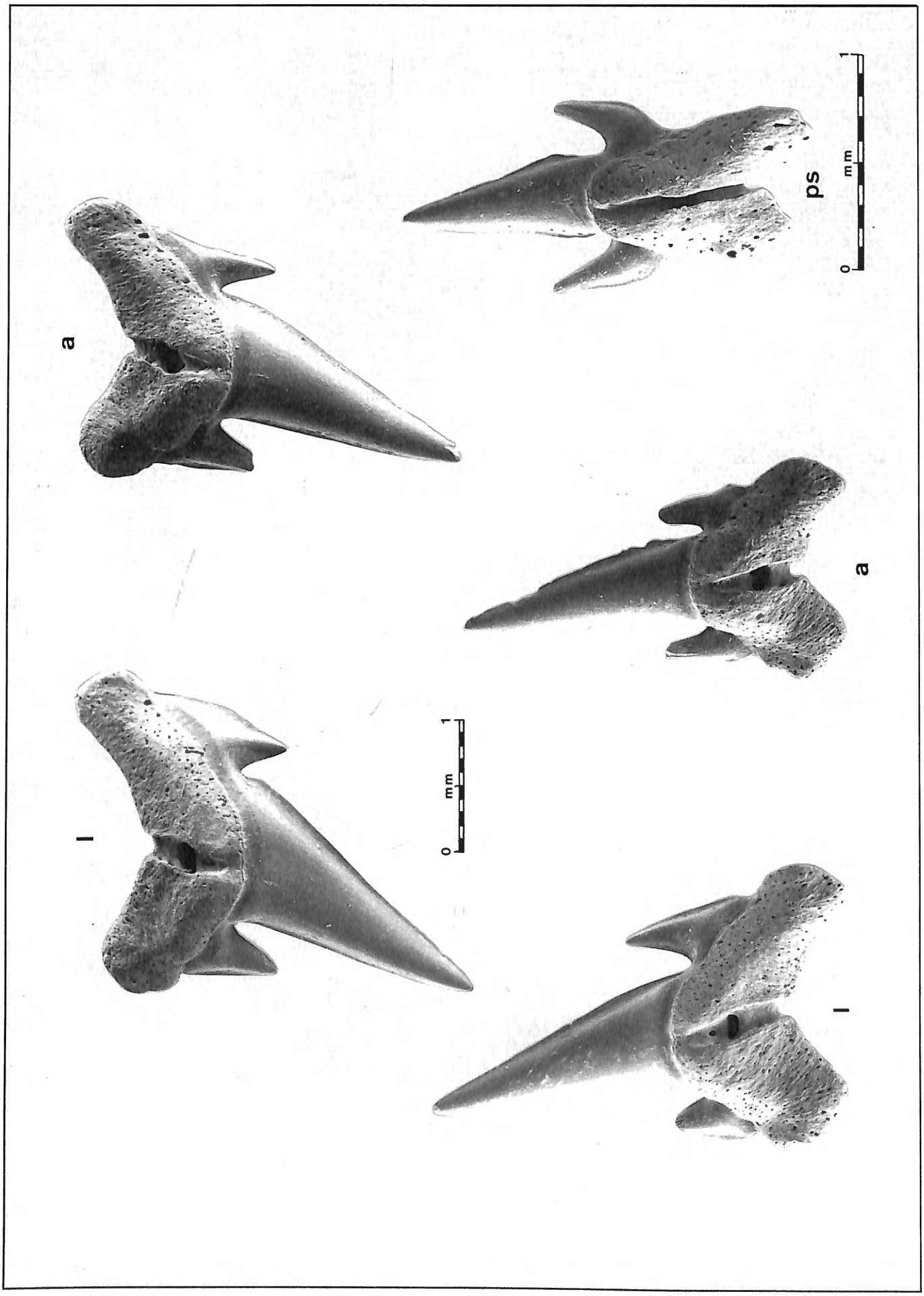

Plate 20. – Triaenodon obesus *RÜPPELL, 1837, female 88 cm (t.l.), Indonesia.*

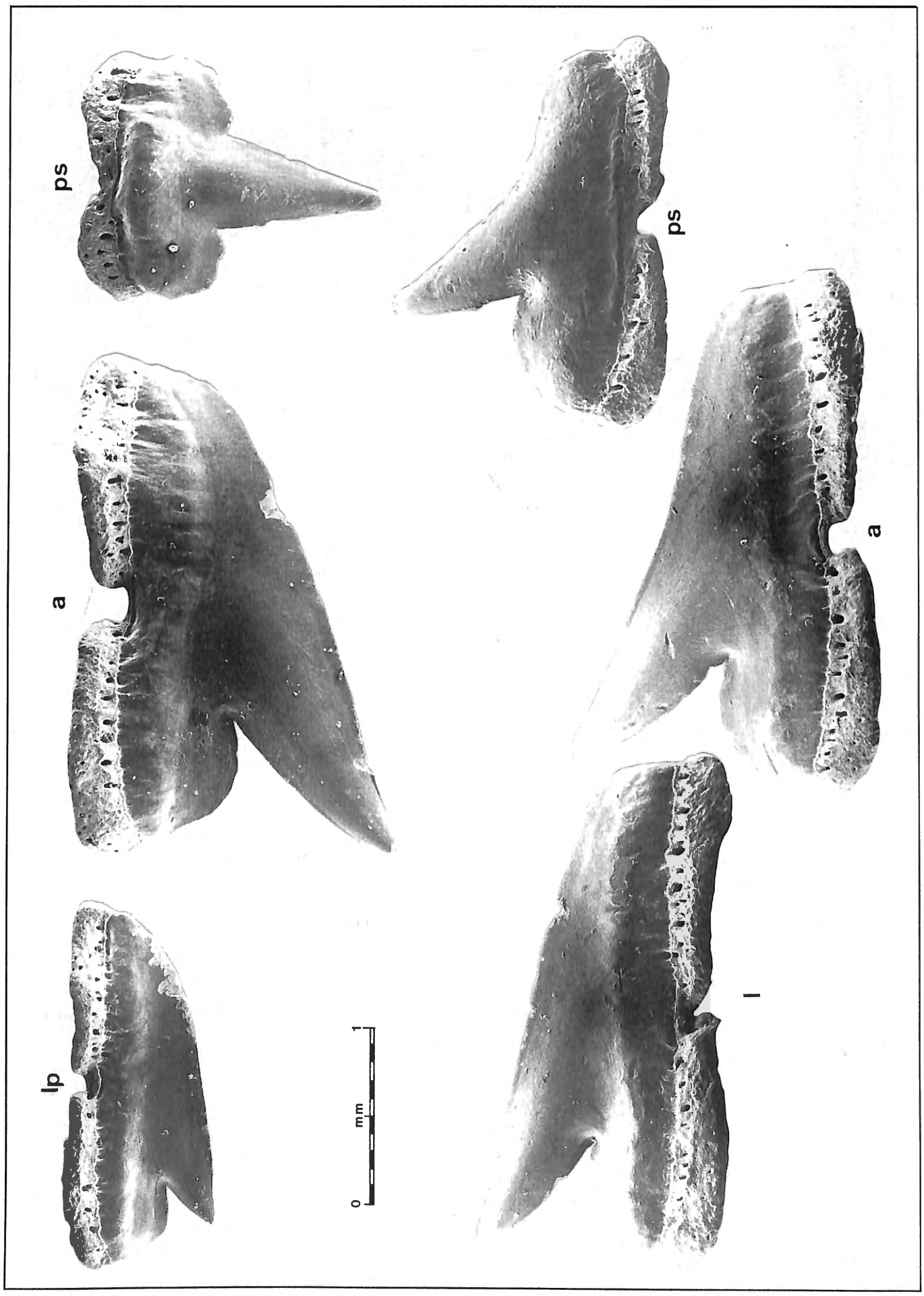

Plate 21. – Loxodon macrorhinus *Müller & Henle, 1839, female 80 cm (t.l.), Sri-Lanka.*

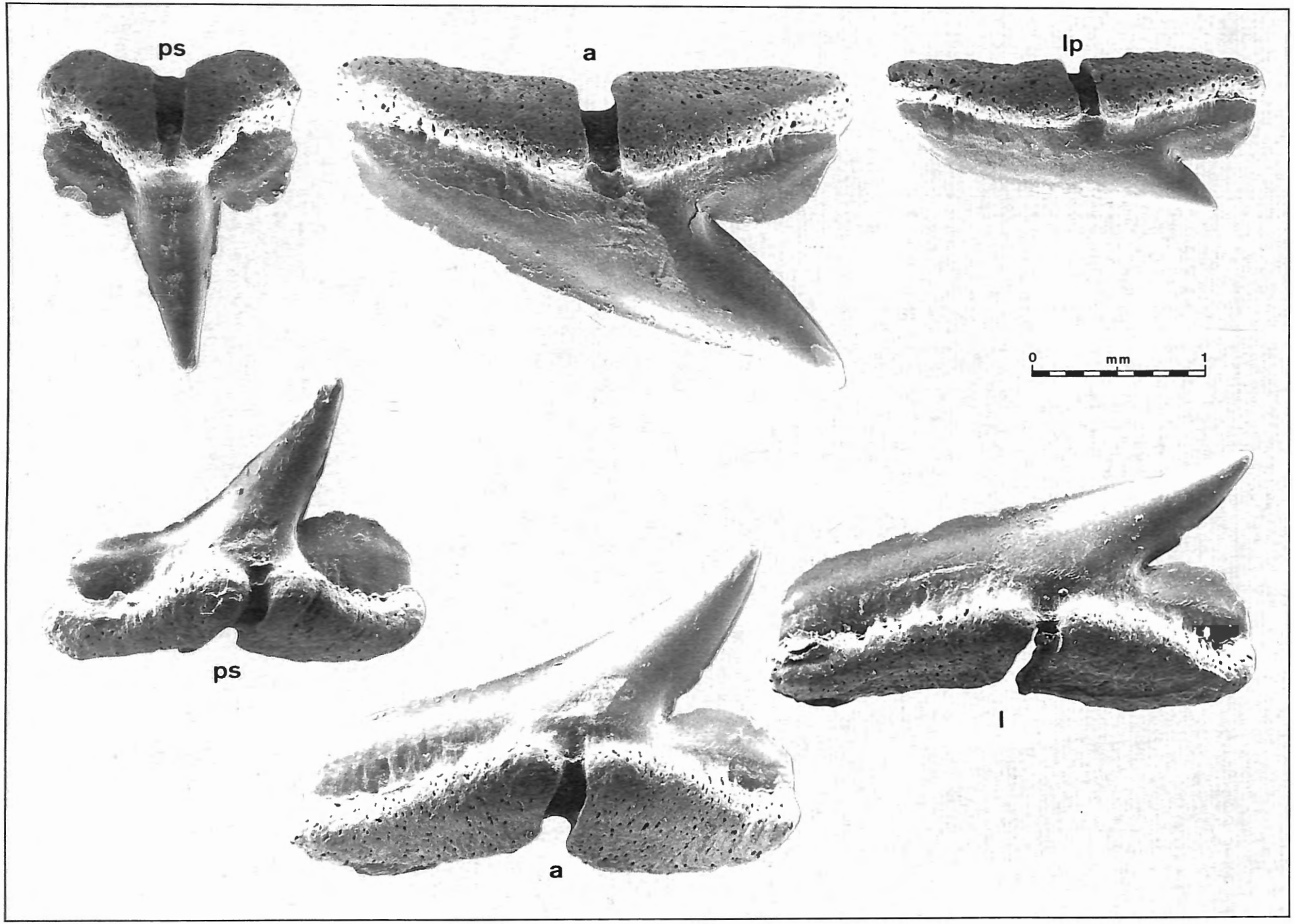

Plate 22. – Loxodon macrorhinus *Müller & Henle, 1839, female 80 cm (t.l.), Sri-Lanka.*

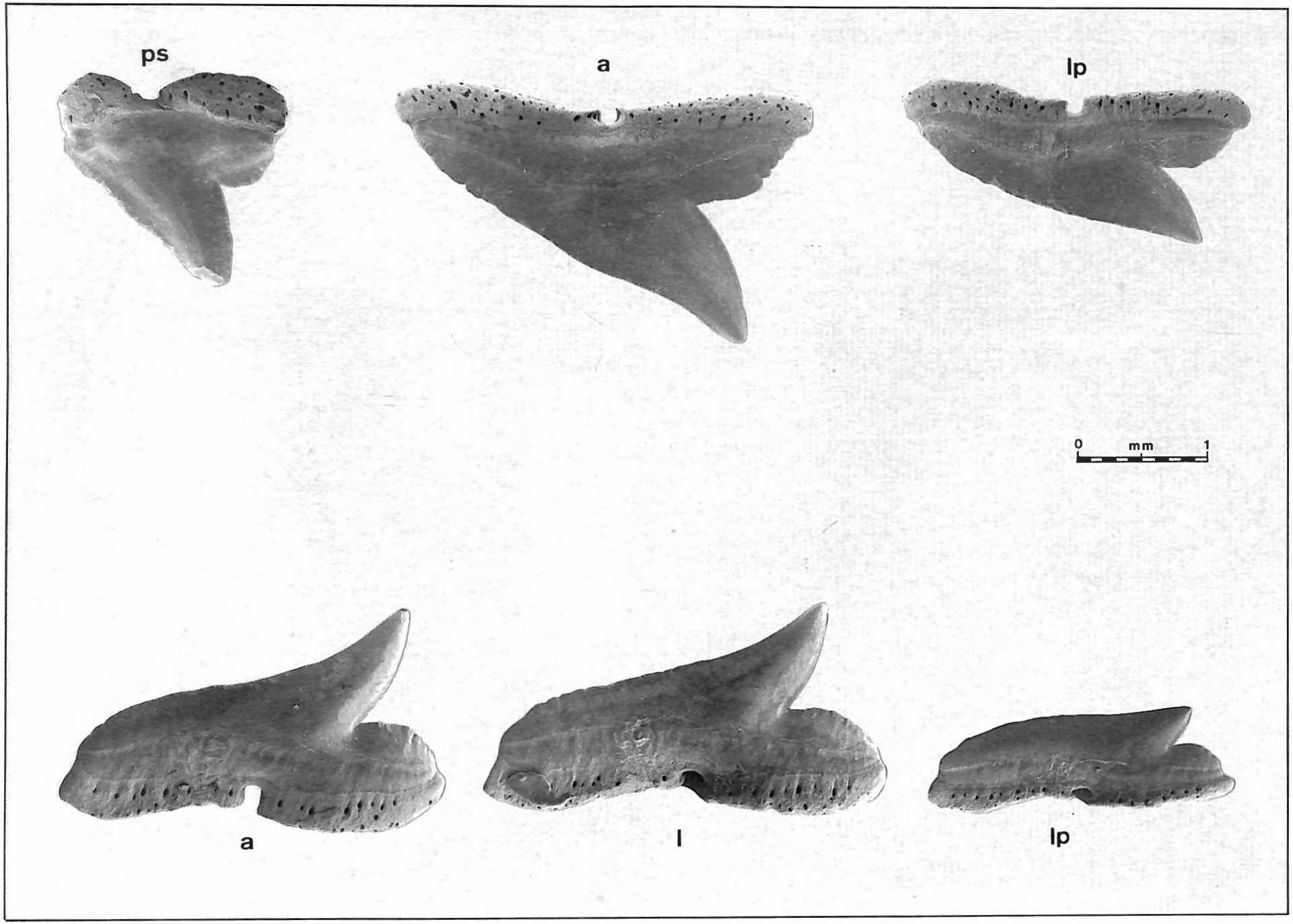

Plate 23. – Rhizoprionodon acutus *(RÜPPELL, 1837), male 46 cm (t.l.), Red Sea.*

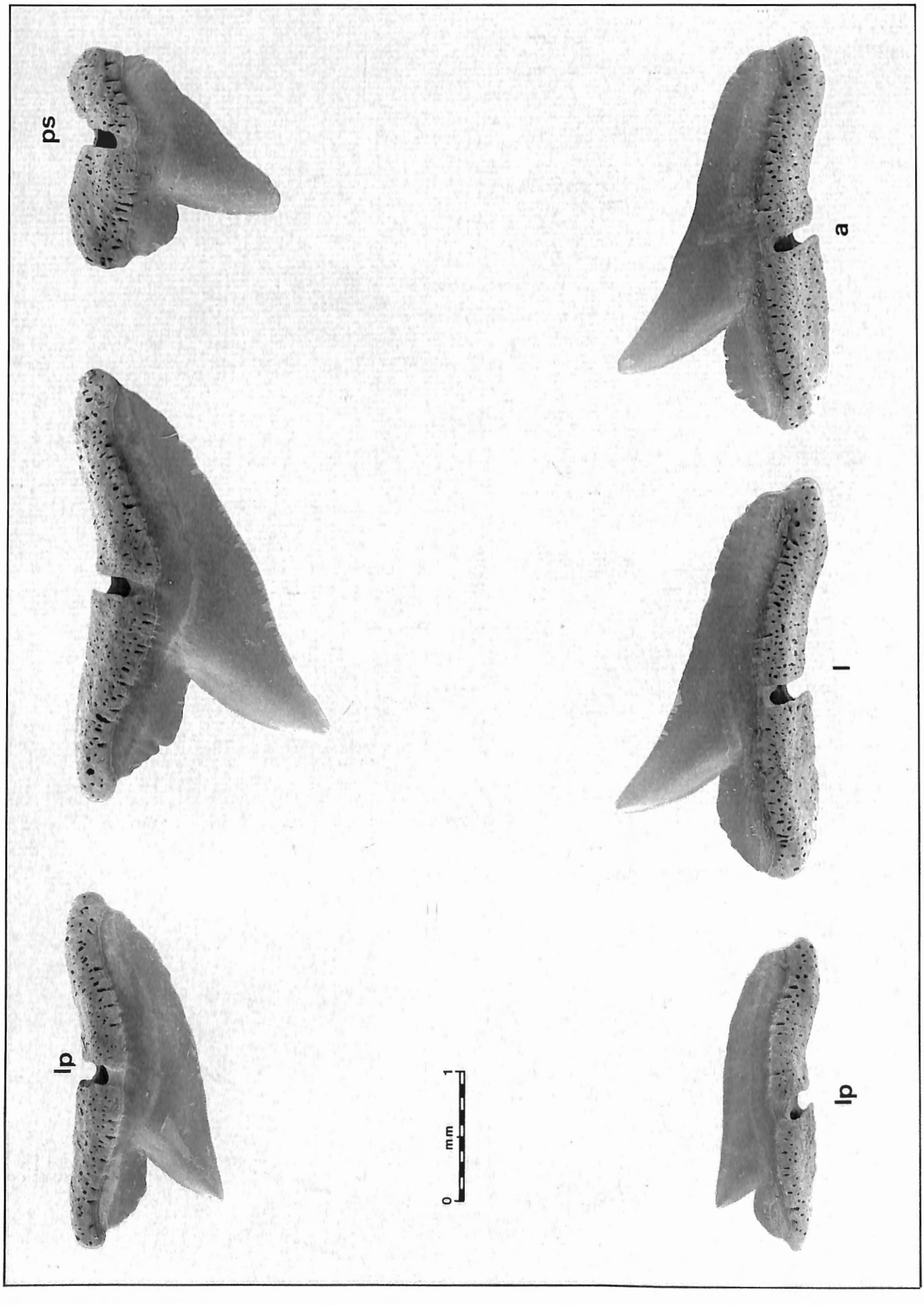

Plate 24. – Rhizoprionodon acutus *(Rüppell, 1837), male 46 cm (t.l.), Red Sea.*

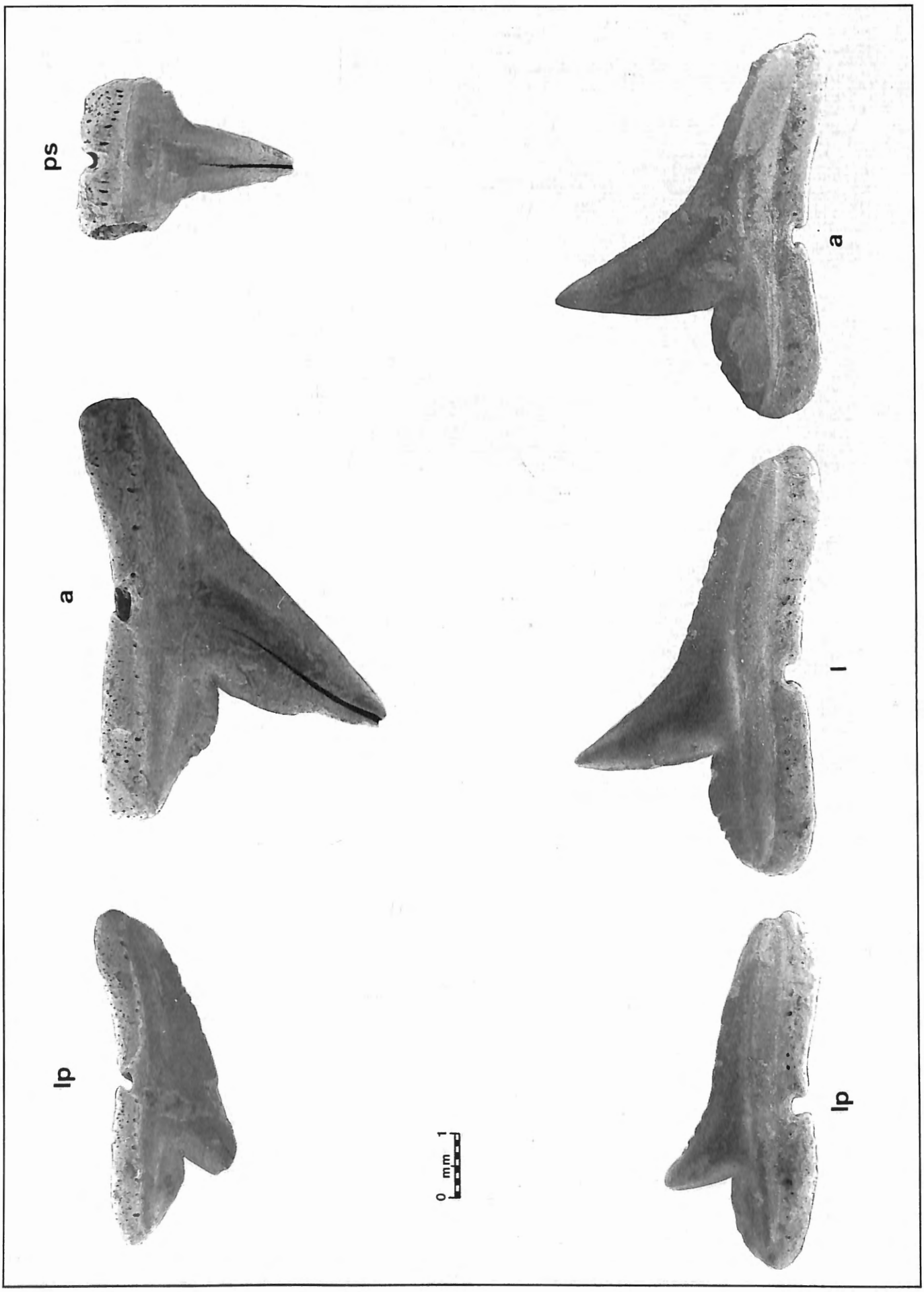

Plate 25. – Rhizoprionodon acutus *(Rüppell, 1837), female 92 cm (t.l.), Gambia.*

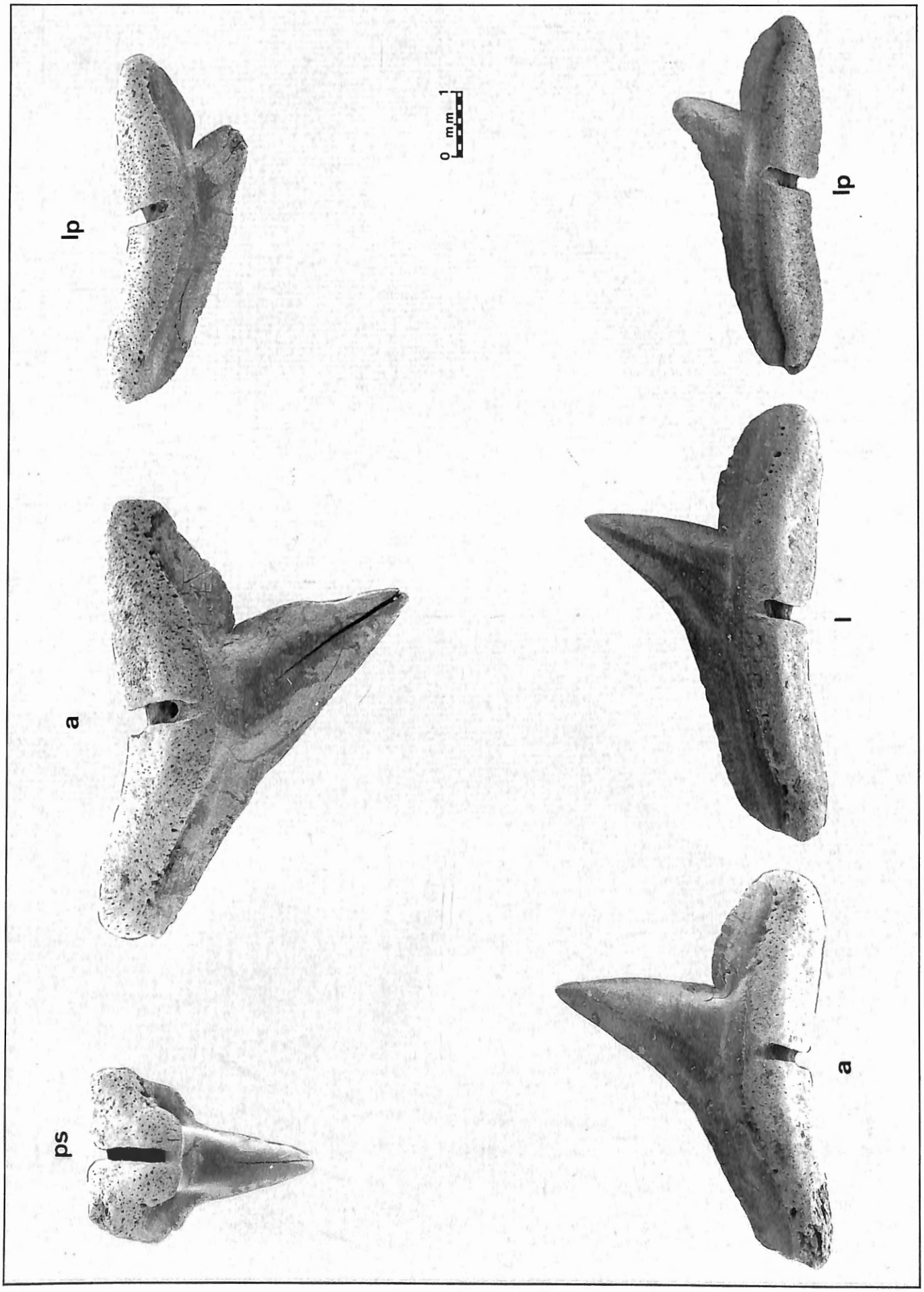

Plate 26. – Rhizoprionodon acutus *(Rüppell, 1837), female 92 cm (t.l.), Gambia.*

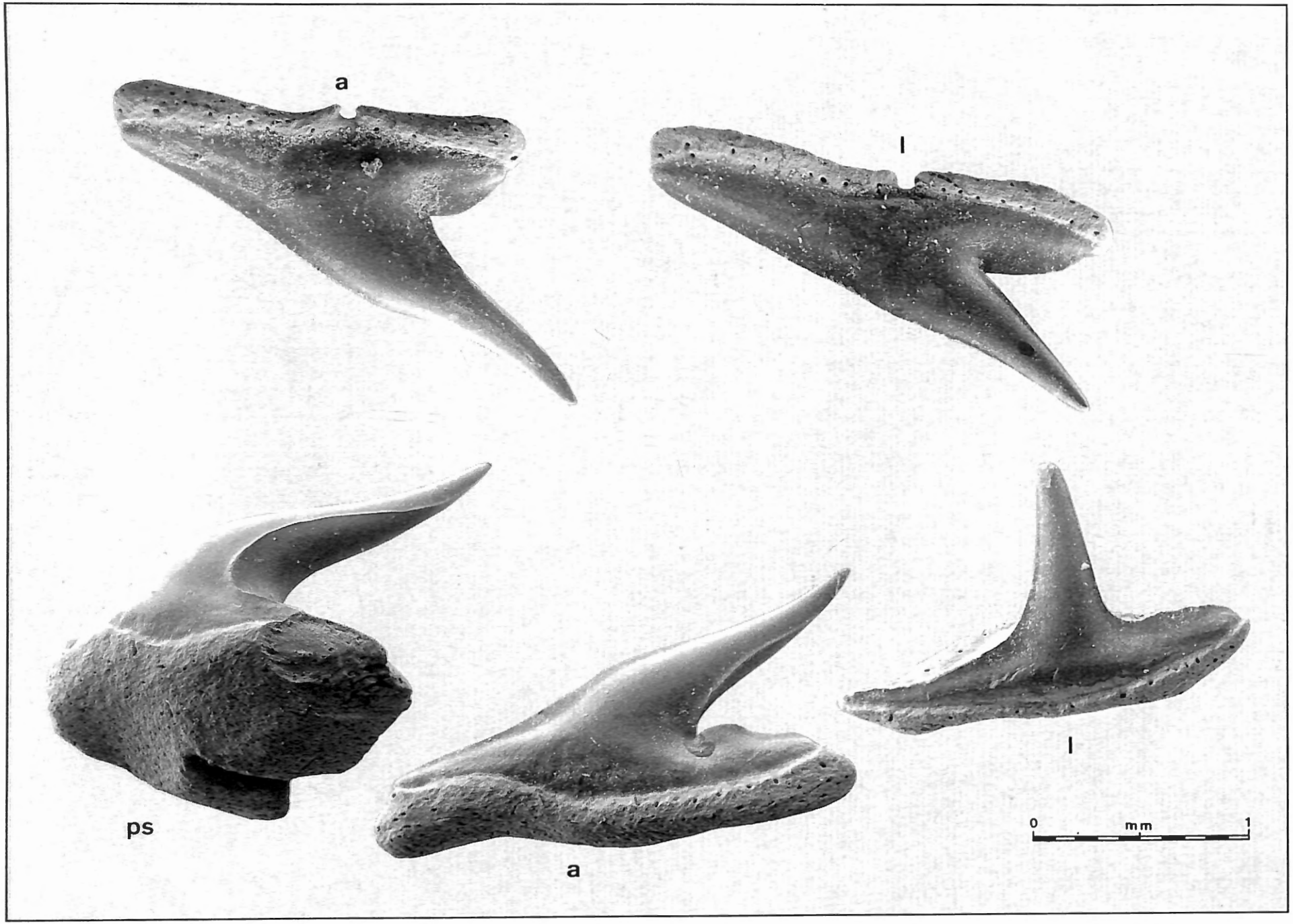

Plate 27. – Scoliodon laticaudus *MÜLLER & HENLE, 1838, male 48 cm (t.l.), holotype of* Physodon muelleri *VALENCIENNES, 1839, Bengal.*

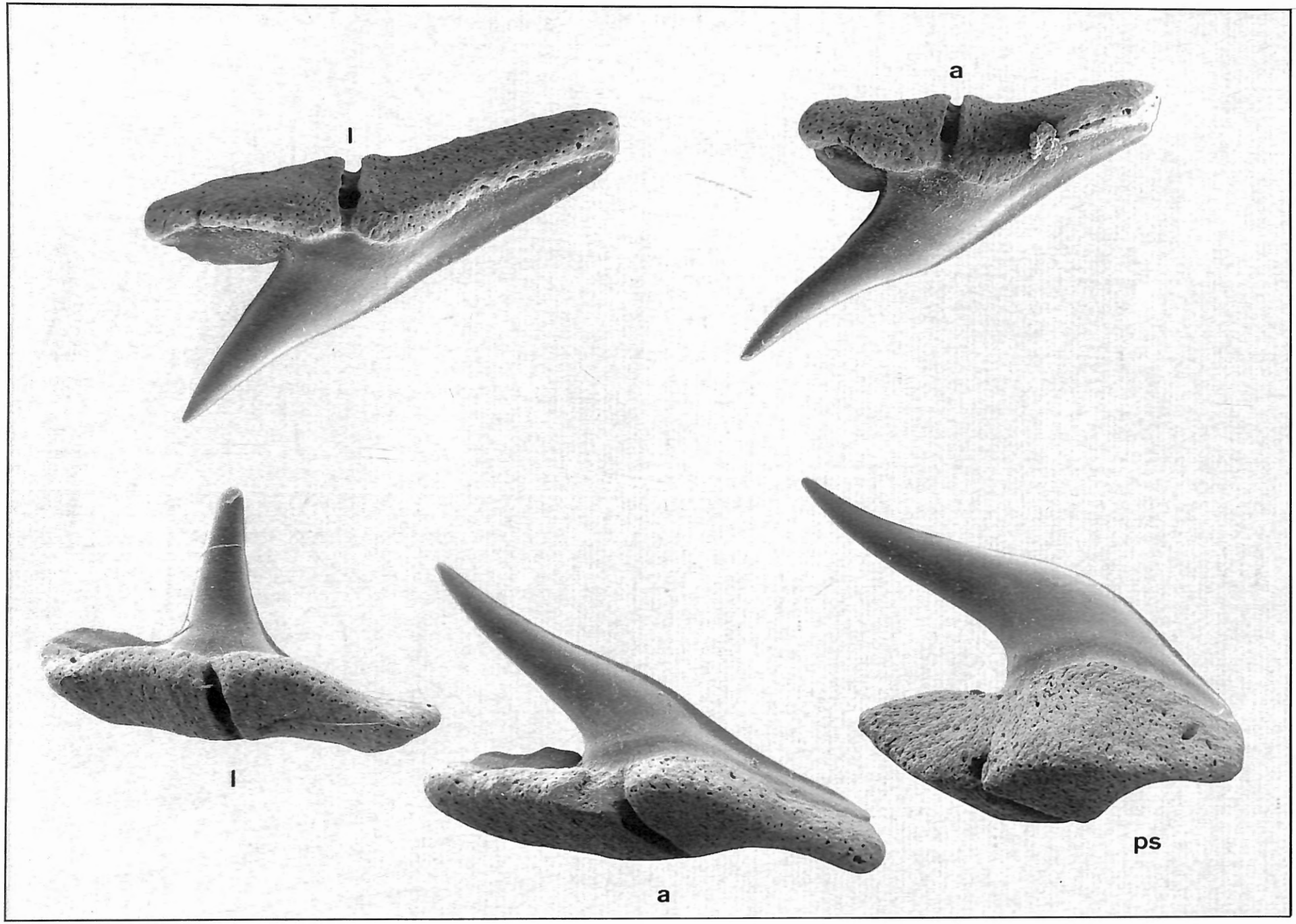

Plate 28. – Scoliodon laticaudus *Müller & Henle, 1838, male 48 cm (t.l.), holotype of* Physodon muelleri *Valenciennes, 1839, Bengal.*

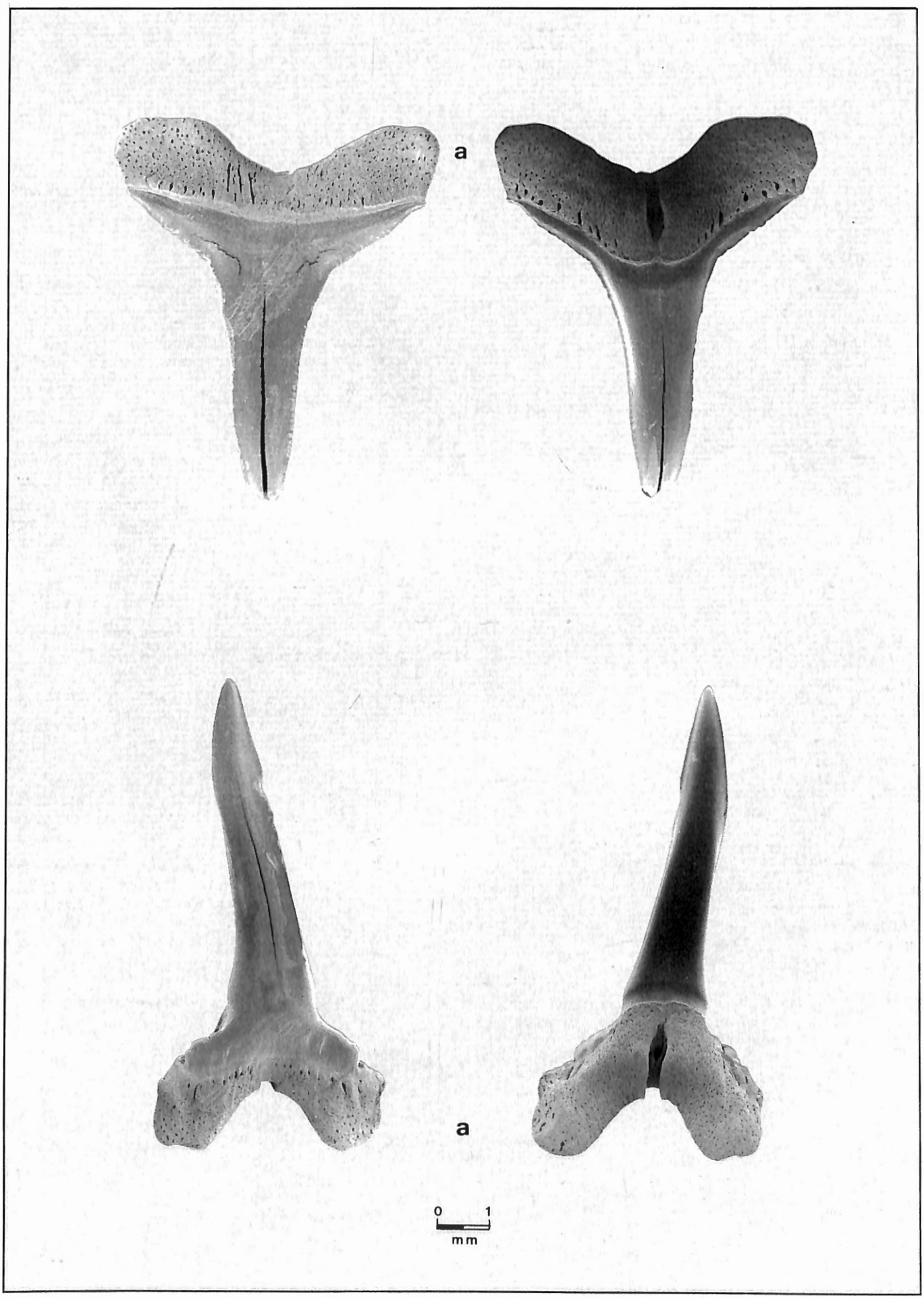

Plate 29. – Isogomphodon oxyrhynchus *(Müller & Henle, 1839), no data, French Guyana.*