

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. 2b :

Order : Carcharhiniformes - Family : Scyliorhinidae

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Abstract

The tooth morphology of all the genera and subgenera of the Scyliorhinidae, with the unique exception of *Pentanchus* (not available for examination), is described and illustrated.

Several systematic considerations are given.

The odontology of the genera *Centroscyllium* and *Aculeola*, which are rather aberrant among the Squaliformes, is compared with that of all the Scyliorhinidae taxa presently described.

Key-words : Elasmobranchii, Selachii, Scyliorhinidae, odontology.

Résumé :

A l'exception de celle du genre *Pentachus* (non disponible), la morphologie des dents des genres et des sous-genres des Scyliorhinidae est décrite et figurée.

Diverses considérations systématiques sont formulées.

L'odontologie des genres *Centroscyllium* et *Aculeola*, si isolés au sein des Squaliformes, est comparée avec celle de tous les taxa de Scyliorhinidae présentement décrits.

Mots-clés : Elasmobranchii, Selachii, Scyliorhinidae, odontologie.

Kurzfassung

Die Zahnmorphologie aller Gattungen und Untergattungen der Scyliorhinidae werden beschrieben und illustriert, mit Ausnahme von der Gattung *Pentachus*, die zum untersuchen nicht verfügbar war.

Mehrere systematische Erwägungen werden vorgeschlagen.

Die Odontologie der Gattungen *Centroscyllium* und *Aculeola*, abweicht von den Squaliformes, werden verglichen mit allen hier beschriebenen Scyliorhinidentaxa.

Schlüsselwörter : Elasmobranchii, Selachii, Scyliorhinidae, Odontologie.

Introduction

The teeth of the Scyliorhinidae, in general, were occasionally described but never properly illustrated. Previous

authors always restricted their illustrations to simplified drawings.

A careful examination was initiated of the teeth of almost all living genera of the Scyliorhinidae, comprising (after COMPAGNO, 1988) the subfamilies Atelomycterinae with the genera *Atelomycterus* and *Aulohalaelurus*, Schroederichthyinae with the single genus *Schroederichthys*, Scyliorhininae with the genera *Scyliorhinus*, *Poroderma* and *Cephaloscyllium*, and Pentanchinae, which is divided into the tribe Galeini with the genera *Asymbolus*, *Cephalurus*, *Galeus*, *Parmaturus*, *Haploblepharus*, *Holohalaelurus* and *Halaelurus*, and the tribe Pentanchini with the genera *Pentanchus* and *Apristurus*. The latter genus comprises the *brunneus*-, *indicus*-, *laurussonii*-, *longicephalus*-, *manis*-, *profundorum*-, *platyrhynchus*-, *riveri*-, *sibogae*- and *spongiceps*-groups. The *Halaelurus* has the two subgenera *Halaelurus* and *Bythaelurus*.

Teeth of the genus *Pentanchus* were not available for examination and could not be described nor illustrated.

COMPAGNO (1988) indicates differences between the type species of *Cephalurus* and specimens from off Peru. The teeth of one of these specimens were examined, described and illustrated.

Description of the odontological morphotypes

ORDER : CARCHARHINIFORMES,
sensu COMPAGNO (1988)

This order comprises, after COMPAGNO (1988), eight families : Triakidae, Proscylliidae, Leptochariidae, Scyliorhinidae, Pseudotriakidae, Sphyrnidae, Carcharhinidae and Hemigaleidae. Besides the Scyliorhinidae, the tooth morphology of which will be described and illustrated in this fascicle, the remaining families include the following subfamilies, tribes and genera :

Family : Proscylliidae				Family : SCYLIIORHINIDAE GILL, 1862
Subfamily : Proscylliinae				
<i>Proscyllium</i>	HILGENDORF,	1904		This family includes, after COMPAGNO (1988), the following subfamilies :
<i>Eridacnis</i>	SMITH,	1913		
<i>Ctenacis</i>	COMPAGNO,	1973		
Subfamily : Golluminae				<i>Atelomycterinae</i>
<i>Gollum</i>	COMPAGNO,	1973		<i>Schroederichthyinae</i>
Family : Leptochariidae				<i>Scyliorhininae</i>
<i>Leptocharias</i>	SMITH, in MÜLLER & HENLE,	1838		<i>Pentanchinae</i>
Family : Pseudotriakidae				
<i>Pseudotriakis</i>	BRITO CAPELLO,	1867		The subfamily <i>Atelomycterinae</i> comprises the genera :
Family : Triakidae				<i>Atelomycterus</i> GARMAN, 1913, type species : <i>Scyllium marmoratum</i>
Subfamily : Triakinae				<i>Aulohalaelurus</i> FOWLER, 1934, type species : <i>Catulus labiosus</i>
<i>Triakis</i>	MÜLLER & HENLE,	1838		
<i>Mustelus</i>	LINCK,	1790		
<i>Scylliogaleus</i>	BOULENGER,	1902		The subfamily <i>Schroederichthyinae</i> comprises the genus :
Subfamily : Galeorhininae				<i>Schroederichthys</i> SPRINGER, 1966, type species : <i>Schroederichthys maculatus</i>
Tribe : Iagini				
<i>Hemitriakis</i>	HERRE,	1923		
<i>Furgaleus</i>	WHITLEY,	1951		The subfamily <i>Scyliorhininae</i> comprises the genera :
<i>Gogolia</i>	COMPAGNO,	1973		<i>Cephaloscyllium</i> GILL, 1862, type species : <i>Scyllium laticeps</i>
<i>Iago</i>	COMPAGNO & SPRINGER,	1971		<i>Poroderma</i> SMITH, 1837, type species : <i>Squalus africanus</i>
Tribe : Galeorhinini				<i>Scyliorhinus</i> BLAINVILLE, 1816, type species : <i>Scyliorhinus canicula</i>
<i>Galeorhinus</i>	BLAINVILLE,	1816		
<i>Hypogaleus</i>	SMITH,	1957		
Family : Sphyrnidae				
<i>Eusphyrna</i>	GILL,	1862		The subfamily <i>Pentanchinae</i> comprises the tribes :
<i>Sphyrna</i>	RAFINESQUE,	1810		Galeini, including the genera :
Family : Carcharhinidae				<i>Asymbolus</i> WHITLEY, 1939, type species : <i>Scyllium anale</i>
Subfamily : Galeocerlinae				<i>Cephalurus</i> BIGELOW & SCHROEDER, 1941, type species : <i>Catulus cephalus</i>
<i>Galeocerdo</i>	MÜLLER & HENLE,	1837		<i>Galeus</i> RAFINESQUE, 1810, type species : <i>Galeus melastomus</i>
Subfamily : Scoliodontinae				<i>Halaelurus</i> GILL, 1862, type species : <i>Halaelurus bürgeri</i>
<i>Scoliodon</i>	MÜLLER & HENLE,	1837		<i>Haploblepharus</i> GARMAN, 1913, type species : <i>Haploblepharus edwardsii</i>
Subfamily : Carcharhininae				<i>Holohalaelurus</i> FOWLER, 1934, type species : <i>Scyliorhinus regani</i>
Tribe : Rhizoprionini				<i>Parmaturus</i> GARMAN, 1906, type species : <i>Parmaturus polius</i>
<i>Loxodon</i>	MÜLLER & HENLE,	1838		Pentanchini, including the genera :
<i>Rhizoprionodon</i>	WHITLEY,	1929		<i>Apristurus</i> GARMAN, 1913, type species : <i>Scyliorhinus indicus</i>
Tribe : Isogomphodontini				<i>Pentanchus</i> SMITH & RADCLIFFE, 1912, type species : <i>Pentanchus profundicolus</i>
<i>Isogomphodon</i>	GILL,	1862		
Tribe : Carcharinini				
<i>Carcharhinus</i>	BLAINVILLE,	1816		
<i>Glyphis</i>	AGASSIZ,	1843		
<i>Prionace</i>	CANTOR,	1849		
<i>Nasolamia</i>	COMPAGNO & GARRICK,	1983		
<i>Lamiopsis</i>	GILL,	1862		
<i>Negaprion</i>	WHITLEY,	1940		
Tribe : Triaenodontini				
<i>Triaenodon</i>	MÜLLER & HENLE,	1837		The following 136 specimens belonging to 28 species were examined :
Family : Hemigaleidae				
Subfamily : Hemigaleininae				
<i>Hemigaleus</i>	BLEEKER,	1852		<i>Apristurus maderensis</i> 2 males
<i>Paragaleus</i>	BUDKER,	1935		<i>Apristurus laurussoni</i> 15 males 9 females
<i>Chaenogaleus</i>	GILL,	1862		<i>Asymbolus analis</i> 2 males 1 female
Subfamily : Hemipristinae				<i>Atelomycterus marmoratus</i> 2 males
<i>Hemipristis</i>	AGASSIZ,	1843		<i>Aulohalaelurus labiosus</i> 1 male 1 female
				<i>Bythaelurus canescens</i> 1 male
				<i>Cephaloscyllium isabellum</i> 1 male 1 female
				<i>Cephaloscyllium sufflans</i> 1 male
				<i>Cephalurus cephalus</i> 1 male

<i>Cephalurus</i> sp. (SE-Pacific)		1 female
<i>Galeus melastomus</i>	14 males	18 females
<i>Galeus murinus</i>	7 males	9 females
<i>Galeus polli</i>	1 male	1 female
<i>Halaelurus bürgeri</i>		1 female
<i>Halaelurus natalensis</i>	1 male	
<i>Haploblepharus edwardsii</i>	1 male	
<i>Holohalaelurus regani</i>	1 male	
<i>Parmaturus melanobranchius</i>		1 female
<i>Parmaturus pilosus</i>	1 male	
<i>Parmaturus xaniurus</i>	1 male	1 female
<i>Poroderma africanum</i>		1 female
<i>Poroderma pantherinum</i>	1 male	
<i>Scyliorhinus canicula</i>	5 males	9 females
<i>Scyliorhinus capensis</i>		1 female
<i>Scyliorhinus stellaris</i>	7 males	6 females
<i>Scyliorhinus torazame</i>	1 male	
<i>Schroederichthys chilensis</i>	1 male	
<i>Schroederichthys maculatus</i>	1 male	

The teeth of the species of the family Scyliorhinidae, generally, have a well developed slender principal cusp, flanked by up to three cusplets.

The root is rarely holaulacorhizid, more often secondary hemiaulacorhizid, which is demonstrated by a partly closed median groove, and mostly secondary anaulacorhizid, by a fully closed median groove. Because fossil ancestors of this family mostly have holaulacorhizid roots with a strongly developed median groove, the root types of living Scyliorhinidae can not be hemiaulacorhizid nor anaulacorhizid *sensu stricto* (CASIER, 1947), but these types of hemiaulacorhizy or anaulacorhizy are formed by syncretion of the median groove. Therefore, we follow CAPPETTA (1987) and use the terms secondary hemiaulacorhizy and secondary anaulacorhizy for this type of root.

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 for females. A strong ontogenetic heterodonty is often present by broader cusplets and a much shorter, less convex principal cusp in teeth of juvenile specimens. A gradient monographic heterodonty is always present by little broader lateral teeth with a more inclined or oblique principal cusp. The lateral teeth and those next to the commissure are mostly smaller than the anterior ones.

Genus : *Apristurus* GARMAN, 1913

Many authors have studied this genus but there is till now much uncertainty about the validity of its species. The most recent revision is of COMPAGNO (1988), who included the following 27 species in this genus :

Apristurus atlanticus (KOEFOED, 1932), *Apristurus brunneus* (GILBERT, 1892), *Apristurus canutus* SPRINGER &

HEEMSTRA, 1979, *Apristurus federovi* DOLGANOV, 1985, *Apristurus herklotsi* (FOWLER, 1934), *Apristurus indicus* (BRAUER, 1906), *Apristurus investigatoris* (MISRA, 1962), *Apristurus japonicus* NAKAYA, 1975, *Apristurus kampae* TAYLOR, 1972, *Apristurus laurussoni* (SAEMUNDSSON, 1922), *Apristurus longicephalus* NAKAYA, 1975, *Apristurus macrorhynchus* (TANAKA, 1909), *Apristurus maderensis* CADENAT & MAUL, 1966, *Apristurus manis* (PRINGER, 1979), *Apristurus microps* (GILCHRIST, 1922), *Apristurus nasutus* DE BUEN, 1959, *Apristurus parvipinnis* SPRINGER & HEEMSTRA, 1979, *Apristurus pinguis* DENG, XIONG & ZAHN, 1983, *Apristurus platyrhynchus* (TANAKA, 1909), *Apristurus profundorum* (GOODE & BEAN, 1896), *Apristurus riveri* BIGELOW & SCHROEDER, 1944, *Apristurus saldanha* (BARNARD, 1925), *Apristurus sibogae* (WEBER, 1913), *Apristurus sinensis* CHU & HU, 1981, *Apristurus spongiceps* (GILBERT, 1895), *Apristurus stenseni* (SPRINGER, 1979), *Apristurus verweyi* (FOWLER, 1934).

The type species of this genus is *Scyliorhinus indicus* BRAUER, 1906 by original designation. However, teeth of the type species were not available for examination, and therefore *Apristurus laurussoni* will be used instead, for illustration and description of the tooth morphology.

Apristurus laurussoni (SAEMUNDSSON, 1922) (Plates 1, 2, 3, 4)

Scyllium laurussoni SAEMUNDSSON, 1922, Vidensk. Meddr Dansk Naturhist. Foren. Kobenhavn., 74 : 173.

The teeth of this species have a rather slender and elongated principal cusp, which is more distinct in upper teeth. The principal cusp is strongly inclined toward the commissure and is commonly flanked by two or (in lateral teeth) three also slender and elongated cusplets. The cusplets closest to the principal cusp reach half the height of the principal cusp or even more in lower lateral teeth.

The root varies between holaulacorhizid and secondary anaulacorhizid, showing two root lobes, that are relatively long and narrow, forming an angle at the root base. The dimensions of the teeth are plurimillimetrical in range.

The outer face of the principal cusp and cusplets is flat to very weakly convex, presenting well developed striae, that run from crown base toward the apex of the principal cusp and cusplets. Although those striae are rather regular in shape, they are sometimes slightly sigmoidal. They reach a maximum density of six striae on the principal cusp in anterior teeth, decreasing to two on the lower lateral one. Striae on cusplets are always less distinct than on the principal cusp.

Reticulated ornamentation is present on the crown base between the striae, which is more distinct on posterior teeth.

The inner face of the principal cusp and cusplets is strongly convex, also presenting striae, which are a little less distinct than the outer ones.

They also run from crown base toward the apex of the principal cusp and cusplets in a more or less regular way.

Their density is rather steady with six striae on the principal cusp and less on cusplets.

Basal ornamentation is absent.

The outer face of the root has a strong central depression, presenting a line of up to ten well developed foramina, of which the central ones are often merged.

The inner face of the root 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 parts, of which the basal face is often called the root base.

Two or four foramina are present on each root lobe, on the part toward the crown and along the ridge. Foramina are absent near the crown root junction. A foramen is always present just below the centre of the ridge, and is sometimes more or less extended toward the root base, forming a partial groove or even sometimes a complete median one.

Some randomly scattered foramina are present on the basal face.

Genus : *Asymbolus* WHITLEY, 1939

The genus *Asymbolus* comprises, after COMPAGNO (1988), the two species *Asymbolus vincenti* (ZEITZ, 1908) and *Asymbolus analis* (OGILBY, 1885). The type species is *Scyllium anale* OGILBY, 1995 by original designation.

Asymbolus analis (OGILBY, 1885)
(Plates 5, 6; Plate 35, figs. 1 & 2)

Scyllium anale OGILBY, 1885. Proceedings of the Linnean Society, New South Wales, 10 : pp. 445-447.

The teeth of this species have a broad based but elongated principal cusp. The principal cusp is more or less oblique toward the commissure and has commonly one also short and broad based cusplet at each side. A vaguely developed second cusplet is present on the extreme edges, next to each cusplet.

The anaulacorhizid root shows two root lobes that are relatively long and narrow, forming an angle at the root base.

The teeth are plurimillimetrical in range.

The outer face of the principal cusp and cusplets is weakly convex, presenting well developed, short basal costules and poorly developed striae. The crown more or less overhangs the root.

A basal ornamentation is absent.

The inner face of the principal cusp and cusplets is strongly convex, presenting striae. They run from the crown base toward the apex of the principal cusp and cusplets in a more or less regular way. Their density is rather high, of about nine to thirteen on the principal cusp and of three to five on the cusplets. Basal ornamentation is absent.

The outer face of the root presents an irregular series of three to six well developed foramina.

The inner face of the root 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 parts and its central section is more or less protuberated.

Sometimes, one or two foramina are present on each root lobe, on the part toward the crown in the depressions, flanking the protuberation of the ridge. Foramina are absent near the crown-root junction. A foramen is always present in the centre of the ridge.

Some randomly scattered foramina are usually present on the basal face.

Genus : *Atelomycterus* GARMAN, 1913

The genus *Atelomycterus* comprises, after COMPAGNO (1988), the two species *Atelomycterus macleayi* WHITLEY, 1939 and *Atelomycterus marmoratus* (BENNETT, 1830). The type species is *Scyllium marmoratum* BENNETT, 1830 by original monotypy.

Atelomycterus marmoratus (BENNETT, 1830)
(Plates 7, 8)

Scyllium marmoratum BENNETT, 1830. Memoir of the life and public Services of Sir Stamford Raffles, London, p. 693.

The teeth of this species have a rather broad based but elongated principal cusp in both upper and lower jaws. The principal cusp is erect on anterior teeth, becoming slightly oblique on lateral and commissural ones. A cusplet is always present at each side, broad based, like the principal cusp, and they tend to curve to its apex.

The root is always secondary hemiaulacorhizid and shows two root lobes, which are relatively broad and subquadrate, forming a straight line at the root base.

The teeth are plurimillimetrical in range.

The outer face of the principal cusp and cusplets is rather convex, presenting little developed striae that run from 1/4 to about 3/4 of the height of the principal cusp and cusplets. These striae are rather irregular in shape. They reach a maximum density of five to eight striae on the principal cusp in both upper and lower teeth. One or two striae are always present on the cusplets.

The crown base is slightly depressed near the crown-root junction. Ornamentation is absent.

The inner face of the principal cusp and cusplets is strongly convex, also presenting well developed striae.

They also run from 1/4 to 3/4 of the height of the principal cusp and cusplets in a more or less irregular way. Their density is rather steady, of seven to eight on the principal cusp and of two to three on both cusplets.

Basal ornamentation is absent.

There is a deep depression on both mesial and distal parts of the principal cusp, which is caused by two strong root depressions. The outer face of the root is very low and divided into mesial and distal root parts by the remains of a median groove.

Both mesial and distal root parts present three to four foramina along the crown-root junction.

The inner face of the root shows a ridge, which is strongly protuberated in the central part. It divides the inner face of the root into two sections.

One or two foramina are present on each root lobe in a deep mesial and distal depression. An aperture is present just above the centre of the protuberated part of the ridge. The relict of a median groove is present on the basal root face, running from the root base up to half the height of the basal root face.

Numerous randomly scattered foramina are present on the basal face of both root lobes.

Genus : *Aulohalaelurus* FOWLER, 1934

The monotypic genus *Aulohalaelurus* was described by FOWLER, 1934 as a subgenus of *Halaelurus* GILL, 1862. However, SPRINGER (1979) elevated *Aulohalaelurus* to the generic rank, and was followed by COMPAGNO (1984). The type species of the genus is *Catulus labiosus* WAITE, 1905 by original designation.

Aulohalaelurus labiosus (WAITE, 1905)
(Plates 9, 10)

Catulus labiosus WAITE, 1905. Records of the Australian Museum, 6 (2) : 57.

The teeth of this species have a rather slender, elongated principal cusp in both upper and lower jaws. The principal cusp is erect in anterior teeth, becoming slightly oblique in lateral and commissural teeth. One well developed short cusplet is always present, with a poorly developed second one on its extreme mesial and distal parts. The cusplets are broad based and tend to curve toward the principal cusp.

The root is always secondary hemiaulacorhizid and shows two root lobes, which are relatively broad and subquadrate, forming a straight line at the root base.

The teeth are plurimillimetrical in range.

The outer face of the principal cusp and cusplets is rather convex, presenting little developed costules.

Ornamentation is absent.

The inner face of the principal cusp and cusplets is strongly convex, sometimes presenting poorly developed striae.

Basal ornamentation is absent.

There is a deep depression on both mesial and distal parts of the principal cusp, which is caused by two strong root depressions.

The outer face of the root is divided into mesial and distal root sections by the remains of a median groove. Both mesial and distal root sections present one or two foramina along the crown-root junction.

The inner face of the root shows a ridge, which is strongly protuberated in the central part. It divides the inner face of the root into two sections.

One or two foramina are present on each root lobe in a deep mesial and distal depression. An aperture is present

just above the centre of the protuberated part of the ridge. The relict of a median groove is present on the basal root face, running from root base up to half the height of the basal root face.

Numerous randomly scattered foramina are present on the basal face of both root lobes.

Genus : *Cephaloscyllium* GILL, 1862

The genus *Cephaloscyllium* was described by GILL, 1862 and comprises, after COMPAGNO 1988), the species *Cephaloscyllium fasciatum* CHAN, 1966, *Cephaloscyllium isabellum* (BONNATERRE, 1788), *Cephaloscyllium laticeps* (DUMERIL, 1853), *Cephaloscyllium nascione* WHITLEY, 1932, *Cephaloscyllium silasi* (TALWAR, 1974), *Cephaloscyllium sufflans* (REGAN, 1921) and *Cephaloscyllium ventriosum* (GARMAN, 1880). The type species is *Scyllium laticeps* DUMERIL, 1853 by original designation, but was not available for examination, and therefore, *Cephaloscyllium isabellum* will be used instead, which is very closely related to the type species (COMPAGNO, 1984, 1988).

Cephaloscyllium isabellum (BONNATERRE, 1788)
(Plates 11, 12)

Squalus isabella BONNATERRE, 1788. Tableau encyclopédique et méthodique des trois règnes de la terre : Ichthyologie, 6. La mer du sud.

The teeth of this species have a broad based, relatively short principal cusp, which is more or less oblique toward the commissure. A short and broad based cusplet is present at each side. A vaguely developed second cusplet is present on the extreme edges, next to each cusplet.

The root varies between holaulacorhizid and secondary anaulacorhizid, showing two root lobes that are relatively long and narrow and form an angle at the root base.

The teeth are plurimillimetrical in range.

The outer face of the principal cusp and cusplets is weakly convex, presenting well developed, short basal costules. The crown overhangs the root.

Some striae are occasional on the principal cusp and cusplets, in males only.

Basal ornamentation is absent.

The inner face of the principal cusp and cusplets is strongly convex, presenting striae that are more distinct in males. They run from the crown base to the apex of the principal cusp and cusplets in a more or less regular way. Their density is rather high with about fifteen striae on the principal cusp and five to seven on the cusplets.

Basal ornamentation is absent.

The outer face of the root is rather high, presenting an irregular series of five to eight well developed foramina, of which the central ones are often merged.

The inner face of the root shows a ridge similar shaped 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 protuberated.

Two to three foramina are present on each root lobe on the part toward the crown in the depressions, flanking the protuberation of the ridge. Foramina are absent near the crown-root junction. A central foramen is always present just below 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 one. Some randomly scattered foramina are usually present on the basal face.

Genus : *Cephalurus* BIGELOW & SCHROEDER, 1941

This monotypic genus was erected by BIGELOW & SCHROEDER (1941) for *Catulus cephalus* GILBERT, 1892. COMPAGNO (1984, 1988) cited previous authors regarding *Cephalurus* — like sharks from the Eastern central and SE-Pacific differing from the type species.

The teeth of one of the latter specimens were examined and are described and illustrated here for comparison with the type species of more Northern Eastern Pacific distribution.

Cephalurus cephalus (GILBERT, 1892)
(Plates 13, 14)

Catulus cephalus GILBERT, 1892. Proceedings of the United States National Museum, 14 : 541.

The teeth of this species have an elongated, slender principal cusp, which is always somewhat inclined toward the commissure. One distal cusplet is always present, and up to two mesial cusplets may be present in addition. All cusplets tend to arise from the lower part of the mesial and distal cutting edges of the principal cusp and have a rather triangular shape.

The root varies between holaulacorhizid and secondary hemiaulacorhizid, showing two root lobes that are relatively long and broad and form a weak angle at the root base. The teeth are plurimillimetrical in range.

The outer face of the principal cusp and cusplets is flat to very weakly convex, presenting some poorly developed striae, which are more developed in lateral teeth.

Costules and ornamentation are absent.

The inner face of the principal cusp is strongly convex and also presents some well developed striae.

Basal ornamentation is absent.

The outer face of the root is low, presenting some irregularly lined foramina.

The inner face of the root shows a ridge of about the same shape as that the angle of the root lobes. It divides the inner face of the root into two parts. One or two foramina are present on each root lobe on the section toward the crown flanking the ridge. Foramina are absent near the crown-root junction. A foramen is always present in the centre of the ridge. The basal section is rather concave.

Some randomly scattered foramina are usually present on the basal face.

Cephalurus sp. cf. *cephalus*
(Plates 15, 16)

COMPAGNO (1988) : Sharks of the Order Carcharhiniformes, Princeton University Press. Princeton New Jersey.

The teeth of this species have a rather short, broad based principal cusp, which is always strongly inclined toward the commissure. One distal cusplet is always present, and up to three mesial cusplets may also be present. All cusplets tend to arise from the lower part of the mesial and distal cutting edges of the principal cusp. They have a rather triangular shape and tend to point inwards.

The root is holaulacorhizid, showing two root lobes that are relatively long and narrow, forming a weak angle at the root base. The teeth are plurimillimetrical in range.

The outer face of the principal cusp and cusplets is flat to very weakly convex, presenting some poorly developed striae that are better developed on lateral teeth. (In juveniles all teeth have better developed striae).

Costules and ornamentation are absent.

The inner face of the principal cusp is strongly convex, also presenting some striae that are slightly more distinct than the outer ones.

The outer face of the cusplets is rather flat and has no striae. Basal ornamentation is absent.

The outer face of the root is low, presenting an aperture with some irregularly lined foramina.

The inner face of the root shows a ridge that is angled as the root lobes. It divides the inner face of the root into two sections.

Two to four foramina are present on each root lobe on the section toward the crown and are lined up near the ridge. Foramina are absent near the crown-root junction.

A foramen is always present in the centre of the ridge. The basal section is rather concave.

Some randomly scattered foramina are usually present on the basal face.

Genus : *Galeus* RAFINESQUE, 1810

This genus comprises (after COMPAGNO, 1988) 11 species : *Galeus arae* (NICHOLS, 1927), *Galeus atlanticus* (VAILLANT, 1888), *Galeus boardmani* (WHITLEY, 1928), *Galeus eastmani* (JORDAN & SNYDER, 1904), *Galeus murinus* (COLLETT, 1904), *Galeus nipponensis* NAKAYA, 1975, *Galeus piperatus* SPRINGER & WAGNER, 1966, *Galeus polli* CADENAT, 1959, *Galeus sauteri* (JORDAN & RICHARDSON, 1909), *Galeus schultzi* SPRINGER, 1979 and the type species *Galeus melastomus* RAFINESQUE, 1810.

Galeus melastomus RAFINESQUE, 1810
(Plates 17, 18)

Caratteri di alcuni nuovi generi e nuove specie di animali (principalmente di pesci) e piante della Scicilia, con varie osservazioni sopra i medisimi. Palermo, pt. 1 : 13.

The teeth of this species have a rather slender and elongated principal cusp, which is more prominent in upper teeth, becoming lower toward the commissure. The principal cusp is slightly inclined toward the commissure. It has more or less sigmoidal mesial and distal cutting edges and has commonly one (in upper and lower anterior teeth), two (in upper and lower lateral and upper posterior teeth) and three (in the lower commissural tooth). Also slender and elongated cusplets are present at each side. The cusplets closest to the principal cusp reach half the height of the principal cusp or even more in lower lateral teeth.

The root is always secondary anaulacorhizid and shows two root lobes that are relatively long and narrow, forming an angle at the root base. The teeth are plurimillimetrical in range.

The outer face of the principal cusp and cusplets is flat or very weakly convex, presenting well developed striae that run from just above the crown base to half the height of the principal cusp and apex of cusplets. Although these striae are rather regular in shape, they are sometimes slightly sigmoidal. They reach a maximum density of seven or eight striae on the principal cusp on anterior and lateral teeth, decreasing to three or four on the lower posterior teeth. Striae on cusplets are always less distinct than on the principal cusp.

Reticulated ornamentation is present on the crown base between the striae, which is more distinct on posterior teeth.

The outer central crown base is depressed, caused by a deep depression of the root.

The inner face of the principal cusp and cusplets is strongly convex, also presenting striae that are slightly less distinct than the outer ones.

They also run from the crown base toward the apex of the principal cusp and cusplets in a more or less regular way. Their density is rather steady, with eight to ten striae on the principal cusp and three to four on the cusplets. The striae do not fully reach the apex of the principal cusp. Basal ornamentation is absent.

The outer face of the root has a strong central depression, presenting a series of up to eight well developed foramina, of which the central ones are often merged in anterior teeth.

The inner face of the root shows a ridge similar shaped as the angle of the root lobes. It divides the inner face of the root into two sections.

Two to four foramina are present on each root lobe on the part toward the crown and are lined along the ridge. Foramina are absent near the crown-root junction. A foramen is always present just above the centre of the ridge. Some randomly scattered foramina are usually present on the basal face.

Genus : *Halaelurus* GILL, 1862

This genus comprises, after COMPAGNO (1988), 2 subgenera : *Halaelurus* and *Bythaelurus*. *Halaelurus* comprises *Halaelurus boesemani* SPRINGER & D'AUBREY, 1972,

Halaelurus bürgeri (MÜLLER & HENLE, 1838), *Halaelurus lineatus* BASS, D'AUBREY & KISTNASAMY, 1975, *Halaelurus natalensis* (REGAN, 1904), *Halaelurus quagga* (ALCOCK, 1899) with the type species *Halaelurus bürgeri*. *Bythaelurus* comprises *Halaelurus canescens* (GÜNTHER, 1878), *Halaelurus dawsoni* SPRINGER, 1971, *Halaelurus hispidus* (ALCOCK, 1891), *Halaelurus immaculatus* CHU & MENG, 1982, *Halaelurus lutarius* SPRINGER & D'AUBREY, 1972 and *Halaelurus alcocki* GARMAN, 1913, which is of uncertain status. The type species is *Halaelurus canescens*, generotype *Halaelurus bürgeri*.

Halaelurus (Bythaelurus) canescens (GÜNTHER, 1878) (Plates 19, 20)

Scyllium canescens GÜNTHER, 1878. Annal and Magazine of Natural History, (ser. 5), 2 (8) : 18.

The teeth of this species have a broad based, relatively short principal cusp, which is more distinct in the lower jaw. The principal cusp is more or less oblique toward the commissure. Commonly, one also short and broad based cuplet is present at each side. On the extreme edges, next to each cusplet, an undeveloped second cusplet is present, which is more distinct in upper lateral teeth.

The root varies between holaulacorhizid and secondary anaulacorhizid, showing two root lobes that are relatively long and narrow and form an angle at the root base. The teeth are plurimillimetrical in range.

The outer face of the principal cusp and cusplets is weakly convex, with well developed, short basal costules. The crown tends to overhang a rather high, basal depression, which is present over the whole width of the crown base. Striae on the principal cusp and cusplets and basal ornamentation are absent.

The inner face of the principal cusp and cusplets is strongly convex, presenting striae that run from the crown base toward the apex of the principal cusp and cusplets in a more or less regular way. Their density is rather high, with about twelve to seventeen striae on the principal cusp and five to seven on the cusplets. Basal ornamentation is absent.

The outer face of the root is rather high, presenting an irregular series of three to five well developed foramina, of which the central ones are often merged.

The inner face of the root shows a ridge similar shaped 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 protuberated.

Two to three foramina are present on each root lobe on the part toward the crown, in the depressions flanking the protuberation of the ridge. Foramina are absent near the crown-root junction. A foramen is always present in the centre of the ridge, which is sometimes more or less elongated toward the root base, forming a partial groove or even sometimes a complete median one.

Some randomly scattered foramina are usually present on the basal face.

Halaelurus (Halaelurus) bürgeri (MÜLLER & HENLE, 1838)
(Plate 25)

Scyllium bürgeri MÜLLER & HENLE, 1838. *Systematische Beschreibung der Plagiostomen*. Berlin. Part 1 : 8.

The teeth of this species have a broad based, relatively short principal cusp, which is poorly developed in lateral teeth. The mesial and distal cutting edges are extended. Cusplets are absent.

The secondary anaulacorhizid root shows two root lobes that are relatively long and narrow and form a very obtuse angle in anterior teeth and one line at the root base in lateral teeth. The teeth are plurimillimetric in range.

The outer face of the principal cusp is weakly convex, presenting well developed, short basal costules. The crown more or less overhangs the root.

A basal reticulated ornamentation is present between the costules.

The inner face of the principal cusp and cusplets is convex, and some poorly developed striae are present.

A basal reticulated ornamentation is present on lateral teeth.

The outer face of the root is rather high, presenting an irregular series of three or five well developed foramina. The inner face of the root shows a ridge, similar shaped as the angle of the root lobes. It divides the inner face of the root into two sections and its central part is, in anterior teeth, more or less protuberated.

Two to three foramina are present on each root lobe on the part toward the crown on the mesial and distal parts. Foramina are absent on the crown-root junction. A foramen is always present in the centre of the ridge.

Some randomly scattered foramina are usually present on the basal face.

Genus : *Haploblepharus* GARMAN, 1913

This genus comprises, after COMPAGNO (1988), three species : *Haploblepharus fuscus* SMITH, 1950, *Haploblepharus pictus* (MÜLLER & HENLE, 1838) and the type species *Haploblepharus edwardsii* (VOIGT, 1832).

Haploblepharus edwardsii (VOIGT, 1832)
(Plates 21, 22)

Scyllium edwardsii VOIGT, 1832. In CUVIER, 1832, *Tierreich*, 2 : 504.

The teeth of this species have a rather slender and elongated principal cusp.

The principal cusp is slightly inclined toward the commissure and two also slender and elongated cusplets are present at each side.

The cusplets closest to the principal cusp reach half the height of the principal cusp or even more in lower lateral teeth.

The root is secondary anaulacorhizid and shows two root lobes that are relatively long and narrow forming an angle at the root base. The teeth are plurimillimetric in range. The outer face of the principal cusp and cusplets is flat or very weakly convex, presenting well developed, elongated basal costules. A reticulated ornamentation is present on the crown base between the costules, which is more distinct on posterior teeth.

The inner face of the principal cusp and cusplets is strongly convex, presenting striae that run from the crown base to 3/4 of the height of the principal cusp and reach the apex on cusplets in a more or less regular way. Their density varies between seven to twelve on the principal cusp but is less on cusplets.

Basal ornamentation is absent.

The outer face of the root has a strong central depression, presenting a series of four to ten well developed foramina, of which the central ones are often merged.

The inner face of the root shows a ridge that is angled as the root lobes. It divides the inner face of the root into two sections.

Two to four foramina are present on each root lobe on the part toward the crown, lined along the ridge. Foramina are absent near the crown-root junction. A foramen is sometimes present in the centre of the ridge.

Some randomly scattered foramina are usually present on the basal face.

Genus : *Holohalaelurus* FOWLER, 1934

This genus comprises, after COMPAGNO (1988), two species : *Holohalaelurus punctatus* (GILCHRIST, 1914) and the type species *Holohalaelurus regani* (GILCHRIST, 1922).

Holohalaelurus regani (GILCHRIST, 1922)
(Plates 23, 24)

Scyliorhinus regani GILCHRIST, 1922. Special report no. 3. Report of the Fishery and Marine Biological Survey. Union of South Africa, Part 1, 2 : 45.

The teeth of this species have a broad based, but elongated principal cusp. The principal cusp is more or less inclined toward the commissure in lateral and commisural teeth, and two also short and broad based cusplets are present at each side.

The root is always secondary anaulacorhizid and shows two root lobes that are relatively long and narrow and form an angle at the root base. The teeth are plurimillimetric in range.

The outer face of the principal cusp and cusplets is almost flat, presenting well developed, relatively long basal costules. The crown overhangs the root.

A weak reticulated basal ornamentation is present between the costules.

The inner face of the principal cusp and cusplets is strongly convex, presenting well developed striae. These run from 1/4 to 3/4 of the height of the principal cusp and cusplets in a rather irregular way. Their density varies between five and nine on the principal cusp and two to three on cusplets. Basal ornamentation is absent.

The outer face of the root is rather high, presenting an irregular series of five to eight well developed foramina, of which the central ones are often merged.

The inner face of the root shows a ridge that is angled as the root lobes. It divides the inner face of the root into two sections, and its central part is more or less protuberated.

Two to three foramina are present on each root lobe, on the part toward the crown in the depressions flanking the protuberation of the ridge. Foramina are absent near the crown-root junction. A foramen is always present just below the centre of the ridge.

Some randomly scattered foramina are usually present on the basal face.

Genus : *Parmaturus* GARMAN, 1906

The genus comprises, after COMPAGNO (1988), 5 species : *Parmaturus campechiensis* SPRINGER, 1979, *Parmaturus macmillani* HARDY, 1985, *Parmaturus melanobranchius* (CHAN, 1966), *Parmaturus xaniurus* (GILBERT, 1892) and the type species *Parmaturus pilosus* GARMAN, 1906).

Parmaturus pilosus GARMAN, 1906
(Plate 26, Plate 35, figs. 3 & 4)

Parmaturus pilosus GARMAN, 1906. New Plagiostoma. Bulletin of the Museum of Comparative Zoology. Harvard College, 46 (11) : 204.

The teeth of this species have a broad based but elongated principal cusp, which in lateral teeth, is more or less oblique toward the commissure. The principal cusp commonly has one also short and broad based cusplet at each side. On the most extreme mesial and distal part, next to each cusplet, a vaguely developed second cusplet is present. The crown base overhangs a rather high basal depression that is present over the whole crown base.

The root is secondary anaulacorhizid and shows two root lobes that are relatively long and narrow, forming an angle at the root base. The teeth are plurimillimetrical in range. The outer face of the principal cusp and cusplets is weakly convex, presenting well developed, short basal costules. The crown is basally depressed.

Striae may be present on the principal cusp and cusplets. Basal ornamentation is absent.

The inner face of the principal cusp and cusplets is strongly convex, presenting well developed striae. These run from a quarter of the height of the principal cusp and cusplets to their apex in a more or less sigmoidal way. Their density

varies between six to ten on the principal cusp and between two to five on cusplets.

Basal ornamentation is absent.

The outer face of the root represents an irregular series of five to eight well developed foramina, of which the central ones are often merged.

The inner face of the root shows a ridge, which is angled as the root lobes. It divides the inner face of the root into two sections and is more or less protuberated in the centre.

Two to three foramina are present on each root lobe on the part toward the crown in the depressions, flanking the protuberation of the ridge. Foramina are absent near the crown-root junction. A foramen is always present in the centre of the ridge.

Some randomly scattered foramina are usually present on the basal face.

Genus : *Poroderma* SMITH, 1837

This genus comprises two species after COMPAGNO (1988) : the type species *Poroderma africanum* (GMELIN, 1789) and *Poroderma pantherinum* (SMITH, 1837). This latter only was available for examination.

Poroderma pantherinum (SMITH, 1837)
(Plates 27, 28)

Scyllium pantherinum SMITH, 1837, in MÜLLER & HENLE, 1838c. Systematische Beschreibung der Plagiostomen, Berlin (pt. 1) : 13.

The teeth of this species have a broad based, triangularly shaped, but elongated principal cusp in both upper and lower jaws. The principal cusp is erect on anterior teeth, becoming almost lightly oblique on lateral and commissural teeth. One cusplet is always present at each side. They are relatively small, weakly developed, and tend to curve to the principal cusp. The root is always secondary hemiaulacorhizid and shows two root lobes, which are relatively elongated and form an angle at the root base.

The teeth are plurimillimetrical in range.

The outer face of the principal cusp and cusplets is rather convex, presenting well developed rather regular shaped fine costules at crown base. The outer surfaces of the principal cusp and cusplets are smooth.

Ornamentation is absent.

The inner face of the principal cusp and cusplets is strongly convex. The surfaces of the principal cusp and cusplets are smooth.

Basal ornamentation is absent.

The outer face of the principal cusp and cusplets is strongly convex. The surfaces of principal cusp and cusplets are smooth.

Basal ornamentation is absent.

The outer face of the root is rather high, presenting up to twenty foramina along the root base, of which the central ones are often merged.

The inner face of the root shows a ridge that is strongly protuberated in the central part. It divides the inner face of the root into two sections.

A first aperture is present in the centre of the protuberated part of the ridge. Another one appears on the basal root face, as the relict of a median groove. Numerous randomly scattered foramina are present on the basal faces of both root lobes.

Genus : *Schroederichthys* SPRINGER, 1966

This genus comprises, after COMPAGNO (1988), 4 species : *Schroederichthys bivius* (MÜLLER & HENLE, 1838), *Schroederichthys chilensis* (GUICHENOT, 1848), *Schroederichthys tenuis* SPRINGER, 1966 and the type species *Schroederichthys maculatus* SPRINGER, 1966.

Schroederichthys maculatus SPRINGER, 1966
(Plates 29, 30)

Fishery Bulletin of the United States. Fish and Wildlife Service, 65 (3) : 605.

The teeth of this species have a broad based, relatively short principal cusp. The principal cusp is more or less oblique toward the commissure in lateral teeth. One short and poorly developed cusplet is present at each side.

The root is secondary anaulacorhizid and shows two root lobes that are relatively long and narrow and form an obtuse angle or an almost straight line at the root base. The teeth are plurimillimetrical in range.

The outer face of the principal cusp and cusplets is weakly convex, presenting well developed, very short basal costules. The crown overhangs the root.

Striae are present on the principal cusp and cusplets in upper teeth and in lower posterior ones as extensions of the costules. A reticulated basal ornamentation is present on the lower part of the costules.

The inner face of the principal cusp and cusplets is strongly convex, presenting well developed striae. They run from the costules to the apex of the principal cusp and cusplets in a more or less regular way. Their density is rather steady, of about seven striae on the principal cusp and of one or two on cusplets.

Basal ornamentation is absent.

The outer face of the root presents a regular series of five to eight well developed foramina, of which the central ones are sometimes merged.

The inner face of the root shows a ridge that is obtusely angled as the root lobes. It divides the inner face of the root into two sections, and is more or less protuberated in the central part.

Foramina are absent on the root section toward the crown in the depressions flanking the protuberation of the ridge. Nor there are foramina near the crown-root junction. A foramen is always present in the centre of the ridge.

Some randomly scattered foramina are usually present on the basal face.

Genus : *Scyliorhinus* BLAINVILLE, 1816

This genus comprises, after COMPAGNO (1988), 13 species : *Scyliorhinus besnardi* SPRINGER & SADOWSKY, 1970, *Scyliorhinus boa* GOODE & BEAN, 1896, *Scyliorhinus capensis* (SMITH, 1838), *Scyliorhinus cervignoni* MAURIN & BONNET, 1970, *Scyliorhinus garmani* (FOWLER, 1934), *Scyliorhinus haeckeli* (RIBEIRO, 1907), *Scyliorhinus hesperius* SPRINGER 1966, *Scyliorhinus meadi* SPRINGER, 1966, *Scyliorhinus retifer* (GARMAN, 1881), *Scyliorhinus stellaris* (LINNAEUS, 1758), *Scyliorhinus torazame* (TANAKA, 1908), *Scyliorhinus canicula* (LINNAEUS, 1758).

COMPAGNO (1988) proposed to divide *Scyliorhinus* into two groups. The odontological differences are not dramatic, but nevertheless, *Scyliorhinus torazame* is illustrated for comparison (Plates 33, 34).

Scyliorhinus canicula (LINNAEUS, 1758)
(Plates 31, 32)

Squalus canicula LINNAEUS, 1758. Systema naturae, Ed. X : 234.

The teeth of this species have a rather broad based but elongated principal cusp, becoming lower toward the commissure. The principal cusp is slightly oblique toward the commissure and commonly one cusplet is present at each side in upper lateral and posterior teeth and in lower ones. The poorly developed cusplets are absent in upper anterior teeth.

The root is always secondary anaulacorhizid and shows two root lobes that are relatively long and narrow and form an angle at the root base. The teeth are plurimillimetrical in range.

The outer part of the principal cusp and cusplets is flat or very weakly convex and presents poorly developed cusplets, which are even absent on lower anterior teeth. A reticulated basal ornamentation is present in upper posterior teeth only.

The inner part of the principal cusp and cusplets is strongly convex and presents striae that are slightly less distinct than the outer ones. They run from the base to the apex of the crown of the principal cusp and cusplets in a more or less regular way. Their density varies between eleven to sixteen on the principal cusp and from three to four on cusplets. The striae do not fully reach the apex of the principal cusp.

Basal ornamentation is absent.

The outer part of the root presents a series of up to eight well developed foramina, of which the central ones are often merged.

The inner part of the root shows a ridge that is angled as the root lobes. It divides the inner face of the root into two sections.

Foramina are absent on the root part toward the crown as well as near the crown-root junction. A foramen is always present in the centre of the ridge.

Some randomly scattered foramina are usually present on the basal face.

DIFFERENTIAL DIAGNOSIS

Scyliorhinid teeth have a root type, which is in an evolving stage. Their original holaulacorhizid stage is adapting via a secondary hemiaulacorhizid stage into a secondary anaulacorhizid stage. Usually two of the three stages are present in one species. However, all the three stages can sometimes be observed. Though a clear evolutionary trend in root stage developments could not be found, some remarkable features could be noted in root development.

The crown development also presents a remarkable differentiation, which was very useful but the degree of reticulated ornamentation and the amount of striae were not used. Both are variable features depending on sexual and ontogenetic heterodonty.

Atelomycterus and *Aulohalaelurus* have the same extraordinary root type and the same shape of principal cusp. The short and broad root lobes have a basal subquadrangular shape and run almost parallel to each other. However, both genera differ in the shape of the principal cusp and in the amount and development of cusplets flanking the principal cusp: *Atelomycterus* has one well developed cusplet on each side of the elongated but broad based principal cusp, while *Aulohalaelurus* has two rather poorly developed cusplets on each side of the slender and elongated principal cusp.

Scyliorhinus, *Poroderma* and *Cephaloscyllium* share the same massive, short principal cusp, which is relatively convex on the inner face.

Poroderma is distinguished from *Scyliorhinus* and *Cephaloscyllium* by the vertically high inner part of the root. *Cephaloscyllium* differs from *Scyliorhinus* by well developed cusplets and short outer costules.

Apristurus, *Galeus* and *Holohalaelurus* have a very similar tooth morphology, which differs from the other genera by the inclination of the principal cusp toward the commissure. This implies an arched mesial cutting edge of the principal cusp. *Holohalaelurus* can be separated from *Apristurus* and *Galeus* by less developed striae on inner and outer faces, which do not reach the apex in *Holohalaelurus*.

Apristurus is characterized by two or three cusplets flanking the principal cusp, as compared with one or two in *Galeus*.

Apristurus, unlike *Galeus*, has a second well developed cusplet.

The subgenera *Halaelurus* and *Bythaelurus* have such a different tooth morphology that odontologically they could be considered as separate genera, or even as subfamilies (they will be treated so below).

Bythaelurus, *Haploblepharus*, *Parmaturus* and *Asymbolus* all share a very strong similarity in tooth morphology. The principal cusp of their teeth do not incline toward the commissure, but are erect. In some cases, they become slightly oblique toward the commissure, which implies that the mesial cutting edge is not arched nor bended.

Minor but stable characteristic features make possible the separation into subgroups.

Bythaelurus and *Parmaturus* share a high, transversally

deeply concave and longitudinally hollowed crown base. *Asymbolus* and *Haploblepharus* share a rather elongated principal cusp.

Schroederichthys and *Halaelurus* are rather different from the other Scyliorhinidae by their broad root and crown base and by their relatively low, triangularly shaped crown. Furthermore, a strong monognathic heterodonty is present. *Schroederichthys* is separable from *Halaelurus* by the presence of poorly developed cusplets, which are absent in *Halaelurus*.

Cephalurus and the *Cephalurus*-like SE-Pacific specimen have an outstanding root formed by a very flat root, which has merged root lobes and a concave basal surface. It makes this genus very remote from all the other scyliorhinid genera. Both are separable from each other. *Cephalurus* is characterised by the erect or slightly oblique, elongated and slender cusp, flanked by a poorly developed cusplet, while *Cephalurus*-like SE-Pacific specimens are characterised by a short inclined principal cusp, up to three mesial and one distal cusplets.

Key to the scyliorhinid genera based on odontological characters:

- 1a - Root lobes, in basal view, relatively short and subquadrate, forming a straight line at root base: 2
- 2a - Principal cusp elongated but broad based and flanked by one cusplet.
 - Outer and inner striae well developed: *Atelomycterus*
Plates 7 & 8
- 2b - Principal cusp elongated and slender.
 - Poorly developed second cusplet present.
 - Outer and inner striae poorly developed or absent: *Aulohalaelurus*
Plates 9 & 10
- 1b - Root lobes, in basal view, long and narrow: . . . 3
- 3a - Outer view: root very low; root lobes merged, concave at basal view: 4
- 4a - Principal cusp slender and elongated.
 - Cusplets poorly developed, flanking the principal cusp: *Cephalurus*
Plates 13 & 14
- 4b - Principal cusp short, inclined toward commissure.
 - Up to three mesial and one distal cusplets: *Cephalurus*-like SE-Pacific specimen
Plates 15 & 16
- 3b - Root lobes rather plain in basal view: 5
- 5a - Root lobes very long and narrow, forming an obtuse angle: 6
- 6a - Principal cusp massive, with outer face triangularly and strongly convex: 7
- 7a - Outer face of root very high: *Poroderma*
Plates 27 & 28
- 7b - Outer face of root low: 8
- 8a - Cusplets poorly developed: *Scyliorhinus*
Plates 31 & 32
- 8b - Cusplets well developed.

- Outer basal costules on crown well developed :
 *Cephaloscyllium*
 Plates 11 & 12
- 6b - Principal cusp slender, with the outer face weakly convex : 9
- 9a - Principal cusp inclining toward commissure (more clearly visible in lateral teeth) : 10
- 10a - Principal cusp strongly inclined toward commissure. Two or three elongated, narrow mesial cusplets : *Apristurus*
 Plates 1 to 4
- 10b - Principal cusp weakly inclined toward commissure : 11
- 11a - One or two elongated, narrow mesial cusplets (second one less developed) : *Galeus*
 Plates 17 & 18
- 11b - Two or three short mesial cusplets :
 *Holohalaelurus*
 Plates 23 & 24
- 9b - Principal cusp always erect or slightly oblique : 12
- 12a - High outer depression at crown base : 13
- 13a - Outer striae absent. Outer basal costules on crown : *Bythaelurus*
 Plates 19 & 20
- 13b - Striae on inner face of crown, coarse and well developed. Outer basal costules absent on crown : *Parmaturus*
 Plate 26
- 12b - High outer depression at crown base absent : . . 14
- 14a - Secondary cusplets poorly developed or absent : *Asymbolus*
 Plates 5 & 6
- 14b - Secondary cusplets well developed :
 *Haploblepharus*
 Plates 21 & 22
- 5b - Root lobes at basal view very long and narrow, forming sometimes a nearly straight line instead of a very obtuse angle : 15
- 15a - Crown low, more or less triangular. Cusplets poorly developed. Lower teeth : strong outer costulation, striae absent. Upper teeth : strong outer costulation, striae present :
 *Schroederichthys*
 Plates 29 & 30
- 15b - Crown low, triangular in anterior teeth. Principal cusp poorly developed with extended mesial and distal cutting edges. Cusplets absent :
 *Halaelurus*
 Plate 25

PRELIMINARY CONCLUSIONS

It has always been problematical to separate or group the species of the Scyliorhinidae, and their position within the Carcharhiniformes is still uncertain. This study only deals with the Scyliorhinidae, and an odontological comparison with the Proscylliidae, the Pseudotriakidae and perhaps even the Leptochariidae is needed. This matter will be treated in the forthcoming contributions.

Despite some clear distinctions, odontology of several groups of the family Scyliorhinidae shows their close relationship. The genera of this family are much closer related to each other than for example the Squalid genera. This is obvious through the rather minor differences within the Squalidae. The present example of the Scyliorhinidae indicates that the significance of characters, diagnosing supraspecific taxa, should be evaluated more carefully.

The instability of holaulacorhizy, secondary hemiaulacorhizy and secondary anaulacorhizy, not only on generic or specific levels but also intraspecifically, indicates the intermediate evolutionary stage of Scyliorhinids.

From the odontological point of view, 5 groups could very well be seen as subfamilies.

The first group with *Atelomycterus* and *Aulohalaelurus* is well distinguished from the other genera by the shape of the root and the root lobes.

The second group with *Scyliorhinus*, *Poroderma* and *Cephaloscyllium* can be separated by their short massive principal cusp.

The odontological differentiation within the third group is not strongly developed, and tooth morphology is in some cases rather uniform. However, *Apristurus*, *Galeus* and *Holohalaelurus* are clearly separable from *Bythaelurus*, *Haploblepharus*, *Parmaturus* and *Asymbolus*, by the way their lateral teeth are directed toward the commissure.

Apristurus and *Galeus*, as well as *Bythaelurus* and *Parmaturus*, have a very similar tooth morphology with rather minor differences, respectively, and lumping them into only two genera might be possible.

Halaelurus differs so dramatically from *Bythaelurus* and the other genera of the group, that this genus should be reallocated to an other group.

The fourth group with *Schroederichthys* and *Halaelurus* can be separated by extended root lobes, and by low to extremely low triangularly shaped principal cusp both in lateral and in anterior teeth. Cusplets, if present, are small and poorly developed.

The fifth group with *Cephalurus* and the *Cephalurus*-like SE-Pacific specimen can be separated by their peculiar concave basal face of the root.

Five major groups can odontologically be separated by root development :

- | | |
|---|-------------------------|
| 1 | 2 |
| <i>Atelomycterus</i> | <i>Scyliorhinus</i> |
| <i>Aulohalaelurus</i> | <i>Poroderma</i> |
| | <i>Cephaloscyllium</i> |
| 3 | 4 |
| <i>Apristurus</i> | <i>Schroederichthys</i> |
| <i>Galeus</i> | <i>Halaelurus</i> |
| <i>Holohalaelurus</i> | |
| <i>Bythaelurus</i> | |
| <i>Haploblepharus</i> | |
| <i>Parmaturus</i> | |
| <i>Asymbolus</i> | |
| 5 | |
| <i>Cephalurus</i> | |
| <i>Cephalurus</i> -like (SE-Pacific specimen) | |

Ontogenetic heterodonty is strong in Scyliorhinidae. The teeth of juveniles always possess crowns with a very flat outer face. Cuspsets are always merged with the cutting edges of the principal cusp and are very flat on both inner and outer faces.

(See plate 35).

The squalid genera *Centroscyllium* and *Aculeola* have true but modified anaulacorhizid root types, as it is usual for the Squaliformes, and far remote from Scyliorhinidae. However both have more or less scyliorhinid-like crowns, which may indicate a presently unexplained similarity with the Scyliorhinidae (HERMAN *et al.*, 1990).

Acknowledgements

We would like to thank Dr. M.L. BAUCHOT, Musée National d'Histoire naturelle, Paris; Dr. M. BOESEMAN, Rijksmuseum van Natuurlijke Historie, Leiden; Dr. G. BURGESS, Florida State Museum; Dr. J.L.V. COMPAGNO, formerly San Francisco State University, California; Dr. W.N. ESCHMEYER, California Academy of Sciences, San Francisco; Dr. J.P. GOSSE, Institut Royal des Sciences naturelles de Belgique, Brussels; Mrs. S.L. JEWETT, United States National Museum of Natural History; B. SERET, formerly ORSTOM, Dakar; Dr. V.G. SPRINGER, United States National Museum, New York and A. WHEELER, British Museum of Natural History, London, for the permission to examine specimens at their disposal. Dr. M. STEHMANN provided specimens of I.S.H., Hamburg.

We also would like to thank Captain P. GUEGUEN (Lorient) for allowing us to collect specimens during his cruises.

We thank particularly Miss F. LADEUZE, F.N.R.S., Brussels, for her technical assistance and careful corrections of the proofs.

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Glossary

(also applying to previous issues of this series, replacing the previous glossaries)

CONCERNING THE JAW

Anterior

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

Commissural

Tooth position next to the end of jaw.

Dignathic

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

File

Tooth row from symphysis toward the end of jaw.

Heterodonty

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

Homodonty

Equal tooth morphology within a set of teeth.

Lateral

Tooth position half way along the jaw.

Longitudinal

Symphysial/commissural direction of a file.

Monognathic

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

Parasymphysial

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

Posterior

Tooth position toward the angle of jaw.

Pseudosymphysial

One of the parasymphysial tooth rows becomes the character of a symphysial tooth row (symmetry). This phenomenon appears in some species.

Row

Tooth row from the inner to the outer face of jaw.

Symphysial

Teeth at junction of both halves of a jaw.

Transversal

Outer/inner direction of a row.

CONCERNING THE TOOTH

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 Rajidae).

Polyaulacorhizid

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

Apron

Expansion of the central part of the outer crown base.

Basal

Bottom face concerned.

Costule

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

Crown

Enamelated tooth part.

Distal

Tooth edge or part toward the angle of jaw.

Inner face

Viewed from inside the mouth.

Longitudinally

Apico/basally directed.

Median groove

Groove running from the inner root base to the inner crown-root junction, dividing anholaulacorhizid 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 faces.

Mesial

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

Outer face

Viewed from outside the mouth.

Pseudoapron

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

Root

Non-enamelated tooth part that forms the junction with the jaw and provides vascularisation of the tooth.

Striae

Vertical ridge running from the base toward the apex of the crown.

Secondary anaulacorhizy

Syncreted median groove of holaulacorhizid type of root.

Secondary hemiaulacorhizy

Beginning syncretion of a median groove of a holaulacorhizid type of root.

Sulcus

Groove developed by the main vascularisation string leading from root base to the main foramen on anaulacorhizid root types. It differs from the median groove of the holaulacorhizid root type and from the parallel grooves of the polyaulacorhizid root type, in which several foramina are concentrated, respectively.

Transversal

Mesio-/distally directed.

Uvula

Lobate extension of the inner crown base.

Composition of the plates

As far as possible, one plate with SEM-photographs of isolated teeth is presented for each of the genera and subgenera.

Upper teeth are presented with the principal cusp downwards, lower teeth with the principal cusp upwards.

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

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

Legend

s = Symphysial position

a = Anterior position

al = Antero-lateral position

l = Lateral position

lp = Latero-posterior position

p = Posterior position

c = Commissural position

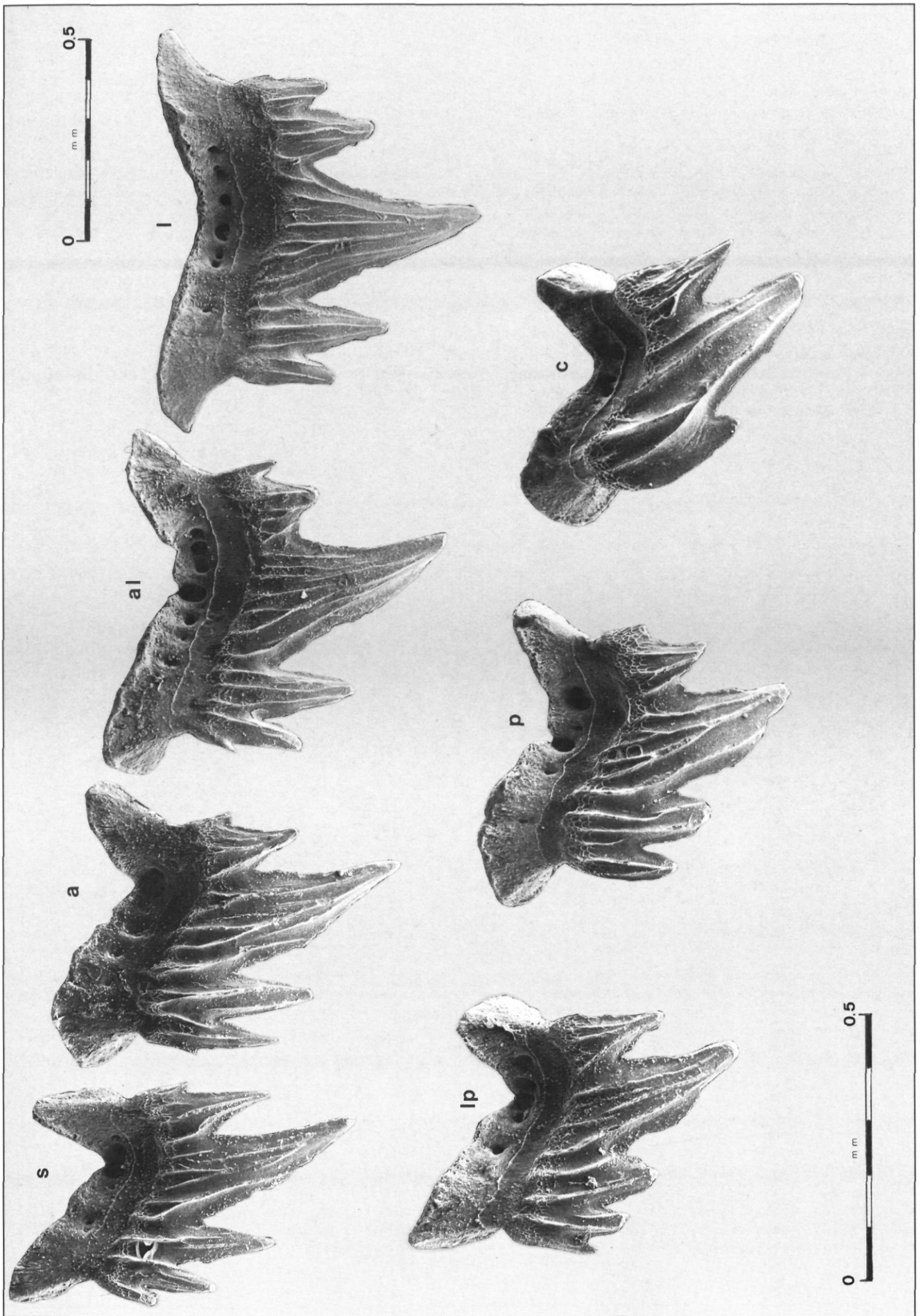


Plate 1. - *Apristurus laurussoni* (SAEMUNDSSON, 1922), Female 68 cm (t.l.), West Ireland.

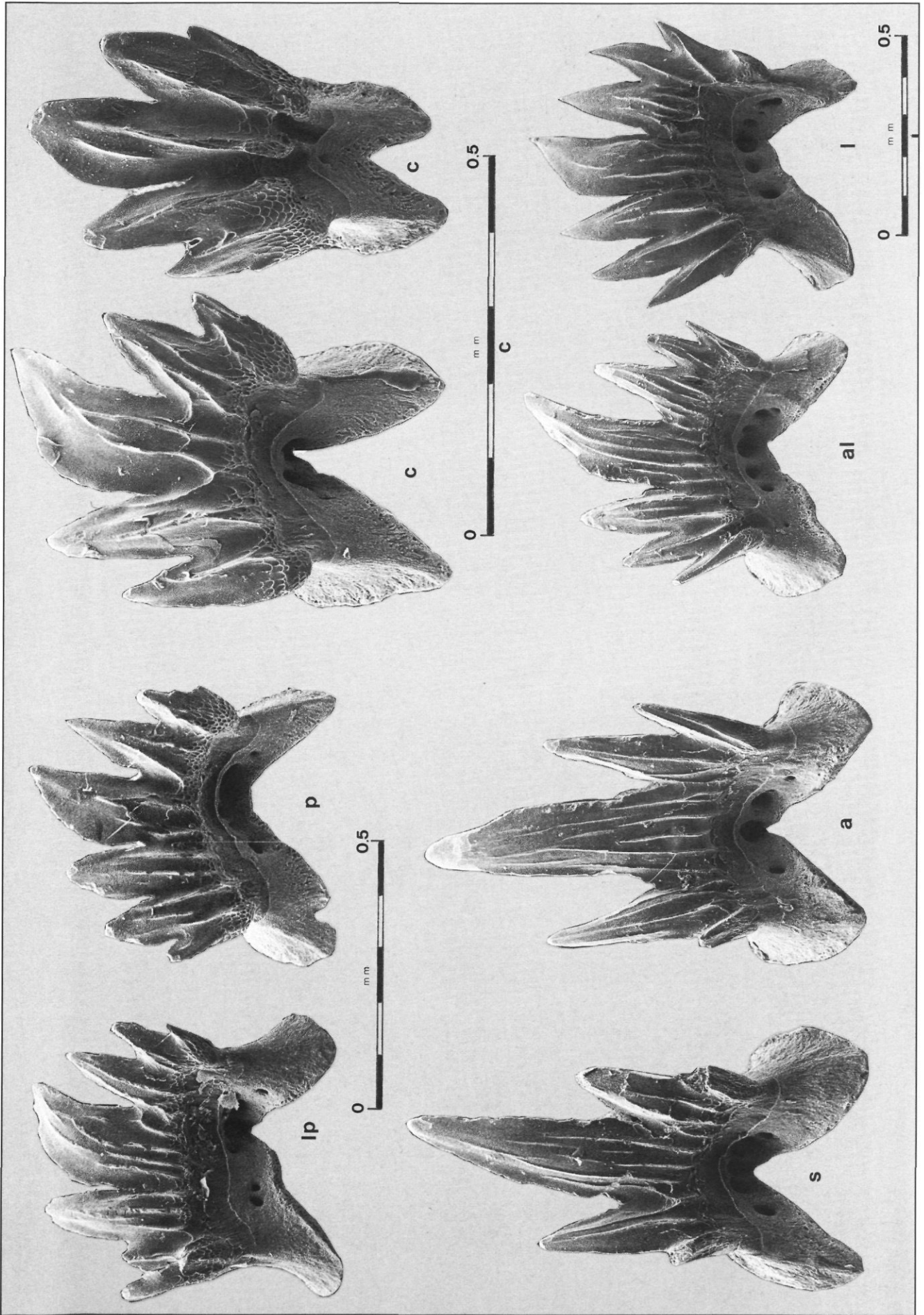


Plate 2. - *Apristurus laurussoni* (SAEMUNDSSON, 1922), female 68 cm (t.l.), West Ireland.

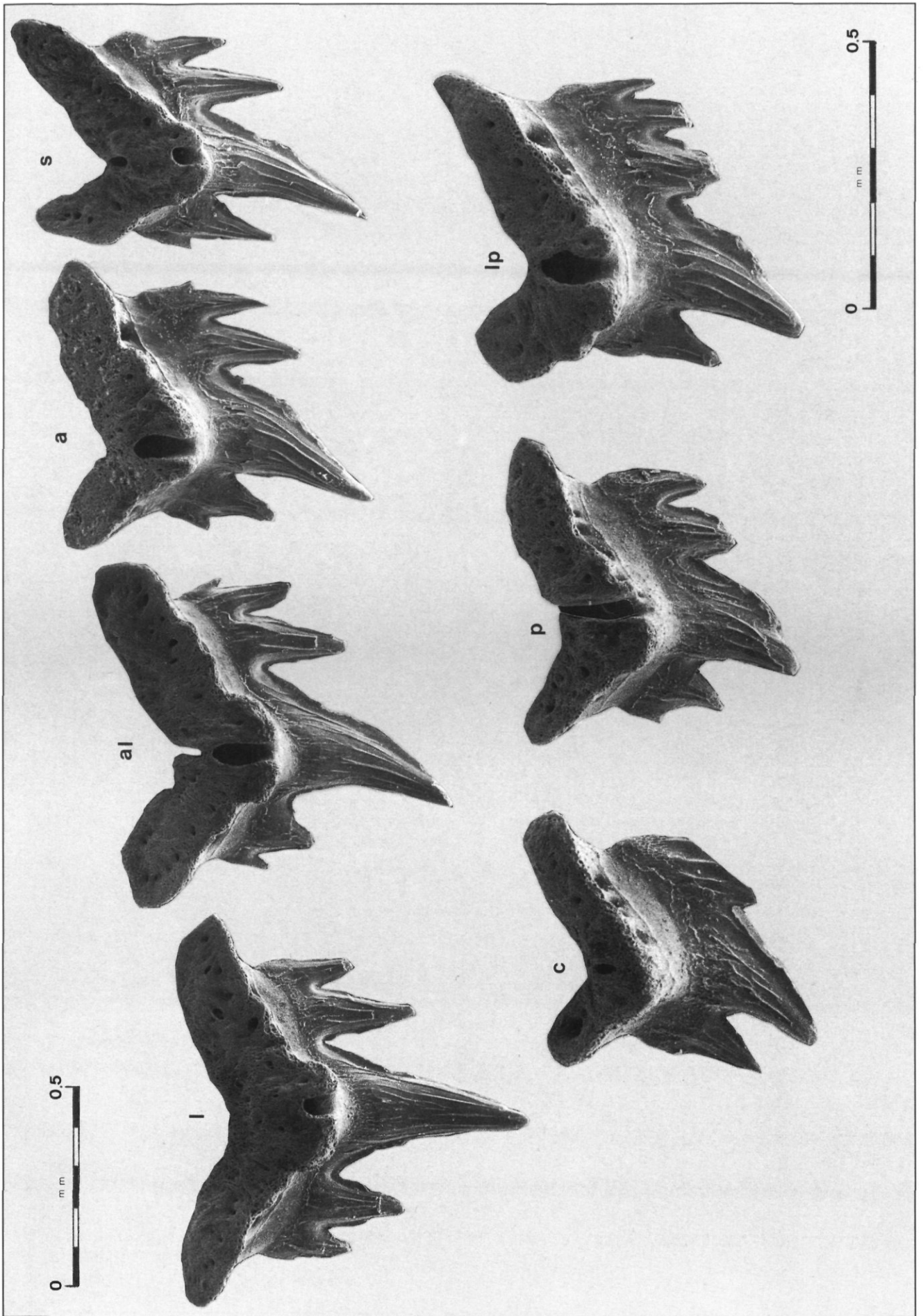


Plate 3. — *Apristurus laurussoni* (SAEMUNDSSON, 1922), female 68 cm (t.l.), West Ireland.

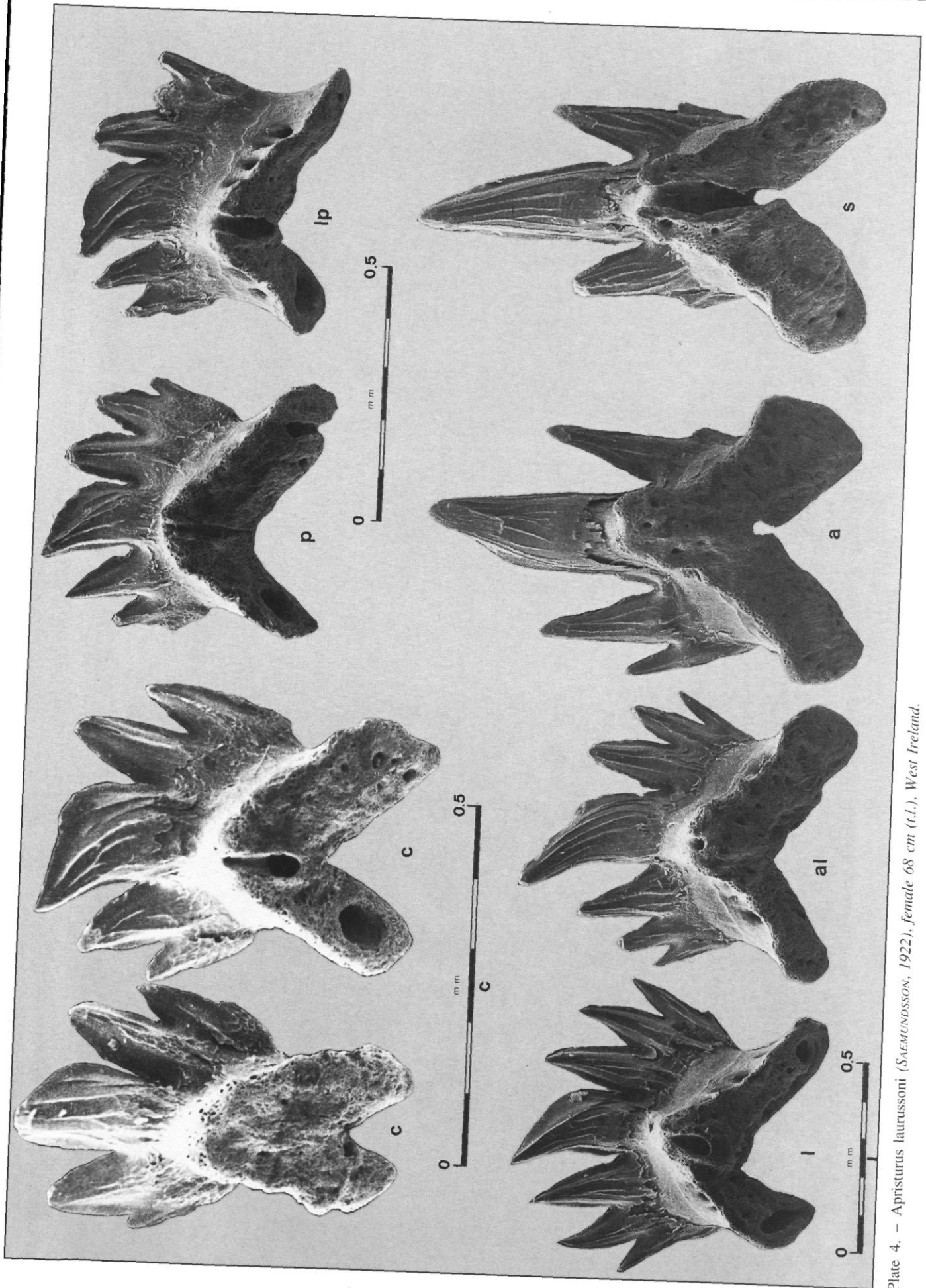


Plate 4. — *Apristurus laurussoni* (SÆMUNDSSON, 1922), female 68 cm (t.l.), West Ireland.

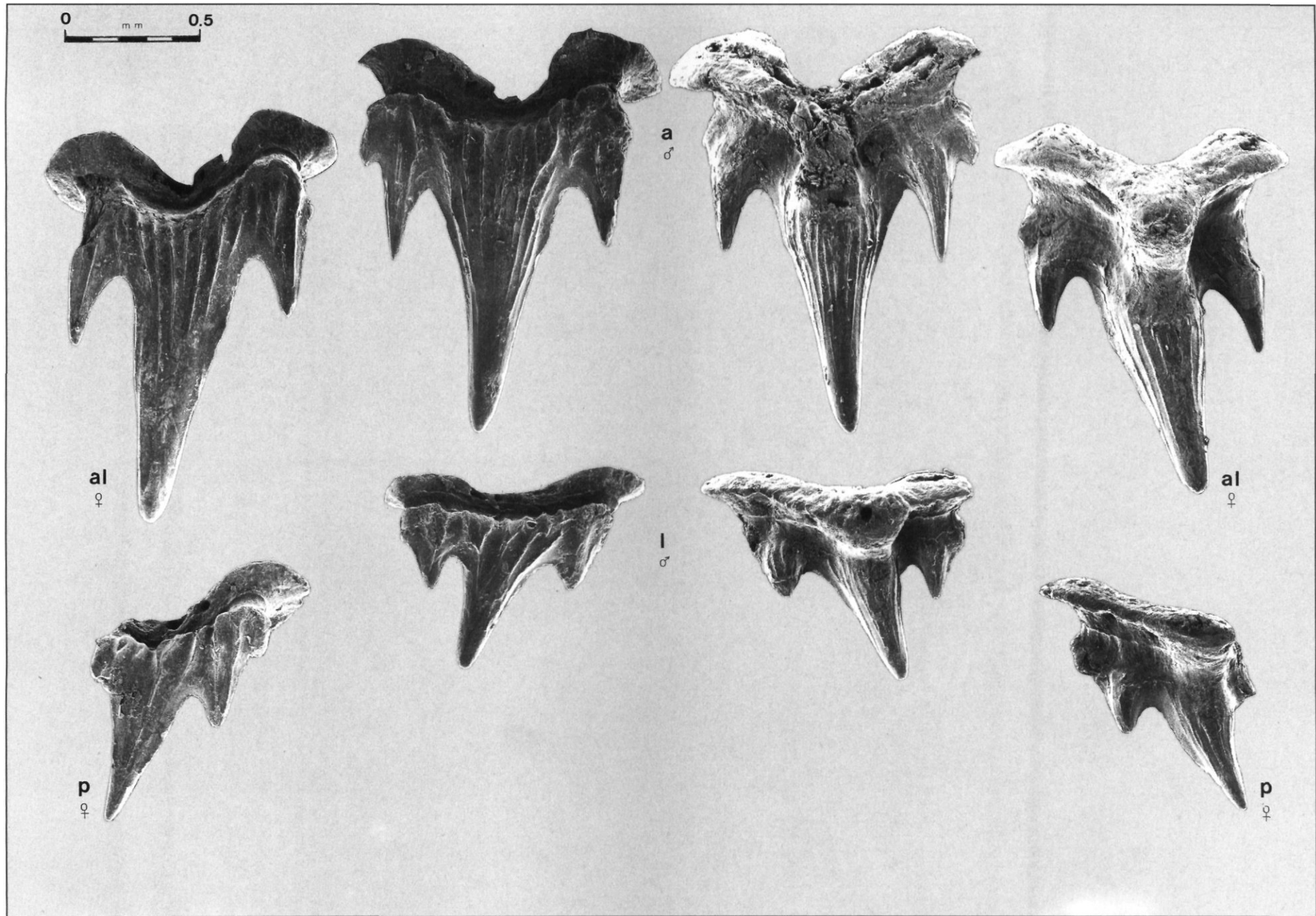


Plate 5. – *Asymbolus analis* (OGILBY, 1885), female 50,5 cm and male 53.5 cm (t.l.), New South Wales, Australia. Courtesy of M. STEHMANN, ISH, Hamburg.

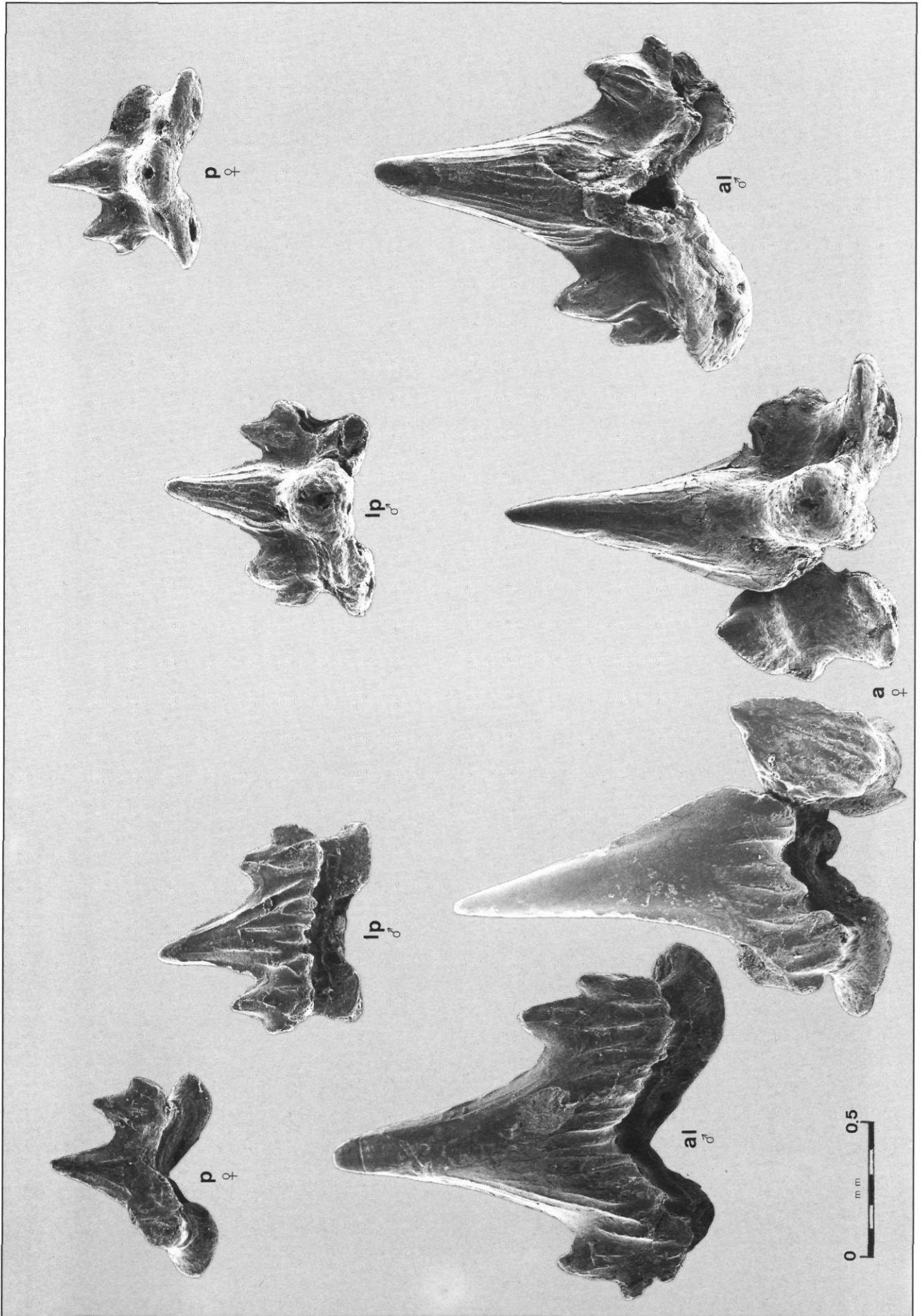


Plate 6. - *Asymbolus analis* (Ogilby, 1885), female 50.5 cm and male 53.5 cm (t.l.), New South Wales, Australia. Courtesy of M. STEHMANN, ISH, Hamburg.

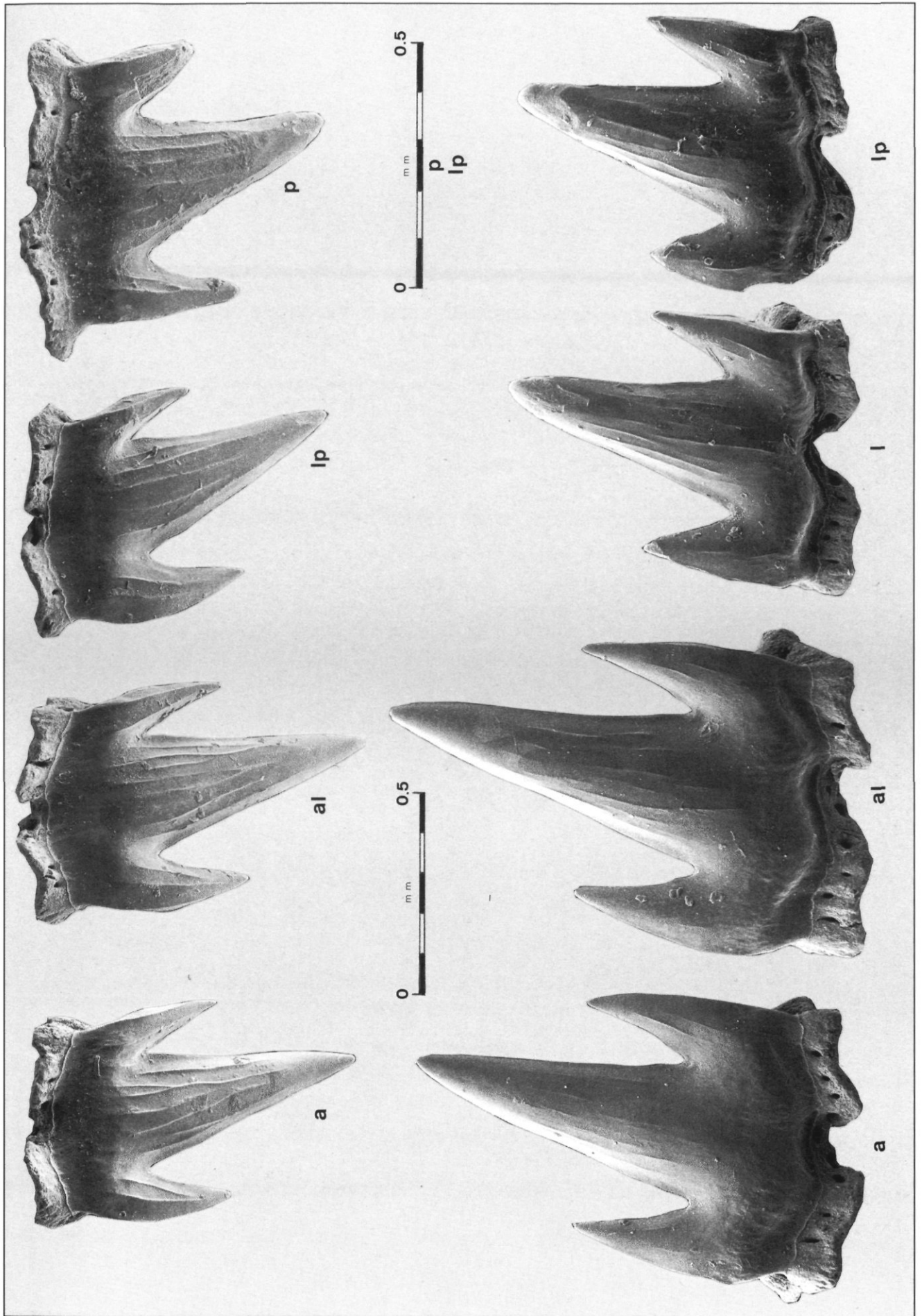


Plate 7. - *Atelomycterus marmoratus* (BENNETT, 1830), male 51 cm (t.l.), I. Molucca, Philippines.

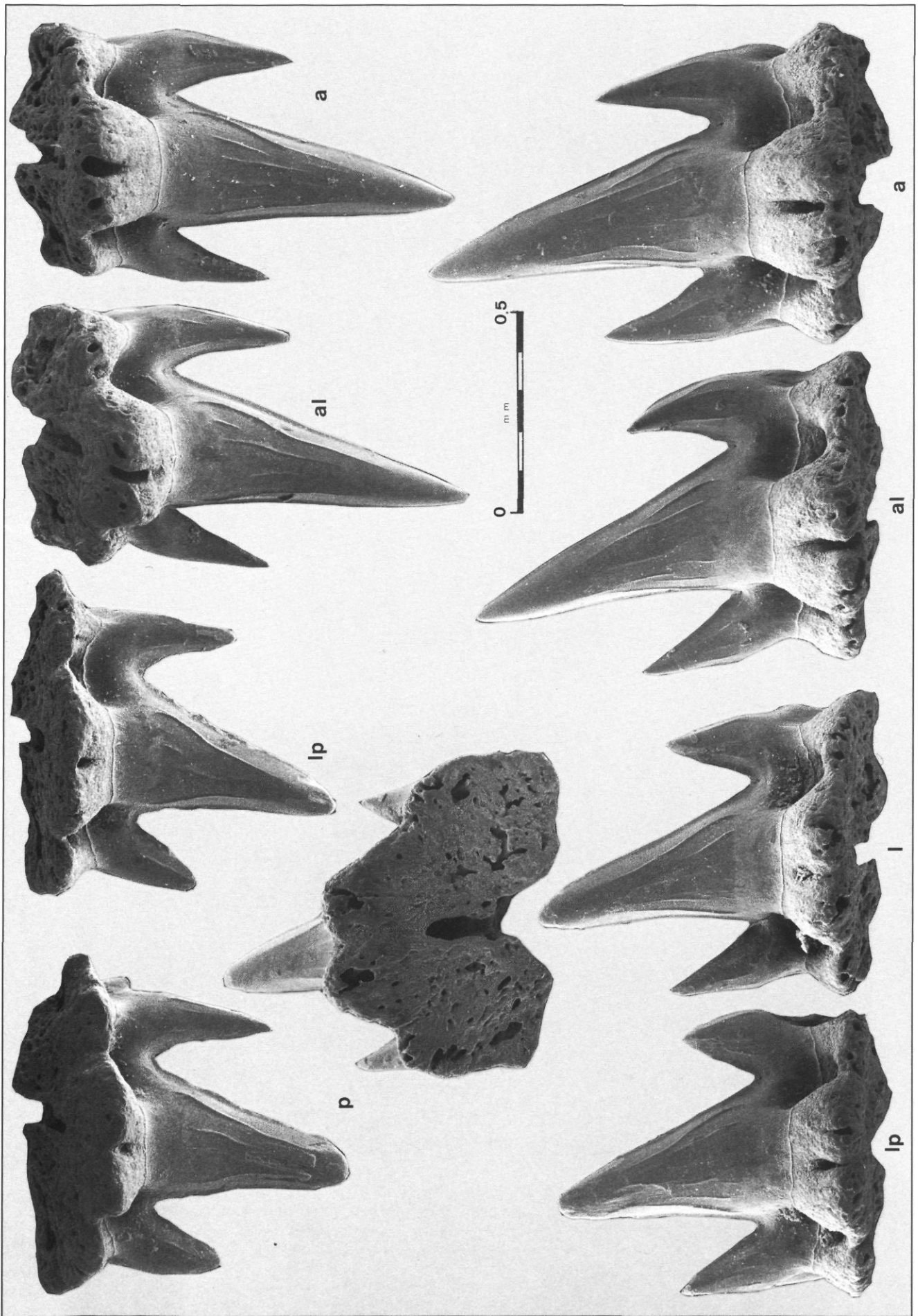


Plate 8. - *Atelomycterus marmoratus* (BENNETT, 1830), male 51 cm (t.l.), I. Molucca, Philippines.
Figures p & lp refer to the same scale bar as figures p & lp of the plate 7.

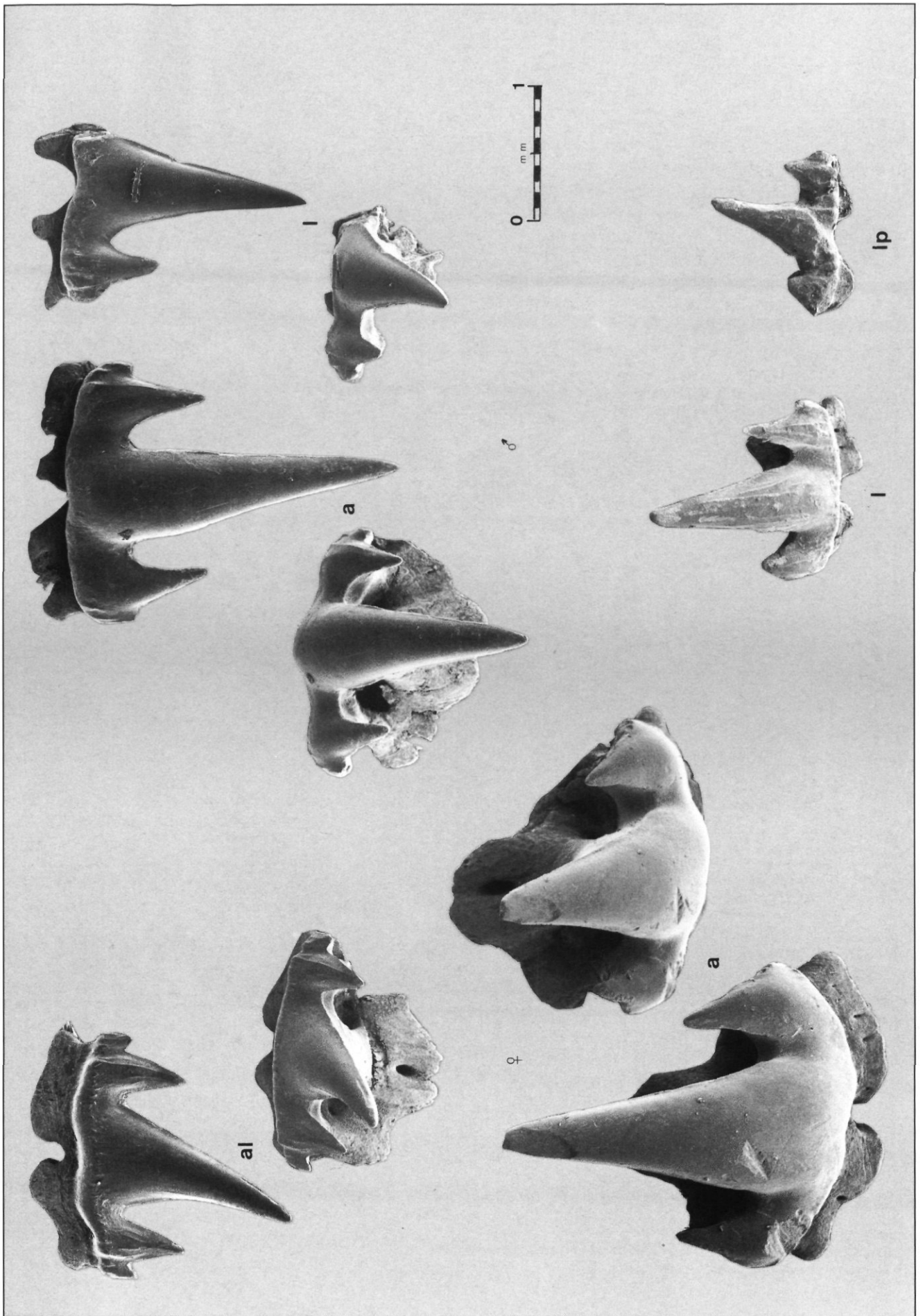


Plate 9. - *Autlohalaelurus labiosus* (WATTE, 1905), female 49 cm and male 59 cm (t.l.), South West Australia.

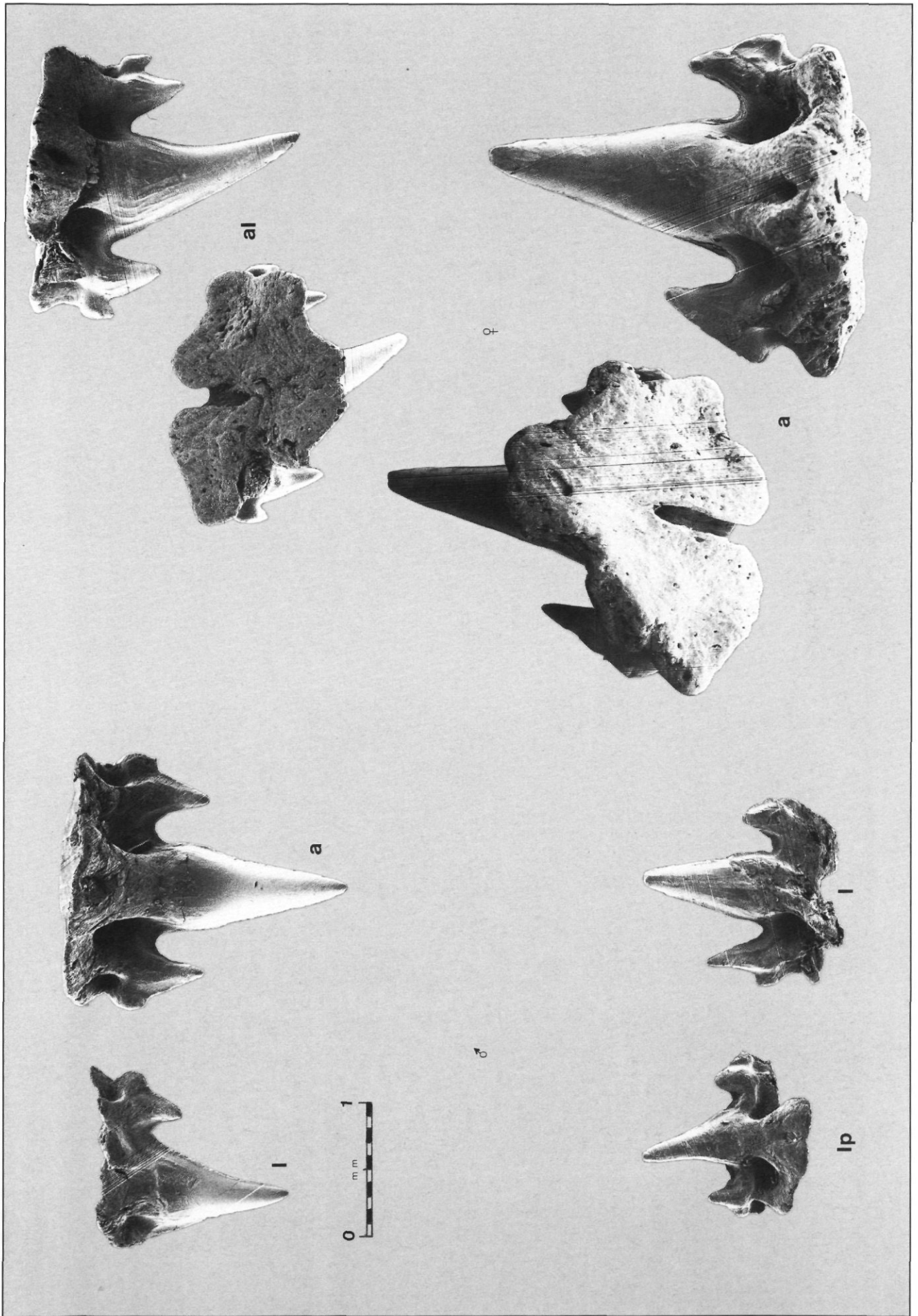


Plate 10. - *Aulohalaelurus labiosus* (WAITE, 1905), female 49 cm and male 59 cm (t.l.), South West Australia.

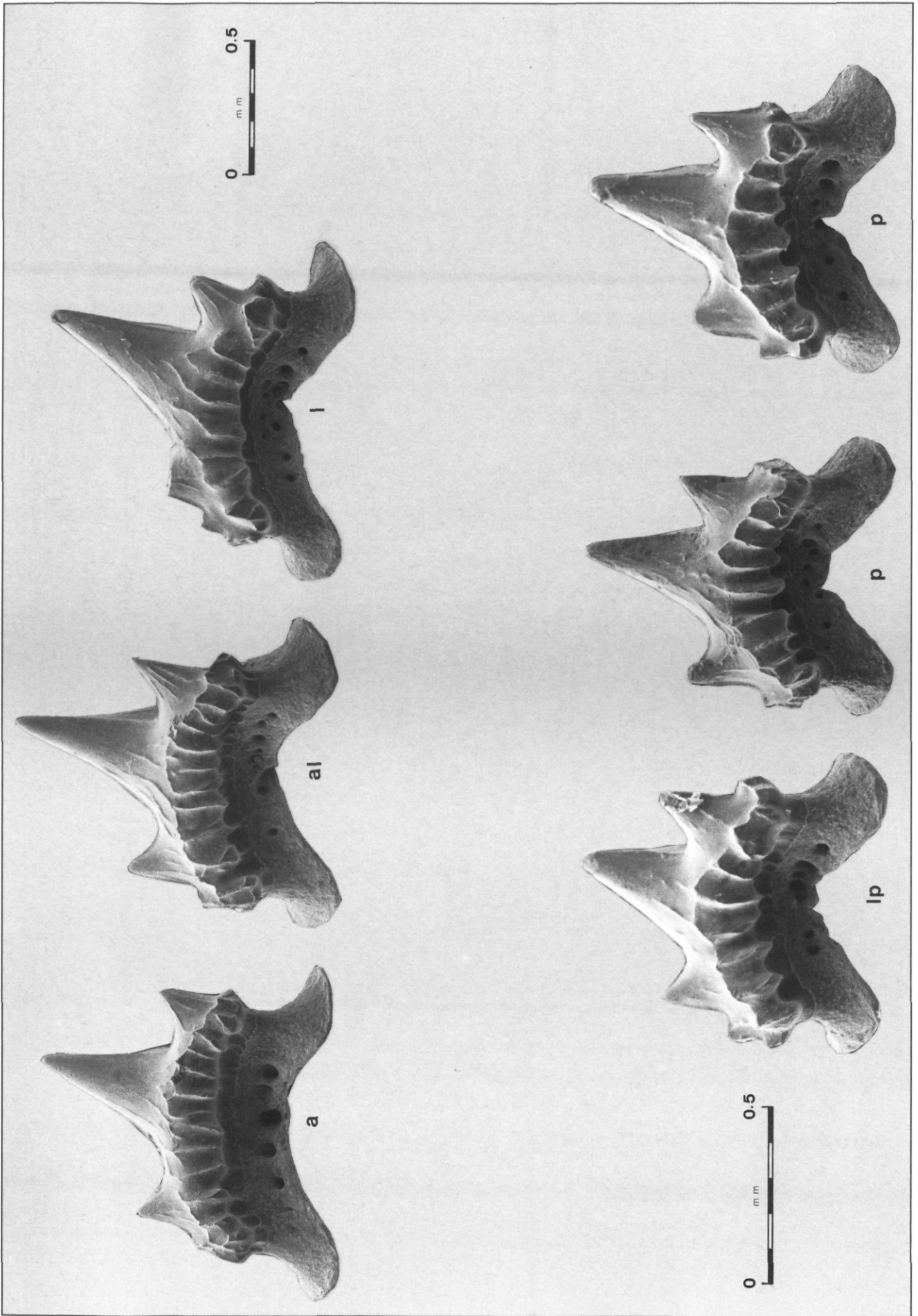


Plate 11. - *Cephaloscyllium isabellum* (BONNATERRE, 1788), female 58 cm (t.l.), Hobart, Tasmania.

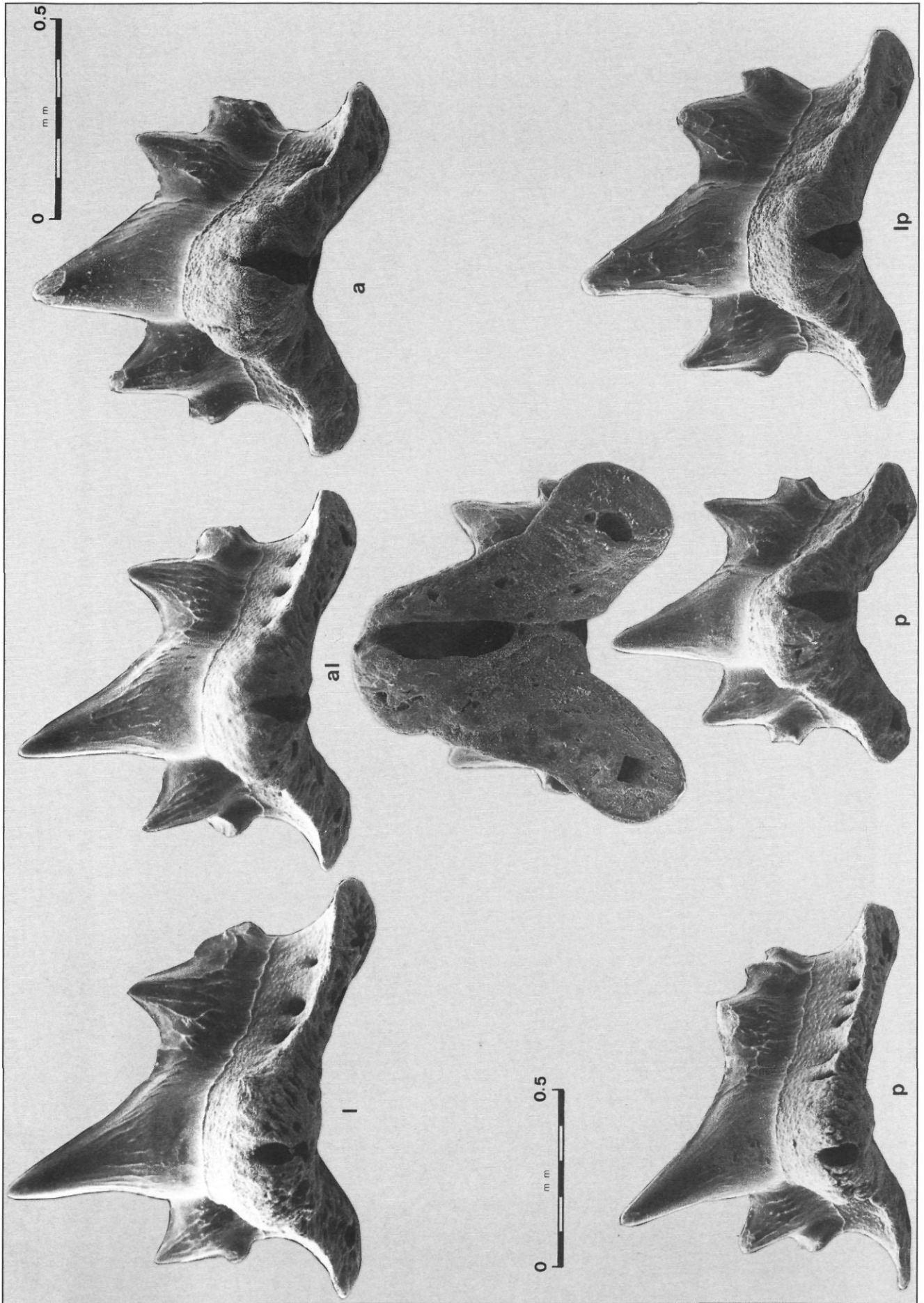


Plate 12. - *Cephaloscyllium isabellum* (BONNATERRE, 1788), female 58 cm (t.l.), Hobart, Tasmania.

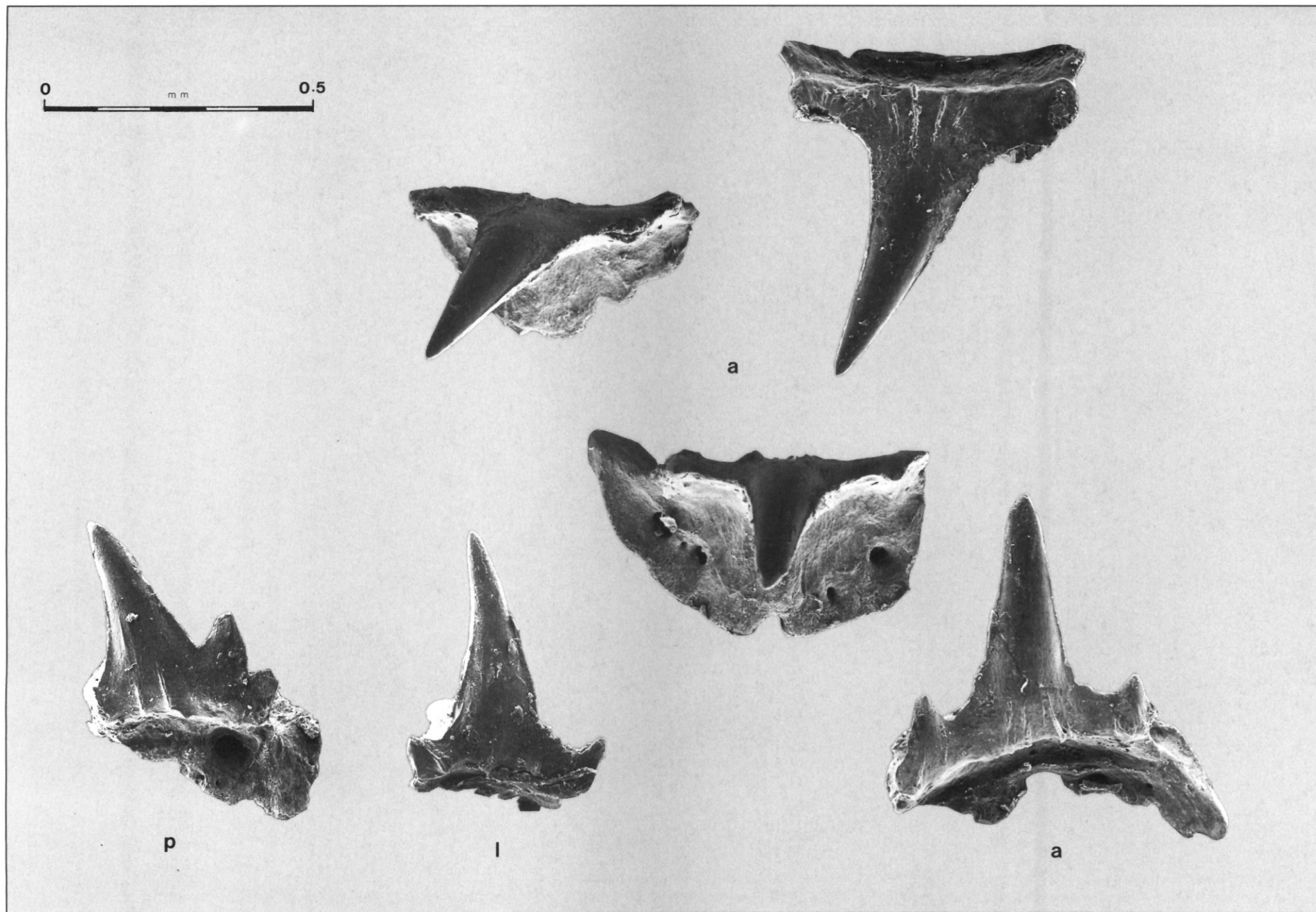


Plate 13. – *Cephalurus cephalus* (GILBERT, 1892), male 21 cm (t.l.), Santa Rosalia, Baja California. Courtesy of M. STEHMANN, ISH, Hamburg.

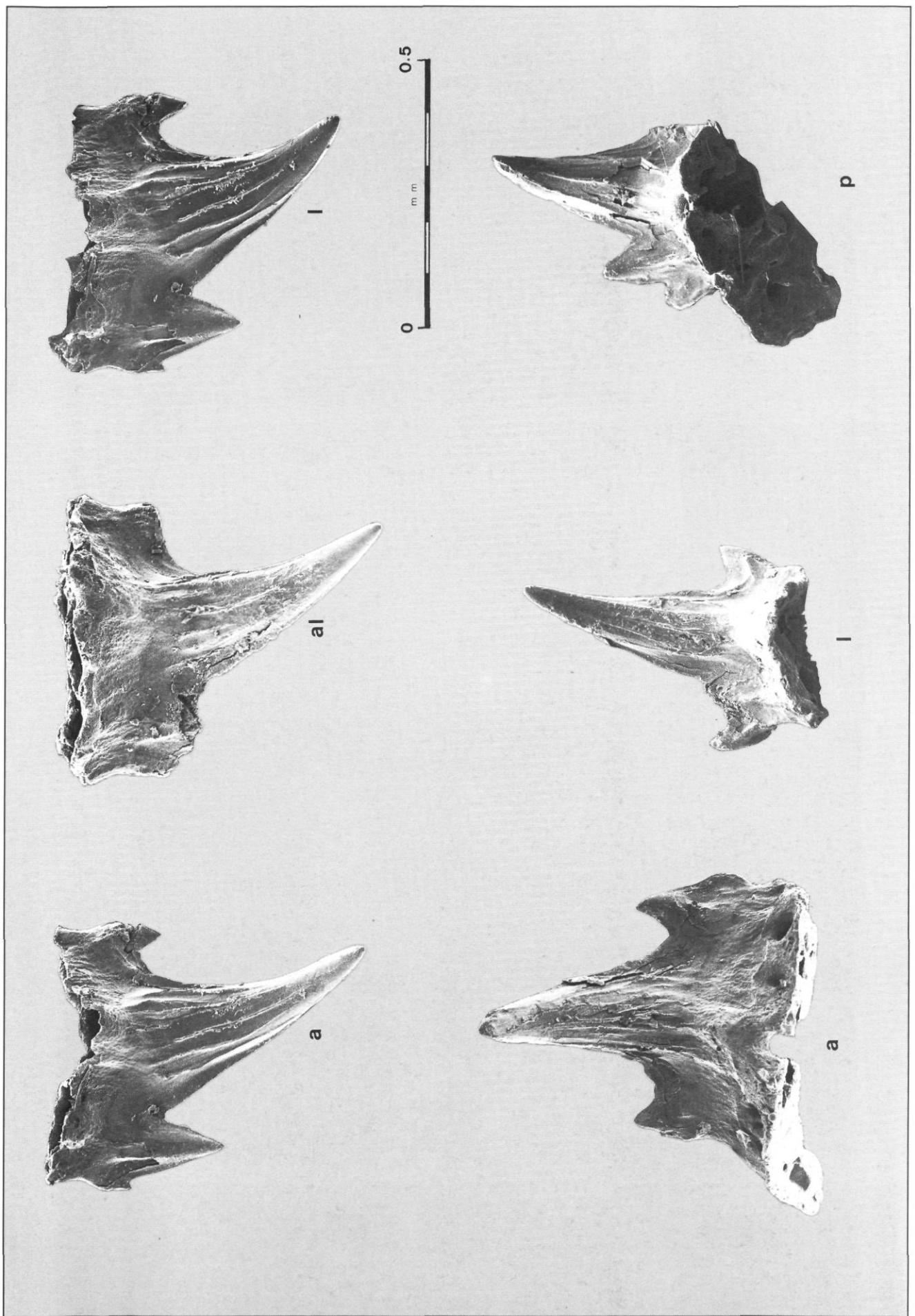


Plate 14. — *Cephalurus cephalus* (GILBERT, 1892), male 21 cm (t.l.), Santa Rosalia, Baja California. Courtesy of M. STEHMANN, ISH, Hamburg.



Plate 15. - *Cephalurus* sp., female 30 cm (t.l.), Peru.

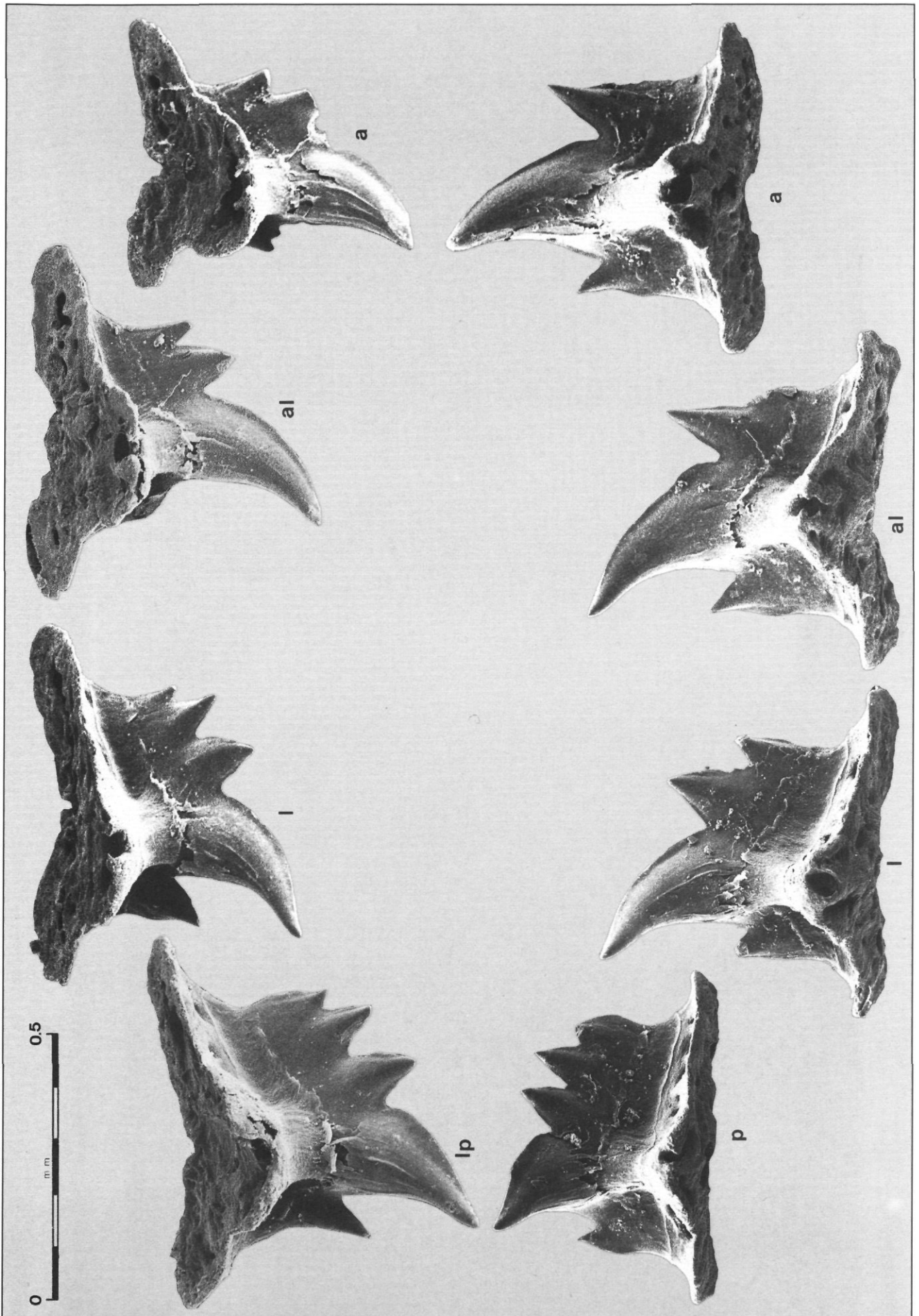


Plate 16. - *Cephalurus* sp., female 30 cm (t.l.), Peru.

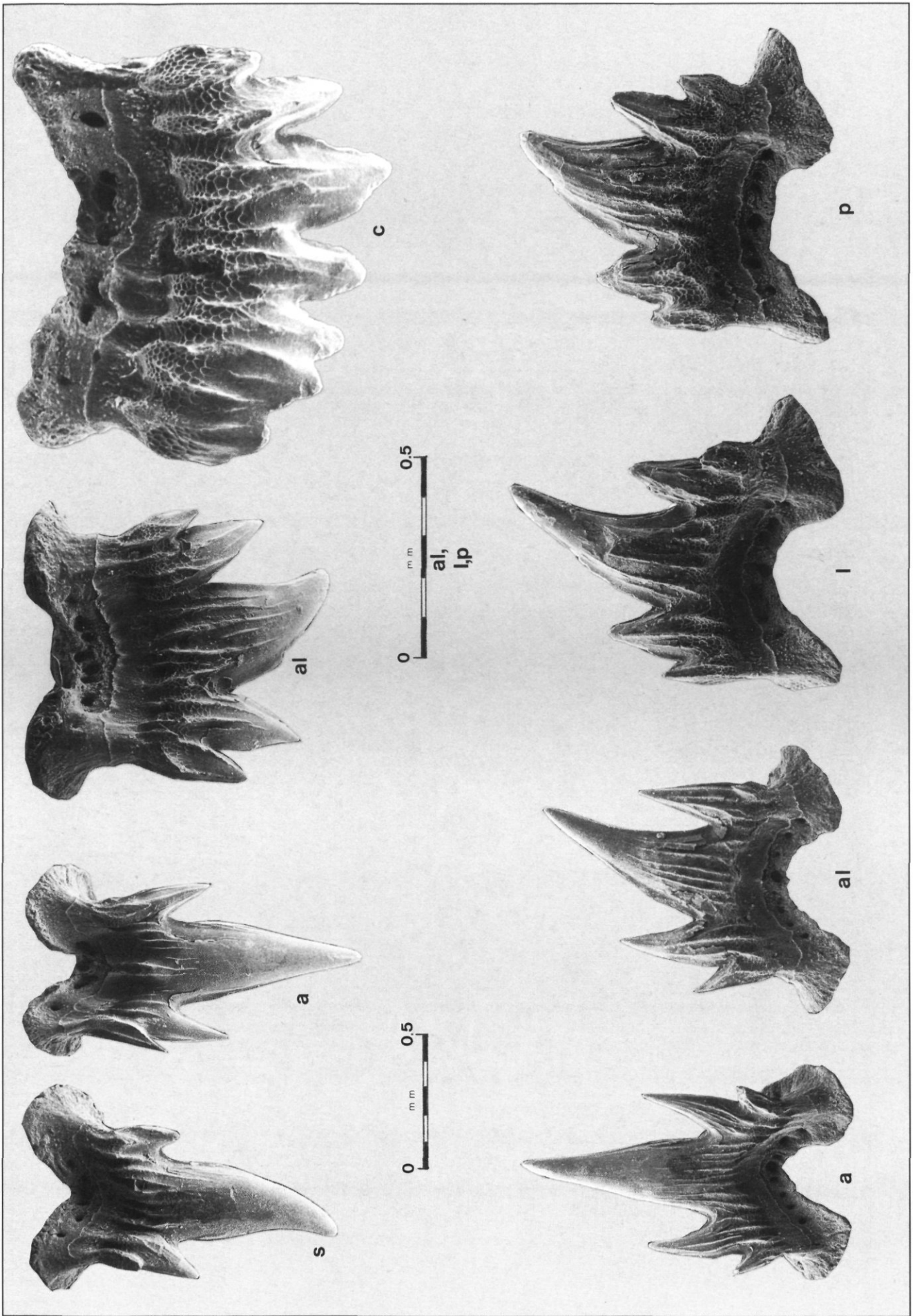


Plate 17. — *Galeus melastomus* RAFINESQUE, 1810, male 64 cm (t.l.), West Flugga, North Atlantic. Enlargement of the upper commissural tooth (c) is twice the one of the upper antero lateral.

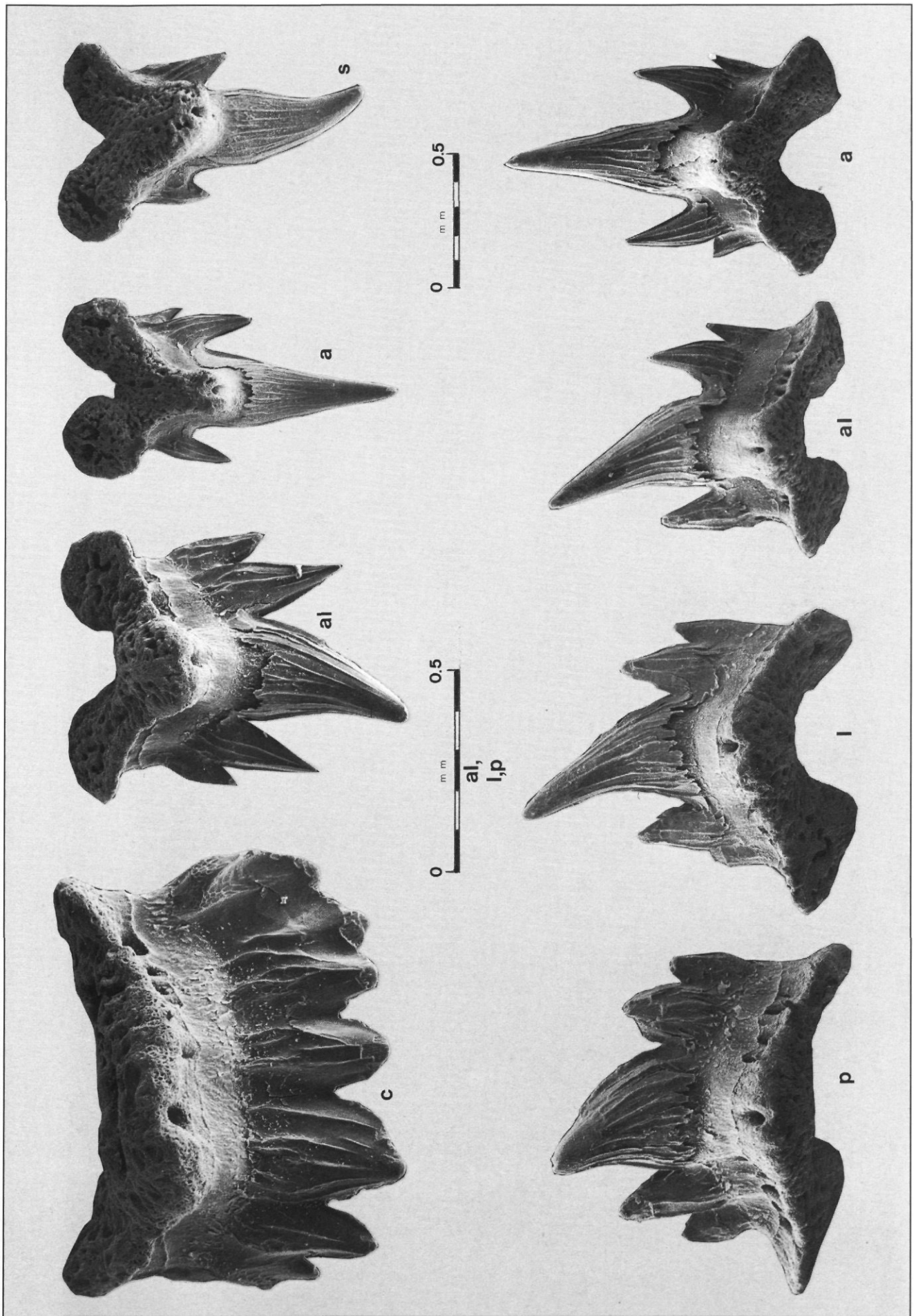


Plate 18. — *Galeus melastomus* RAFINESQUE, 1810, male 64 cm (t.l.), West Flugga, North Atlantic. Enlargement of the upper commissural tooth (c) is twice the one of the upper antero lateral.

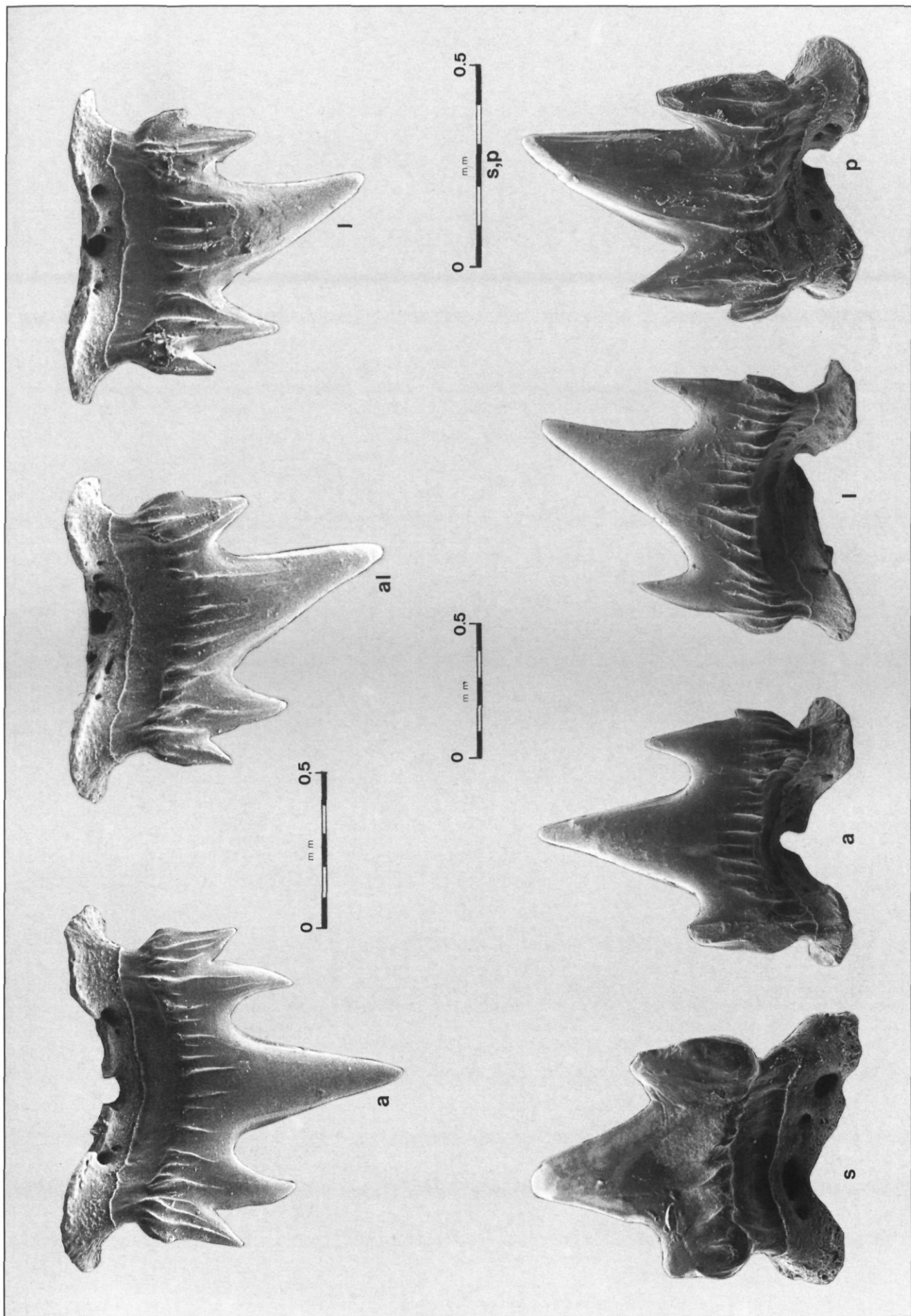


Plate 19. - Halaelurus (Bythaelurus) canescens (GÜNTHER, 1878), male 59 cm (t.l.), Chile.

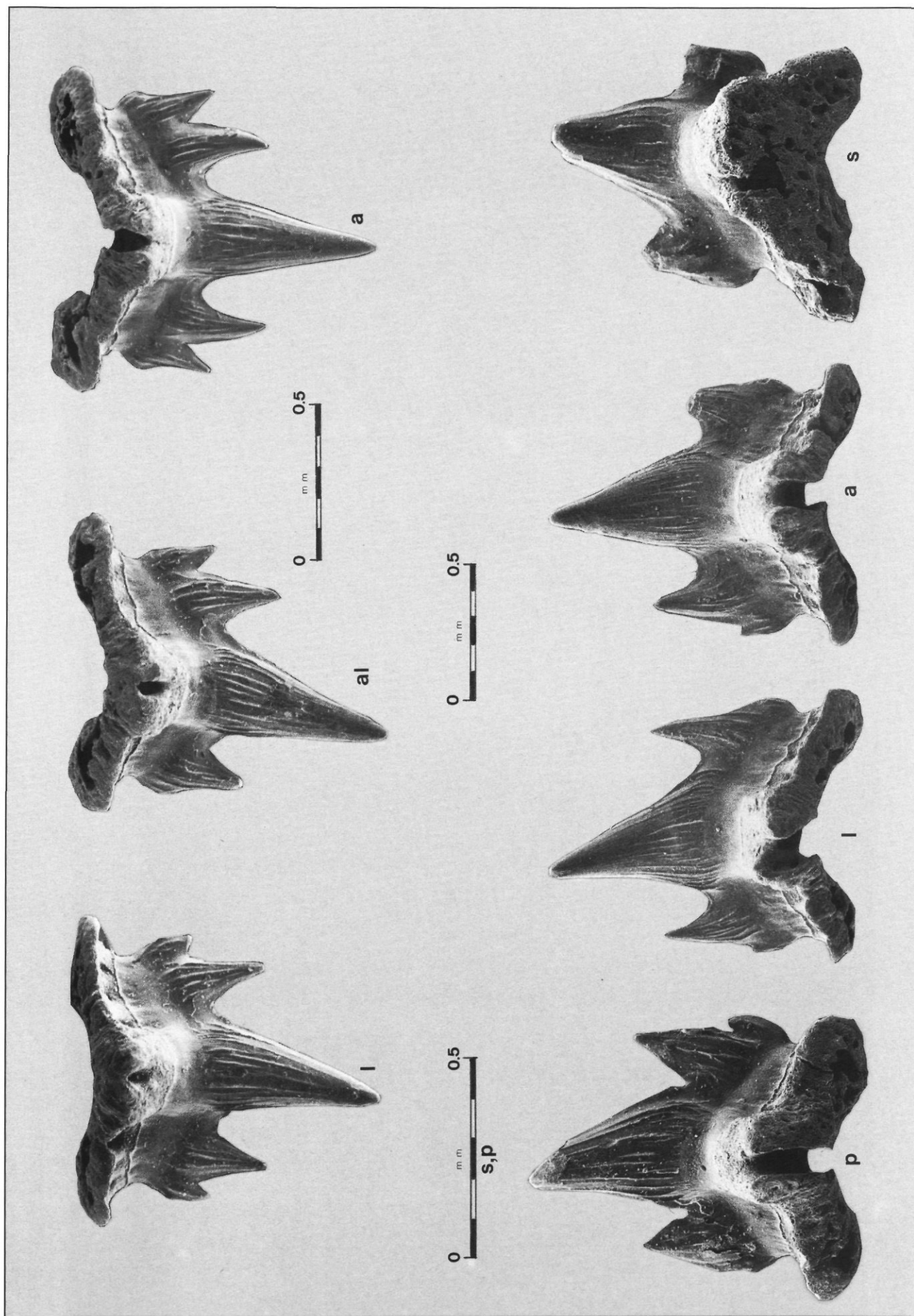


Plate 20. - *Halaelurus (Bythaelurus) canescens* (GÜNTHER, 1878), male 59 cm (t.l.), Chile.

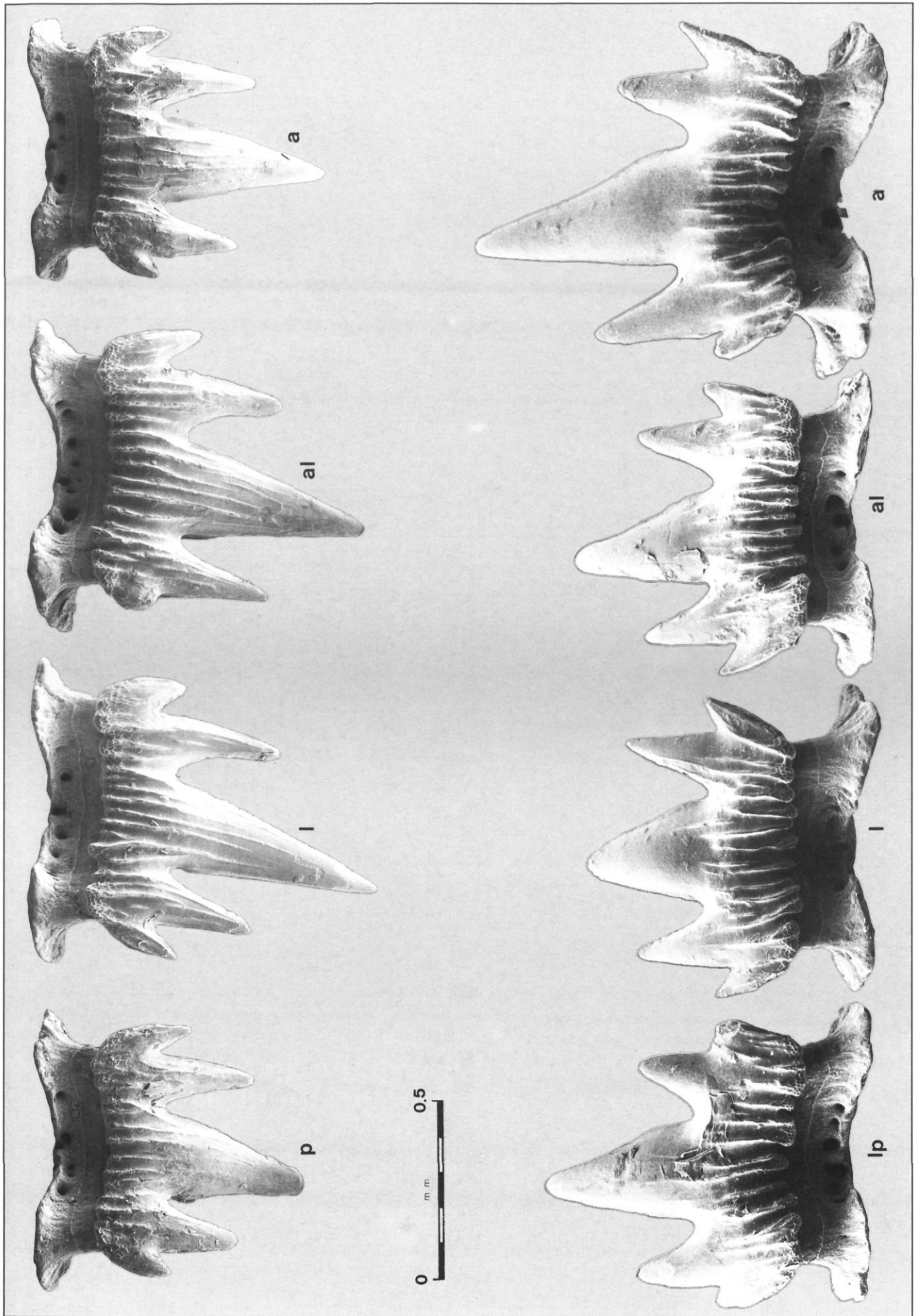


Plate 21. — *Haploblepharus edwardsii* (Voigt, 1832), male 50 cm (t.l.), Capetown, South Africa.

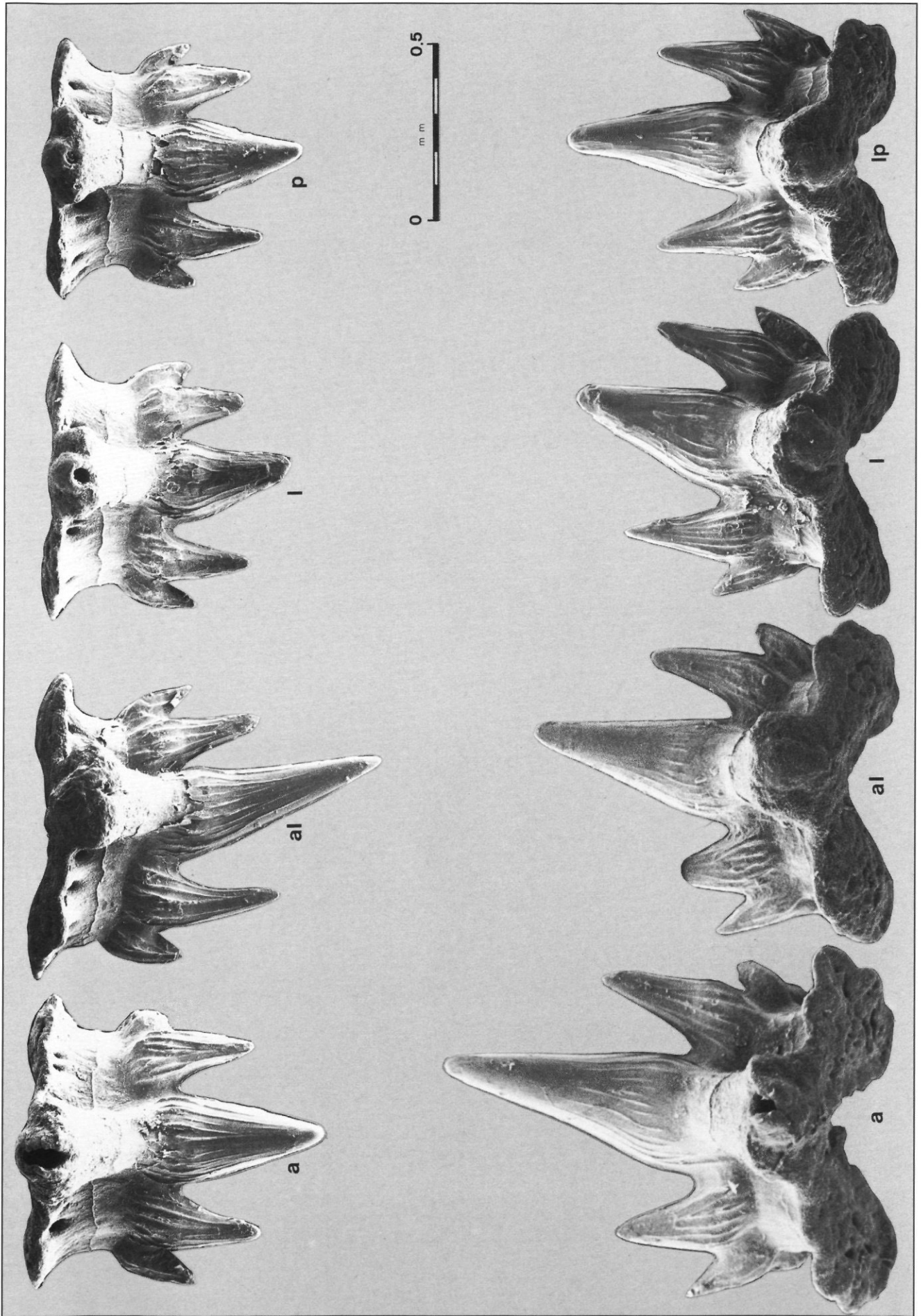


Plate 22. - *Haploblepharus edwardsii* (Vogel, 1832), male 50 cm (t.l.), Capetown, South Africa.

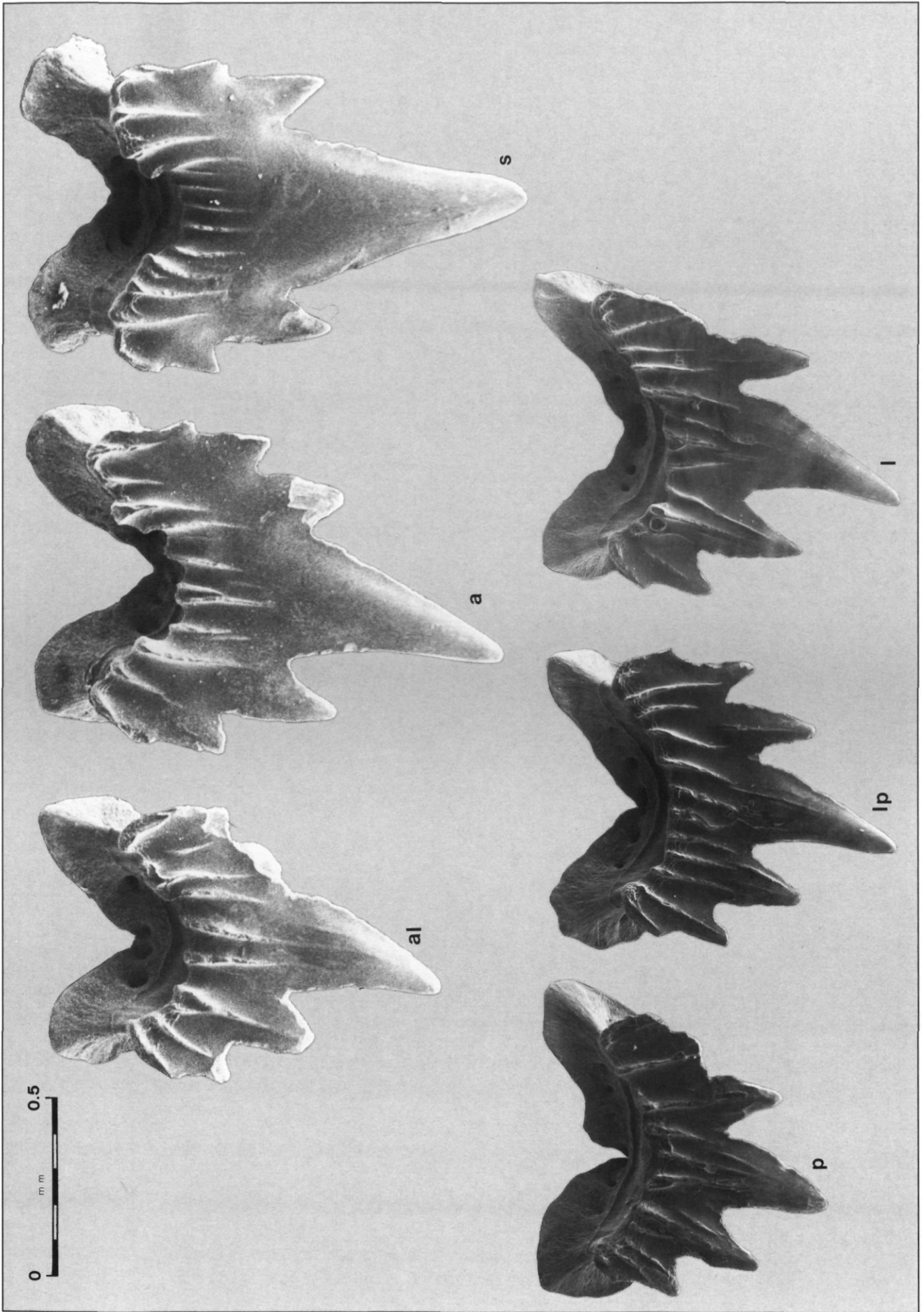


Plate 23. - *Holohalaelurus regami* (GILCHRIST, 1922), male 54 cm (t.l.), Capetown, South Africa.

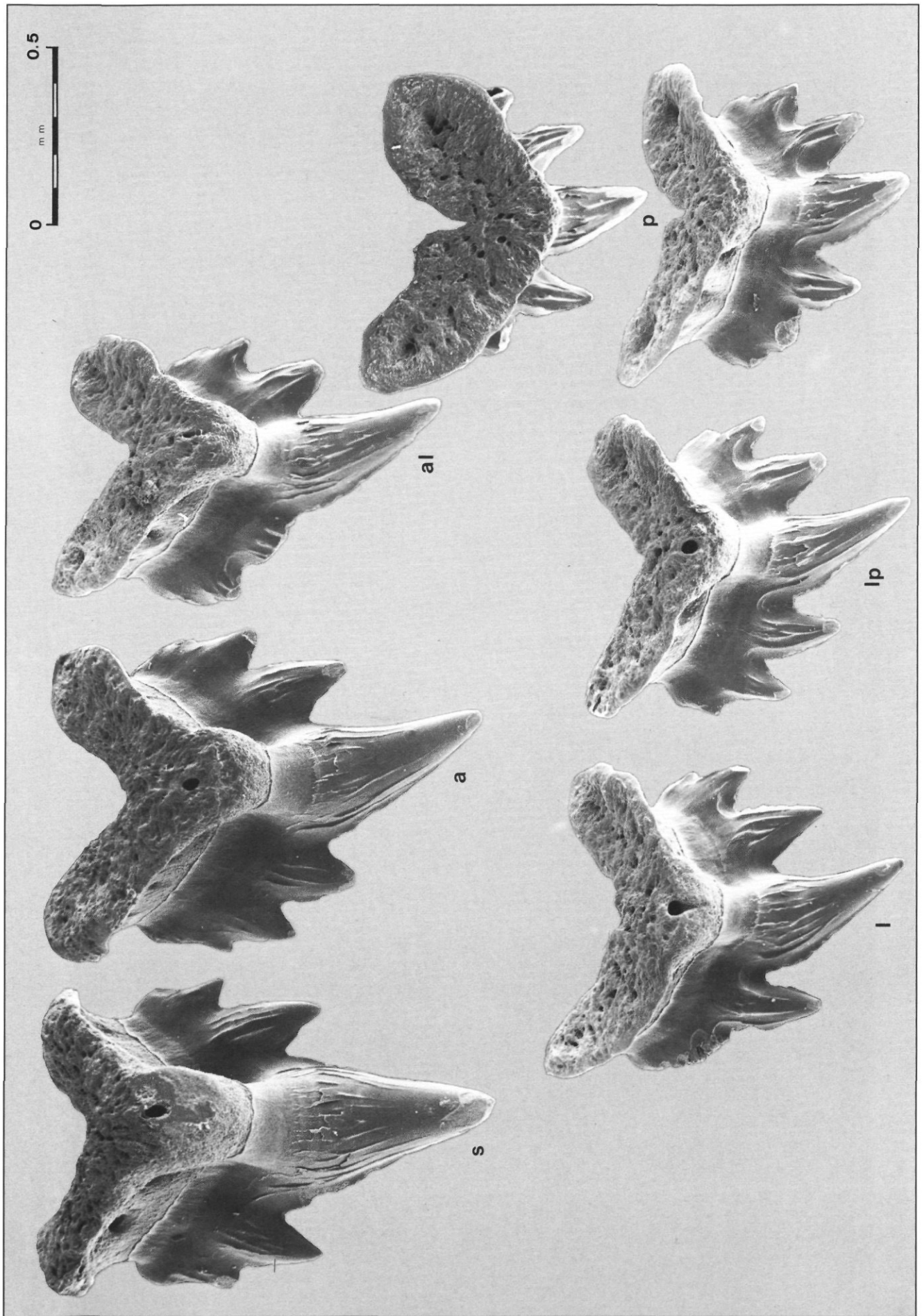


Plate 24. - *Holohalaelurus regami* (GILCHRIST, 1922), male 54 cm (t.l.), Capetown, South Africa.

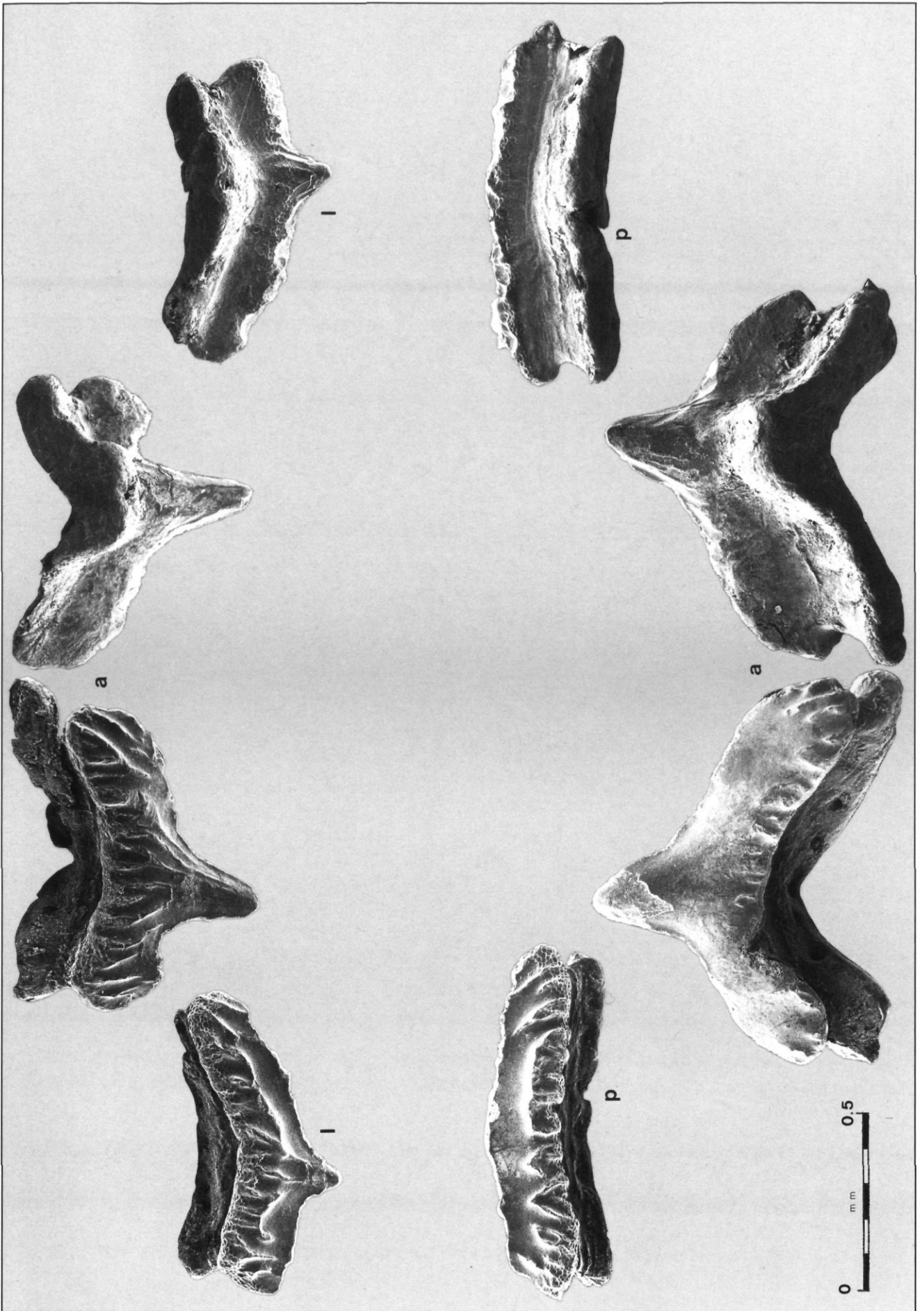


Plate 25. - *Halaelurus (Halaelurus) burgeri* (MULLER & HENLE, 1838), female 42.5 cm (t.l.), South Lombok, Indonesia.

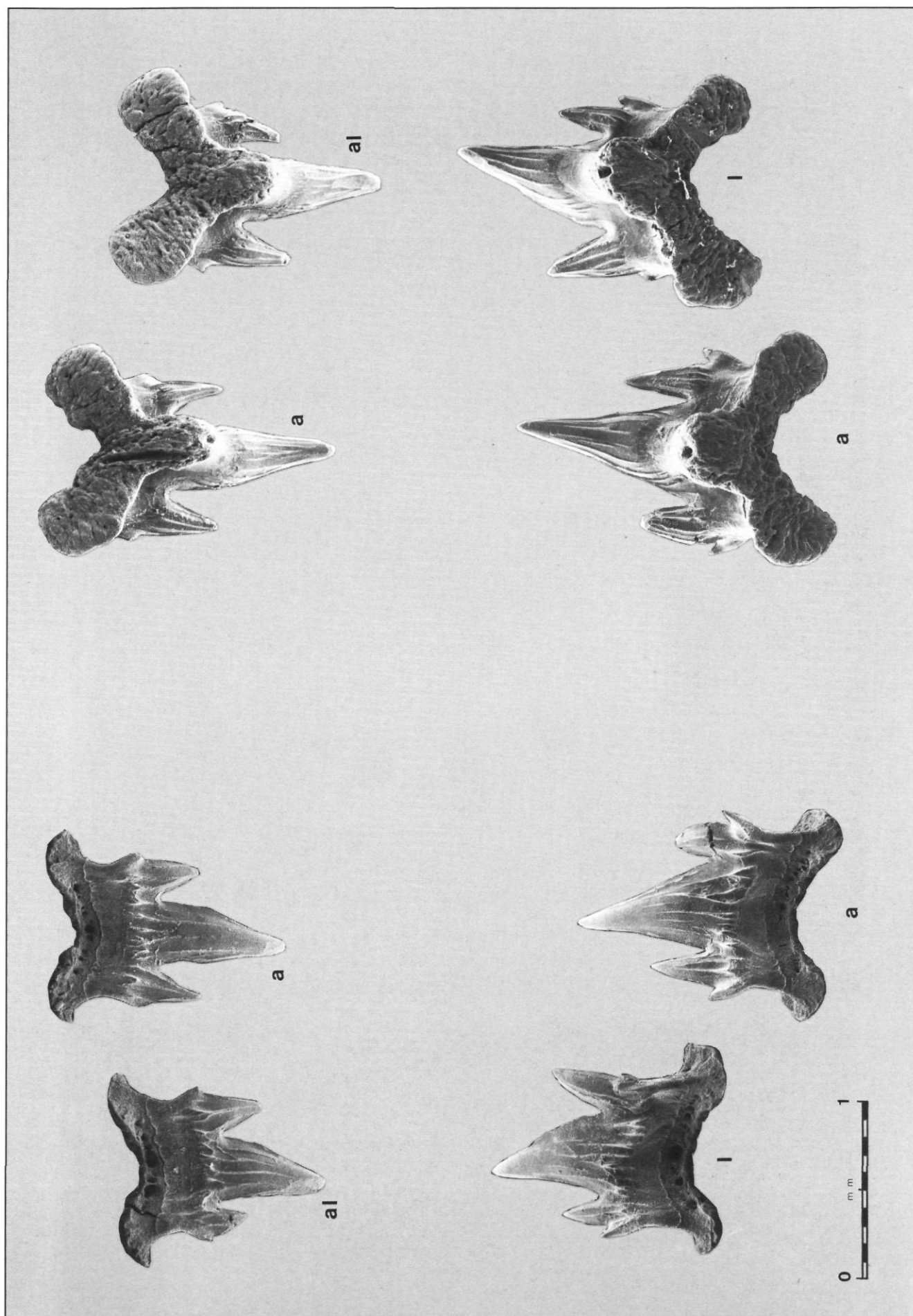


Plate 26. - *Parmaturus pilosus* GARMAN, 1906, male 64 cm (t.l.), Japan.

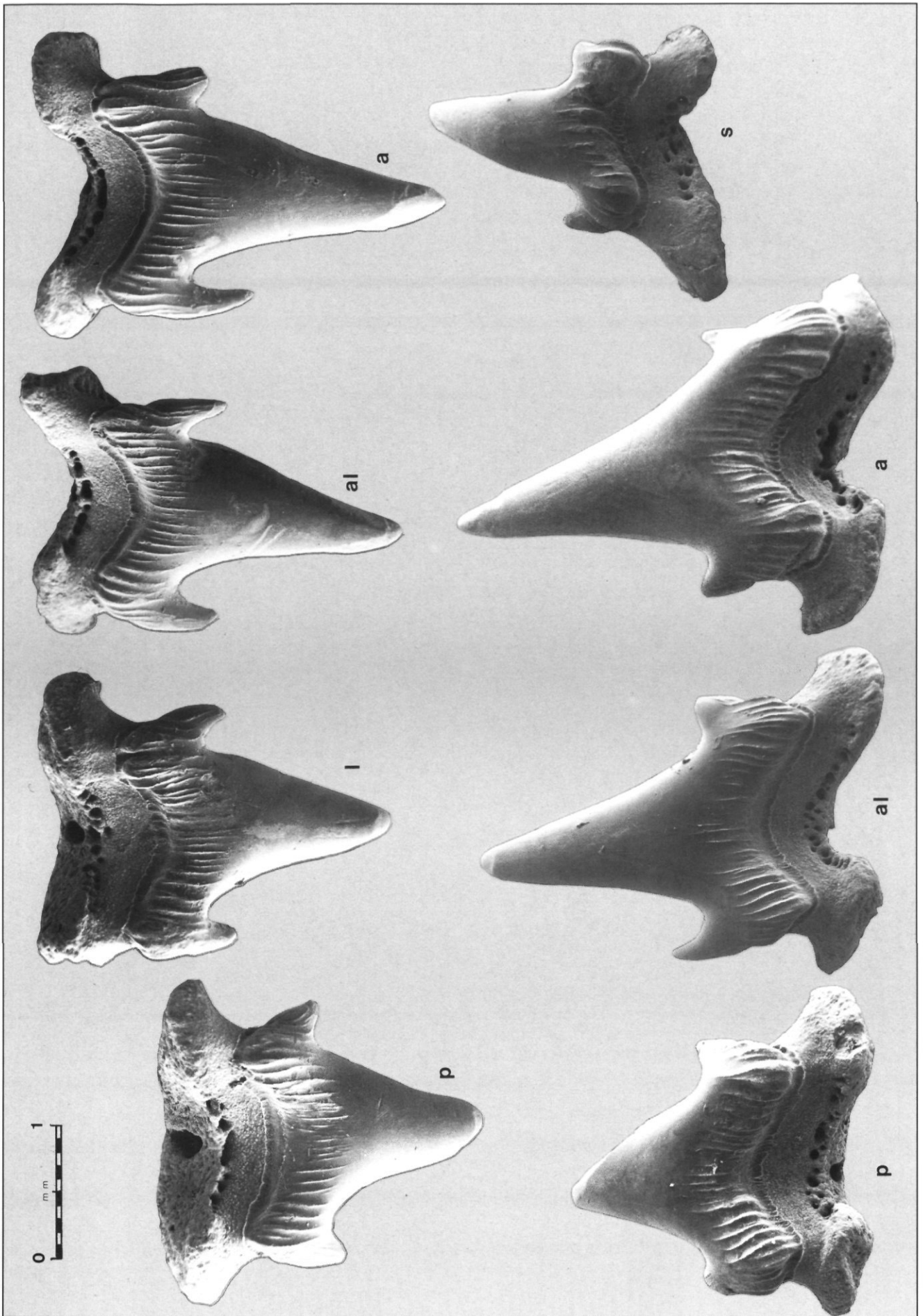


Plate 27. - *Poroderma pantherinum* (SMITH, 1837), male 68 cm (t.l.), Natal, South Africa.

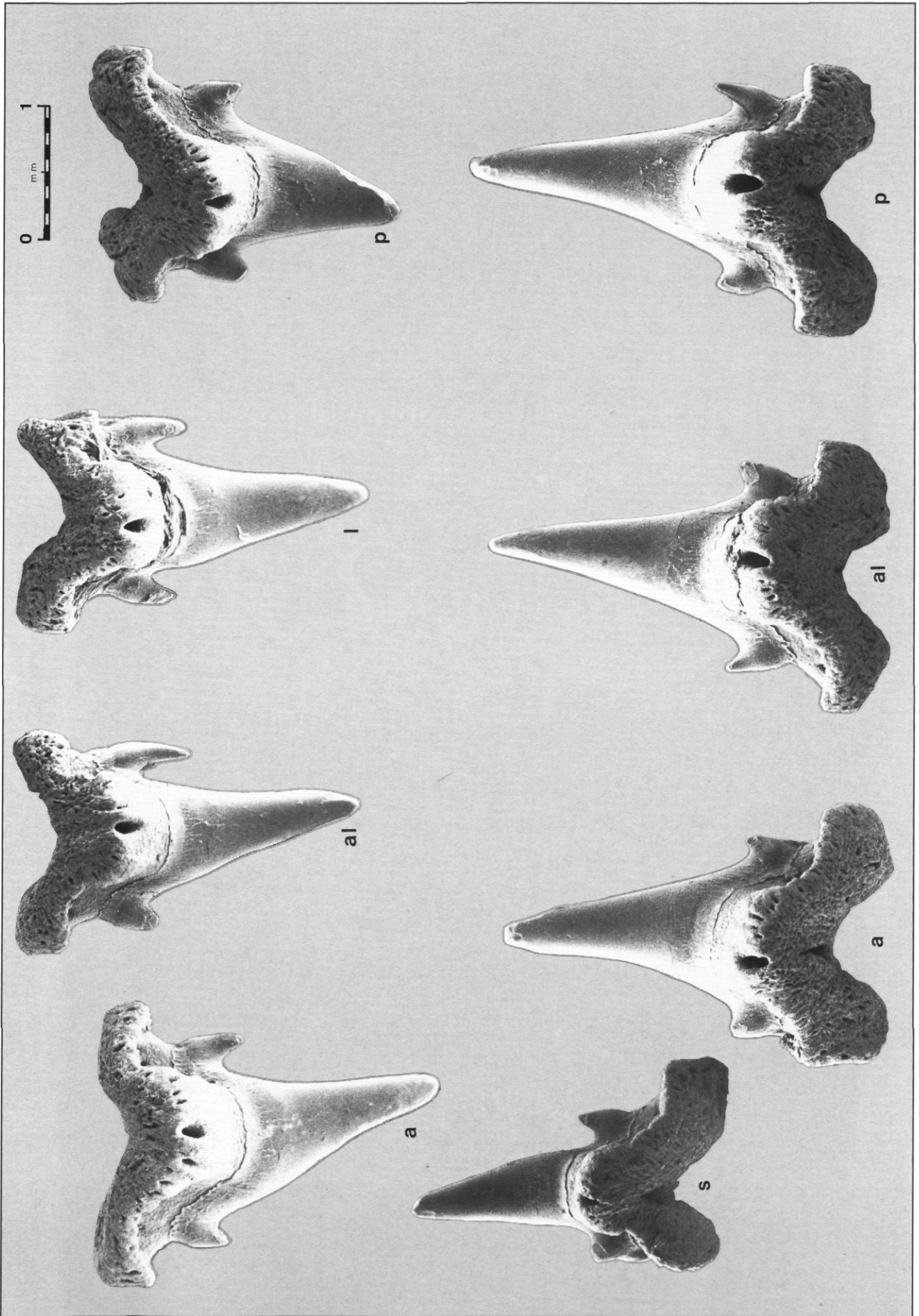


Plate 28. — *Poroderma pantherinum* (SMITH, 1837), male 68 cm (t.l.), Natal, South Africa.

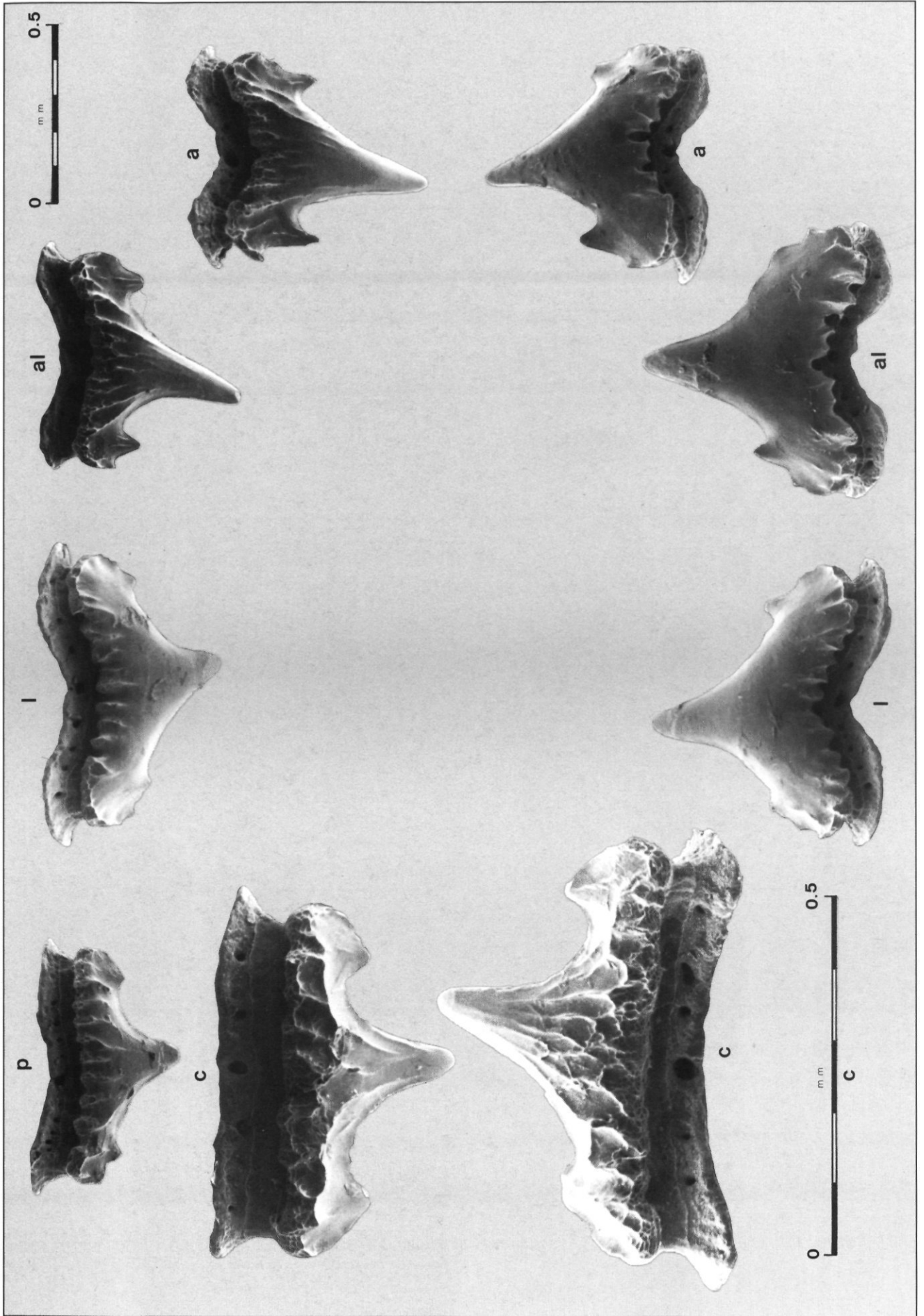


Plate 29. - *Schroederichthys maculatus* SPRINGER, 1966, male 31 cm (t.l.), Honduras.

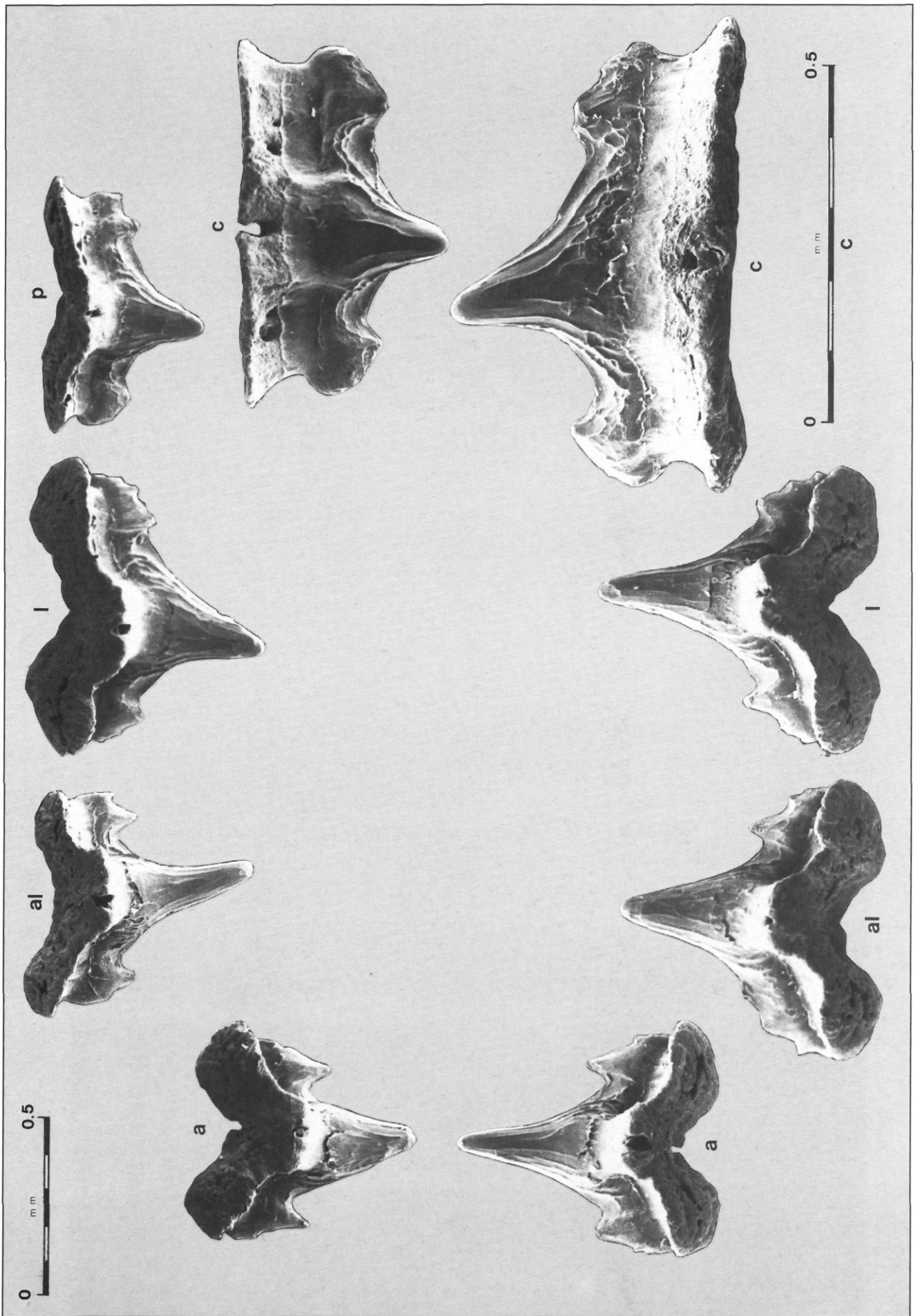


Plate 30. - *Schroederichthys maculatus* SPRINGER, 1966, male 31 cm (t.l.), Honduras.

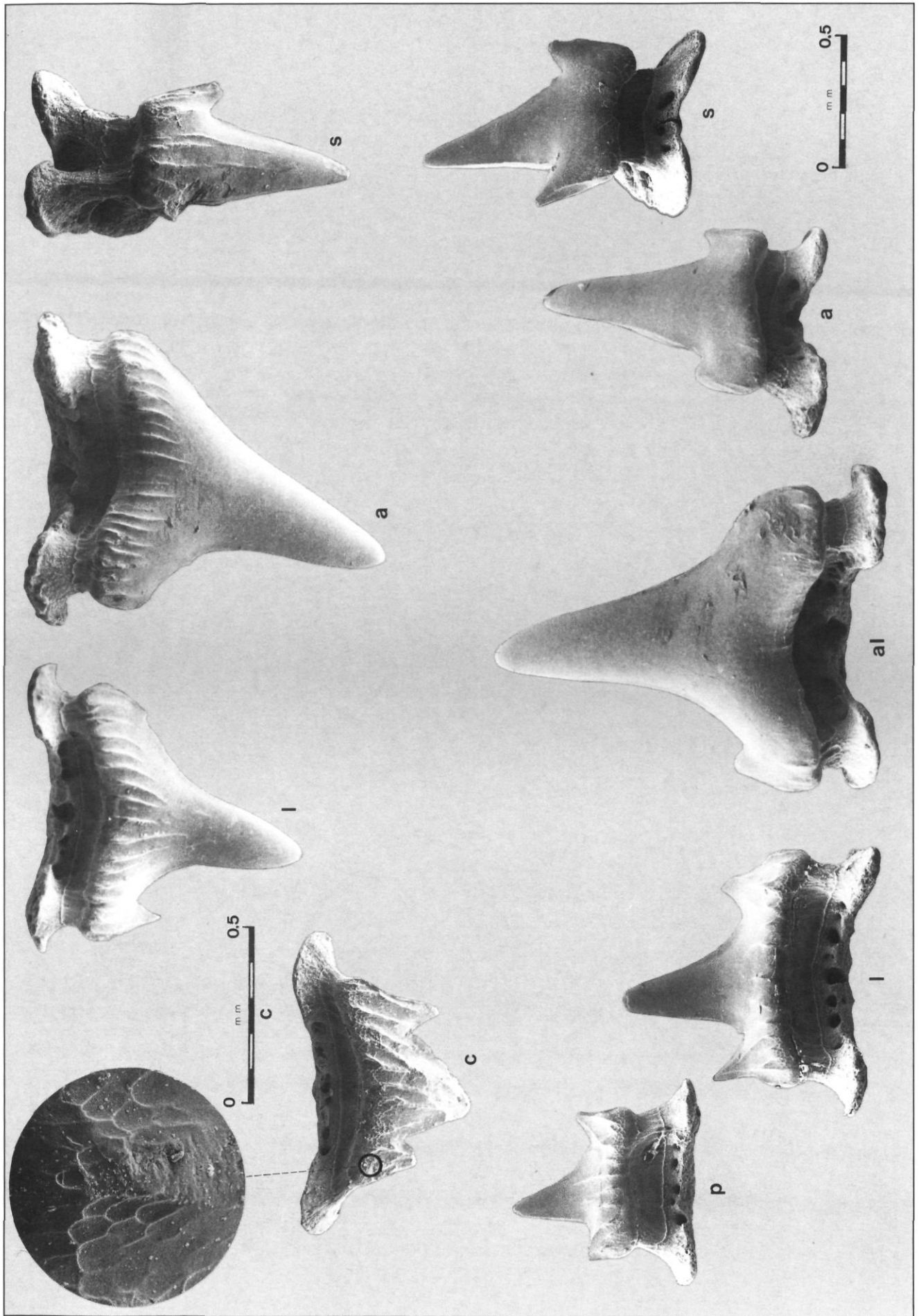


Plate 31. - *Scylliorhinus canicula* (LINNAEUS, 1758), male 53 cm (t.l.), South Dakar, Senegal.

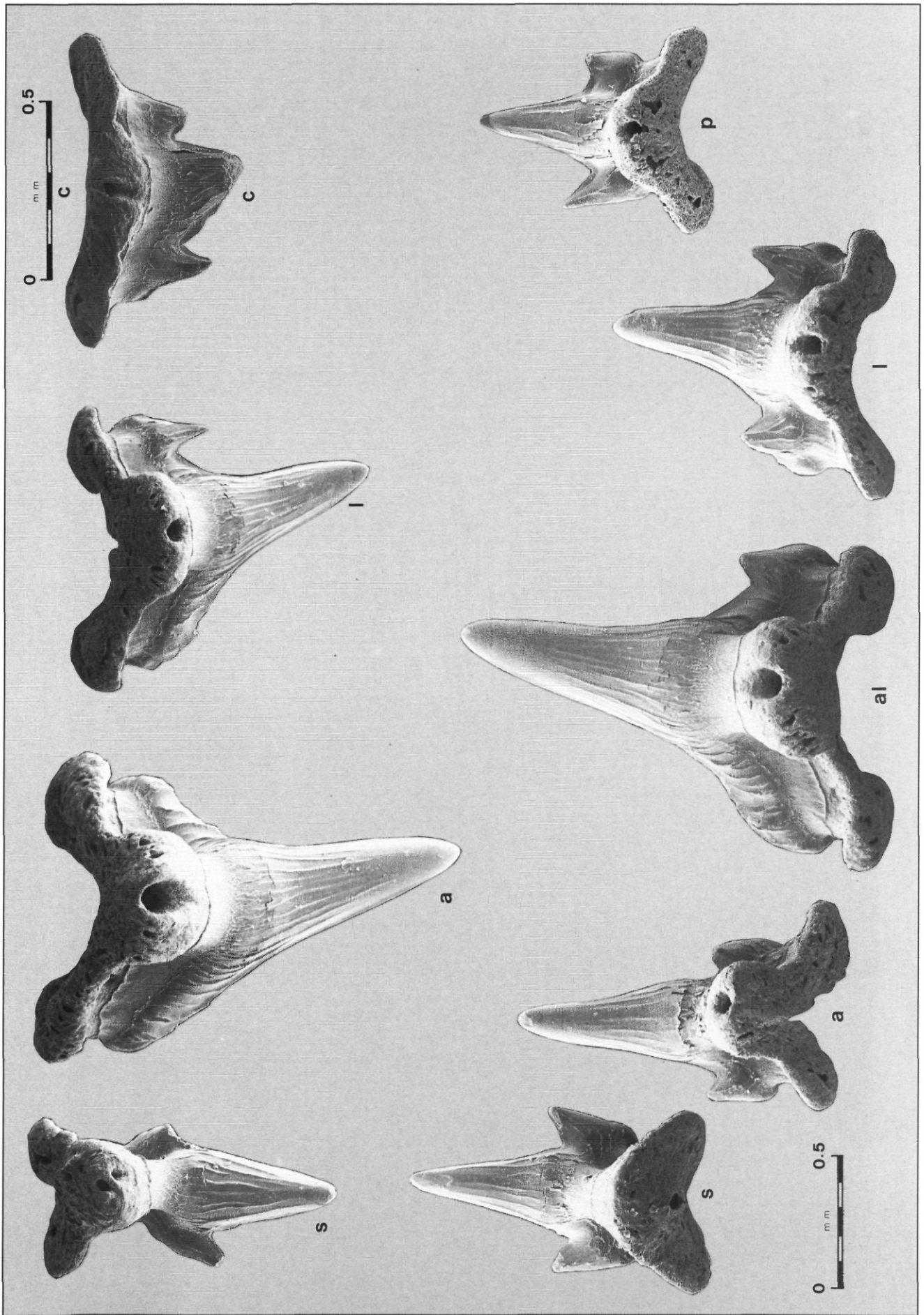


Plate 32. - *Scyliorhinus canicula* (LINNAEUS, 1758), male 53 cm (t.l.), South Dakar, Senegal.

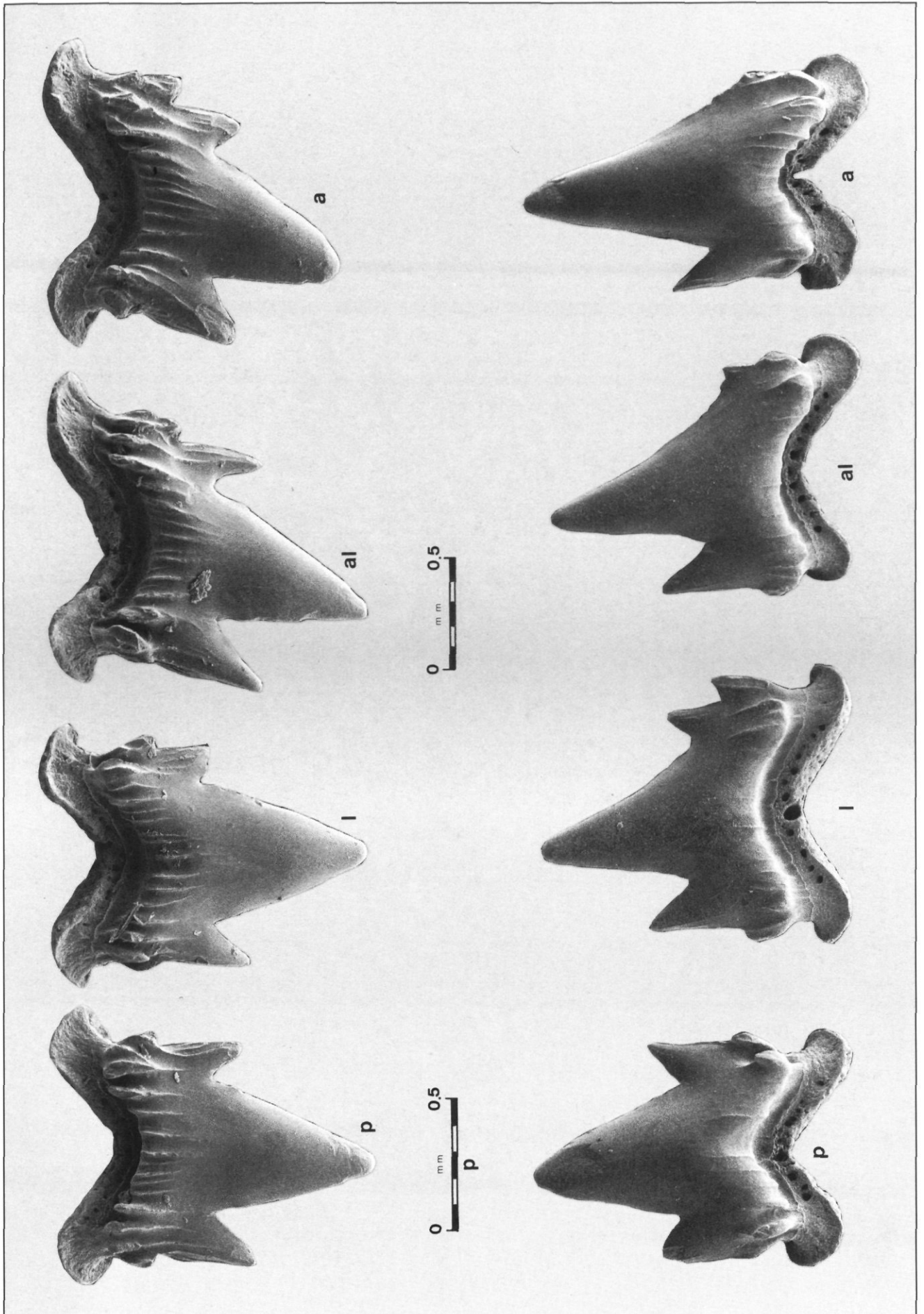


Plate 33. — *Scyliorhinus torazame* (TANAKA, 1908), male 44 cm (t.l.), Japan.

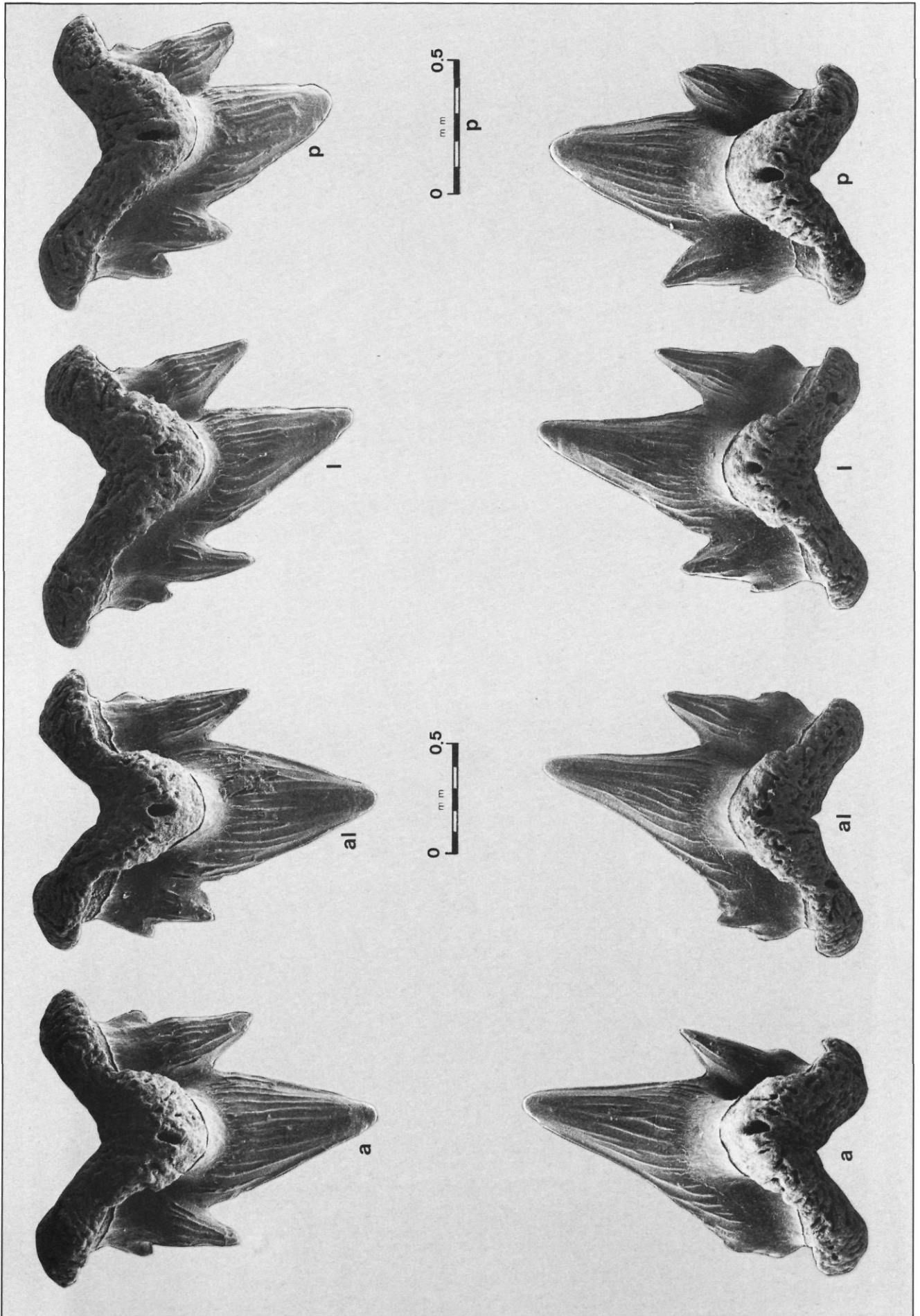


Plate 34. — Scyliorhinus torazame (TAVAKA, 1908), male 44 cm (t.l.), Japan.

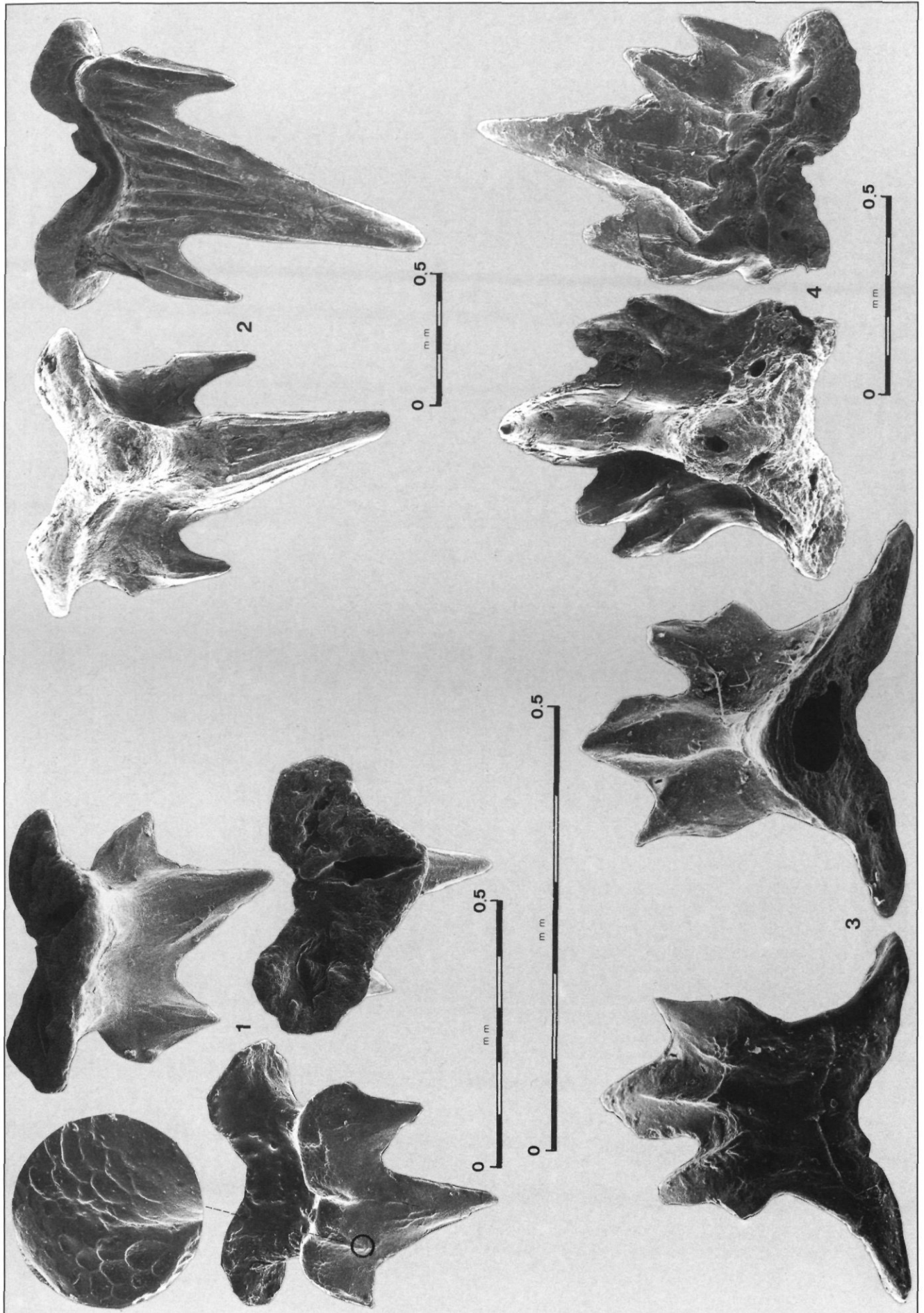


Plate 35. - Comparison between teeth of juvenile (1, 3) and adult (2, 4) specimens of *Asymbolus analis* (Ogilby, 1885), figs. 1 & 2, and *Parmaturus pilosus* (GARMAN, 1906), figs. 3 & 4.