

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

Editor : M. STEHMANN

Part B : Batomorphii No. 1a :

Order Rajiformes - Suborder Rajoidei - Family : Rajidae

Genera and Subgenera : *Anacanthobatis* (*Schroederobatis*), *Anacanthobatis* (*Springeria*), *Breviraja*, *Dactylobatus*, *Gurgesiella* (*Gurgesiella*), *Gurgesiella* (*Fenestrija*), *Malacoraja*, *Neoraja* and *Pavoraja*

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Abstract

Part B of this series, comprising the Batomorphii, is initiated with taxa of the Rajoidei. The tooth morphology of representatives of nine genera and subgenera is described and illustrated by SEM-photographs. An adapted terminology is introduced for the description of rajoid teeth, because their tooth morphology differs markedly in various aspects from that in selachians. A differential diagnosis for and conclusions on rajoid odontology, as well as an odontological key will be given in a forthcoming issue dealing with the last rajoid taxa.

Key-words : Elasmobranchii - Batomorphii - Rajoidei - Odontology - Descriptive terminology.

Résumé

La deuxième partie (B) de cette série concerne les Batomorphii. Dans ce premier fascicule l'odontologie de neuf taxons supraspécifiques de Rajoidei est décrite et illustrée (clichés MEB). Une terminologie adaptée à la problématique de leur odontologie est proposée, car celle-ci diffère grandement de celle des sélaciens. Diagnose différentielle, conclusions systématiques et clef de détermination odontologique seront présentées dans le fascicule qui cloturera l'étude de ce groupe.

Mots-clés : Elasmobranchii - Batomorphii - Rajoidei - Odontologie - Terminologie descriptive.

Kurzfassung

Teil B dieser Serie, der die Batomorphii umfassen wird, beginnt mit der Beschreibung und Illustrierung durch REM-Photos der Zahnmorphologie einer Gruppe von Rajoidentaxa. Auf Grund erheblicher Unterschiede in der Zahnmorphologie bei Selachiern und Rajoiden wird eine entsprechend angepaßte odontologische Terminologie für die Rajoidei vorgestellt. Eine zusammenfassende Differentialdiagnose und Bewertung zur Odontologie der Rajoidei, sowie ein odontologische Bestimmungsschlüssel werden zum Abschluß der Rajoiden in einem späteren Beitrag folgen.

Schlüsselwörter : Elasmobranchii - Batomorphii - Rajoidei - Odontologie - Terminologie Zahnmorphologie.

General introduction

Unlike the principally much more lively interest in shark teeth, never before received teeth of batoid fishes (sawfishes, guitarfishes, rays and skates) a similar degree of attention. In contrast to the majority of sharks, by far most of the batoid species possess very small teeth closely set in plate-like bands on the jaws. The only exceptions are myliobatoid rays with only one row of greatly enlarged teeth (*Aetobatus*), or the median one of only few tooth rows enlarged in a similar way (*Myliobatis*, *Pteromylaeus*, *Aetomylaeus*, *Rhinoptera*), to form massive crunching tooth plates. For a long time, there have also been many more fossil records and publications on teeth of sharks than on those of batoids. This was mainly due to the difference in size, that means the tiny batoid teeth were either often overlooked, or not recognised as such, and they were much less obvious and characteristic than shark teeth. With regard to living species, sharks are easier available and also received always more attention of researchers, because many are dangerous to man, and last but not least are jaws and individual teeth of sharks certainly more spectacular as trophies and collectors items. As a consequence, existing descriptions and illustrations of teeth of living batoids are usually rather superficial and concerning the general type of dentition and eventual sexual dimorphism rather than the detailed complete tooth morphology. Based on the principles of description and illustration, including root structures and vascularization system, introduced for sharks in Part A, Part B of our odontological series will provide the same kind of consistent and detailed information on the morphology of batoid teeth. We begin Part B with a first

contribution on tooth morphology of rajoid skates, the most specious, systematically most problematical, and geographically most widely distributed group of batoids. For the rajoids, as well as later within few other diverse batoid groups, will the sequence of publication of supraspecific taxa not reflect any certain classification or taxonomic ordering but merely depend on availability of study material and progress made in its investigation. If a larger number of supraspecific taxa within an order, suborder, or even family of batoids has to be published, due to technical limitations, in more than one issue of this series, the last contribution will provide for each higher taxonomic category, respectively, the summarizing discussion, conclusion, differential diagnosis, and odontological key. So is the present issue on some supraspecific rajoid taxa only the first of several contributions on rajoid tooth morphology.

Systematics and classification of sharks are not yet fully understood and clarified in the sense, that existing systems uniformly would reflect resolved phylogenetic interrelationships. However, considerably more progress in revisional work has been achieved for this group of chondrichthyan fishes than for the remaining two, namely Batomorphii and Holocephali. So has COMPAGNO (1984) presented a world catalogue of living shark species and somewhat later (1988) added a thorough revision of the Carcharhiniformes. Despite several still existing unresolved problems, these works have offered a good systematic basis for Part A on sharks of this series, the odontological results of which have provided additional arguments for eventually resolving part of still questionable shark taxa and their interrelationships. A similar general revision of the Holocephali is soon to be expected by DIDIER (in press, pers. comm.). Quite different is the situation for systematics of the Batomorphii, although their number of species and supraspecific taxa nearly equals that of sharks; that again documents the by far greater research effort invested in sharks.

A world catalogue of batoid species is still far from being completed, because revisional effort has been quite heterogeneous for a long time regarding the various orders and suborders of batoid fishes and distributional ranges of the species. GARMAN (1913) was the last investigator having revised "The Plagiostomia" (sharks, skates and rays) in total. All following revisional accounts on Batomorphii, or Batoidea only dealt with individual family taxa (e.g., NORMAN, 1926, for the Rhinobatidae), single genera, or mainly defined geographical faunas. As a consequence, unlike the Selachii of Part A, we cannot rely on a relatively recent up to date taxonomic arrangement for the supraspecific batoid taxa for publishing the odontological contributions of Part B. It will therefore be commented on and explained in the introduction to each order, suborder, or family of the batoids, which classification or revision

will form the basis for the taxonomic arrangement chosen.

Like before in Part A on sharks, will the authors also here in Part B on Batomorphii not draw any nomenclatorially valid conclusions. 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. The original reference of each specific taxon will be given in the descriptive section, respectively, and not be repeated under literature references.

Part B : Batomorphii

ORDER : RAJIFORMES

Suborder : *Rajoidei*

Introduction

Considerable revisional progress within the Batomorphii has been made during the past about 40 years especially in rajoid skates. Critical regional faunal inventories and revisions have played a key role in this process, and this kind of revisional approach is less surprising, if the total number of rajoid species is considered. These are about 230, which is nearly 50 % of all batoid species known. In addition, unlike sharks and holocephalans, are rajoid skates distributed almost everywhere in the world oceans from Arctic to Antarctic and from shallow coastal to deep waters of several thousand meters depth. They become scarce in tropical coastal regions only or, like in tropical coral reef areas, are missing. Apparently has this group of batoids been sufficiently flexible and managed to settle in nearly all kinds of marine habitats, resulting in greatly diverse evolutionary lineages of the rajoids.

Regional revisions were, e.g., published by CLARK (1926) for the European rajids, including the Mediterranean, BIGELOW & SCHROEDER (1953) for the entire Western North Atlantic batoid fauna, ISHIYAMA (1958) for the Western North Pacific Rajidae, MENNI (1972, 1973) for the southwestern, STEHMANN (1970) for the northeastern, and HULLEY (1970) for the southeastern Atlantic rajids. Early authors already erected few, now as before valid rajid genera (*Sympterygia* MÜLLER & HENLE, 1841; *Psammobatis* GÜNTHER, 1870; *Dactylobatus* BEAN & WEED, 1909) in addition to the collective genus *Raja* LINNAEUS, 1758. Paralleled by the extension of character complexes used for the analysis of rajid systematics, was the genus *Raja* step by step split up further by more recent authors into a number of genera, and subgenera of some of these. The family Rajidae was even subdivided into few more families to separately

include skates with quite extraordinary features: Anacanthobatidae VON BONDE & SWART, 1923; Arhynchobatidae BIGELOW & SCHROEDER, 1953; Pseudorajidae BIGELOW & SCHROEDER, 1954; Gurgesiellidae DE BUEN, 1959; Crurirajidae HULLEY, 1972. MCEACHRAN (1984) finally summarized relevant revisional results published by authors mentioned above and obtained by himself plus coauthors in a cladistic analysis. This resulted in his definition of two groups of the Rajoidei equalling family rank, of which one (the Rajidae) comprehends the majority of rajoid genera and subgenera, whereas the other one remained unnamed. However, on the one hand could he not consider all supraspecific taxa recognized at that time (e.g. *Atlantoraja*, *Rhinoraja*, *Rioraja* and subgenera of *Anacanthobatis* missing), because his classification was largely based on anatomical structures of neurocranium, scapulocoracoid and claspers, and such information was not equally available for all relevant taxa. On the other hand was his classification concept not unanimously accepted because, e.g., of the heterogeneity of diagnostic characters it was based on. In addition, further supraspecific rajoid taxa were resurrected and established since by authors. MCEACHRAN & MIYAKE (1990a) updated the existing information with a revised, though still incomplete working hypothesis on phylogenetic interrelationships of rajoid skates. The same authors (MCEACHRAN & MIYAKE, 1990b) presented, as an appendix to a zoogeographical and bathymetrical analysis for skates, a list of the nominal species of rajoid skates, with assignment to supraspecific taxa according to their updated classification. Few species, however, had here been reallocated to other genera without a specific explanation for such alterations. Several groups of species also remained with unresolved assignment in both recent papers by MCEACHRAN & MIYAKE (1990a+b) due to lacking investigational results: STEHMANN (1986) had grouped the about 45 species of *Bathyraja* into three morphotypes related to depth distribution (shallow, deep water, and transitional morphotypes) but drew no taxonomic conclusions. MCEACHRAN & MIYAKE (1990a+b) considered two groups of species, namely the North Pacific and Amphi-American *Raja* Assemblages, unresolved within their classification concept and said, that also *Bathyraja*, *Irolita*, *Pavoraja*, *Pseudoraja*, and *Rhinoraja* require further research. Finally, YEARSLEY & LAST (1992) described a third subgenus within *Pavoraja*, namely *P. (Insentiraja)*.

Although the phylogenetic interrelationships within the Rajoidei are still not fully elucidated, and despite thus still existing uncertainties in the recentmost account by MCEACHRAN & MIYAKE (1990a) on rajoid classification, is the latter concept the most up to date and complete one available. It will be used therefore for our consideration of supraspecific rajoid taxa below family level to be studied odontologically, regardless their final ranking as subgenera, genera, tribes and/or subfamilies. It has been the principle from the beginning of this series to

investigate the tooth morphology of all accepted, eventually considered, even questionable supraspecific taxonomic units, with the aim to offer additional arguments for the stabilization of classification and perhaps shed light on open questions from the odontological point of view.

Along with every description of the tooth morphology, the vascularization of the teeth will be described and illustrated. The method of making the vascularization visible follows STENSIÖ, which was kindly brought to our attention by Dr. Talimaa, Institute of Geology, Vilnius (personal communication): completely submerged in anise oil, teeth become totally transparent and internal structures visible in transmittent light.

All supraspecific rajoid taxa taken into consideration for an odontological investigation, availability of the required study material given, in this and following issues of our series (Part B) are listed below:

Family ANACANTHOBATIDAE:

genus *Anacanthobatis* VON BONDE & SWART, 1923 with four subgenera (after HULLEY, 1973) *Anacanthobatis* VON BONDE & SWART, 1923, *Springeria* BIGELOW & SCHROEDER, 1951, *Sinobatis* HULLEY, 1973, and *Schroederobatis* HULLEY, 1973.

Family ARHYNCHOBATIDAE:

genus *Arhynchobatis* WAITE, 1909.

Family CRURIRAJIDAE:

genus *Cruriraja* BIGELOW & SCHROEDER, 1948.

Family GURGESIELLIDAE:

genus *Gurgesiella* DE BUEN, 1959.

Family PSEUDORAJIDAE:

genus *Pseudoraja* BIGELOW & SCHROEDER, 1954.

RAJOIDEI (Group I = unnamed family rank, after MCEACHRAN, 1984, and MCEACHRAN & MIYAKE, 1990a+b): *Sympterygia* MÜLLER & HENLE, 1841; *Psammobatis* GÜNTHER, 1870; *Arhynchobatis* WAITE, 1909; *Irolita* WHITLEY, 1937; *Pavoraja* (*Pavoraja*) WHITLEY, 1939; *Raja* (*Rioraja*) WHITLEY, 1939; *Rhinoraja* ISHIYAMA, 1952; *Pseudoraja* BIGELOW & SCHROEDER, 1954; *Bathyraja* ISHIYAMA, 1958 (incl. three morphotypes after STEHMANN, 1986); *Notoraja* ISHIYAMA, 1958; *Raja* (*Atlantoraja*) MENNI, 1972; *Pavoraja* (A) sensu MCEACHRAN, 1984; *Pavoraja* (*Insentiraja*) YEARSLEY & LAST, 1992.

RAJOIDEI (Group II = family RAJIDAE, after MCEACHRAN, 1984, and MCEACHRAN & MIYAKE, 1990a+b): *Raja* (*Raja*) LINNAEUS, 1758; *Raja* (*Dipturus*) RAFINESQUE, 1810; *Raja* (*Amblyraja*) MALM, 1877; *Raja* (*Leucoraja*) MALM, 1877; *Dactylobatus* BEAN & WEED, 1909; *Anacanthobatis* VON BONDE & SWART, 1923 (incl. four subgenera after HULLEY, 1973, see above); *Breviraja* BIGELOW & SCHROEDER, 1948; *Cruriraja* BIGELOW & SCHROEDER, 1948; *Raja* (*Okamejei*) ISHIYAMA, 1958; *Gurgesiella* (*Gurgesiella*) DE BUEN,

1959; *Malacoraja* STEHMANN, 1970; *Raja* (*Rajella*) STEHMANN, 1970; *Raja* (*Rostroraja*) HULLEY, 1970; *Gurgesiella* (*Fenestraja*) MCEACHRAN & COMPAGNO, 1982; *Neoraja* MCEACHRAN & COMPAGNO, 1982; 'North Pacific *Raja* Assemblage'; 'Amphi-American *Raja* Assemblage'.

NOTE, that part of the supraspecific taxa under both groups of RAJOIDEI are duplicated from the the first five families above due to our consideration of the various concepts of classification.

The first group of genera and subgenera, of which we present here our odontological results, is listed below under Material.

Material and terminology

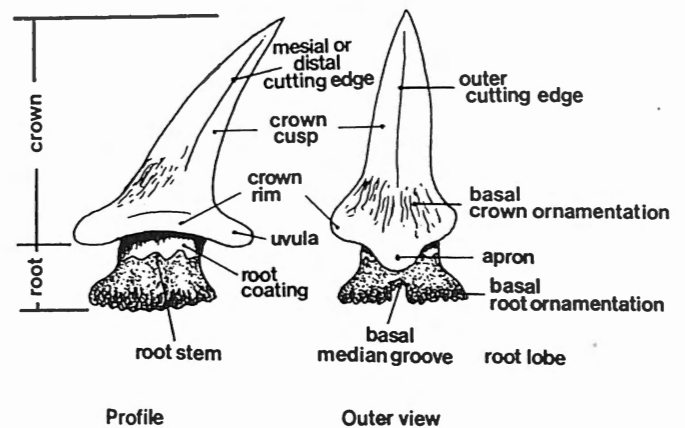
For this fascicle the following 34 specimens of 10 species were examined :

<i>Anacanthobatis</i> (<i>Schroederobatis</i>) <i>americanus</i>	
ISH 260-1981	♀ 353 mm TL
ISH 256-1981	♂ 314 mm TL
ISH 260-1981	♂ 273 mm TL
<i>Anacanthobatis</i> (<i>Schroederobatis</i>) <i>melanosomus</i>	
IRSNB uncatalogued	♀ 270 mm TL
<i>Anacanthobatis</i> (<i>Springeria</i>) <i>longirostris</i>	
ISH 3570-1979	♀ 660 mm TL
ISH 3583-1979	♀ 308 mm TL
ISH 3583-1979	♂ 465 mm TL
<i>Breviraja</i> <i>spinosa</i>	
ISH 3595-1979	♀ 305 mm TL
ISH 3520-1979	♀ 180 mm TL
ISH 3600-1979	♂ 300 mm TL
ISH 3657-1979	♂ 200 mm TL
<i>Dactylobatus</i> <i>armatus</i>	
ISH 3582-1979	♀ 685 mm TL
IRSNB uncatalogued	♀ 160 mm TL
ISH 3582-1979	♂ 270 mm TL
<i>Gurgesiella</i> (<i>Fenestraja</i>) <i>plutonia</i>	
ISH 3542-1979	♀ 267 mm TL
ISH 3522-1979	♂ 232 mm TL
ISH 3580-1979	♀ 147 mm TL
ISH 3522-1979	♂ 232 mm TL
ISH 3580-1979	♂ 164 mm TL
<i>Gurgesiella</i> (<i>Gurgesiella</i>) <i>dorsalifera</i>	
ISH 1931-1968	♀ 526 mm TL
ISH 1948-1968	♂ 417 mm TL
ISH 1943-1968	♂ 383 mm TL
<i>Malacoraja</i> <i>senta</i>	
ISH 251-1985	♀ 571 mm TL
ISH 8-1969	♀ 291 mm TL
ISH 1029-1982	♂ 570 mm TL
ISH 1029-1982	♂ 366 mm TL
<i>Neoraja</i> <i>caerulea</i>	
ISH 175-1983	♀ 277 mm TL
ISH 647-1986	♀ 239 mm TL

ISH 641-1986	♂ 277 mm TL
ISH 641-1986	♂ 187 mm TL
<i>Pavoraja</i> (<i>A</i>) <i>asperula</i>	
ISH uncatalogued	♀ 520 mm TL
ISH uncatalogued	♀ 314 mm TL
ISH uncatalogued	♂ 427 mm TL
ISH uncatalogued	♂ 339 mm TL

Terminology

The odontological characters of batoids differ widely from Selachii and therefore, a modified descriptive terminology for Rajoidei is proposed as used in the descriptions below.



Textfigure 1 - Odontological terminology for rajoid teeth.

Ward (1984) was the first to introduce a specified terminology for describing fossil rajoid teeth. However, further odontological characters for rajoids became known during these investigations, and which are added by modifying Ward's (1984) original drawing (text-figure 1).

The root of the teeth is formed as a stem, often exhibiting a bilobed base with a basal groove. Basal ornamentation may be present on the edges of the root lobes. In addition, root coating may be present in the upper root part. This coating appears to be enameloid, but its nature needs further examination.

The crown shape varies in occlusal outer view from semi-circular, semi-oval, triangular, to quadrangular or even trapezoid. The basal crown rim is mostly rounded, with sometimes an inner uvula or/and outer apron present. The shape and size of the crown cusp, if present, also varies from a small eccentric cone to a elongate or lanceolate cusp, with or without an outer and/or distal

and mesial cutting edges. Sometimes the cusp is replaced by a transversal keel, dividing the crown in an inner and outer part. A basal outer crown ornamentation may be present varying from some coarse costules to a finer reticulation.

Description of the odontological characters

Genus : *Anacanthobatis* VON BONDE & SWART, 1923

So far 11 species are described. The genus *Anacanthobatis* was subdivided into four subgenera by HULLEY (1973, namely *Anacanthobatis*, *Schroederobatis*, *Sinobatis*, *Springeria*, based on seven species known at that time and accepted by HULLEY. Only the subgenera *Schroederobatis* and *Springeria* will be presented here.

Subgenus : *Schroederobatis* HULLEY, 1973

Monotypic with type species *A. americanus* BIGELOW & SCHROEDER, 1962.

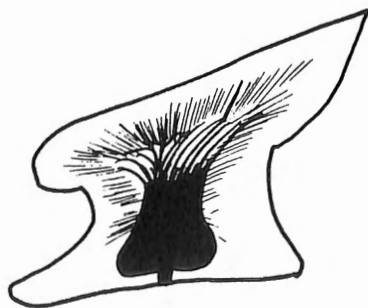
Anacanthobatis (*Schroederobatis*) *americanus*
BIGELOW & SCHROEDER, 1962.
(Plates : 1, 2 & 3; textfigure 2)

Anacanthobatis americanus BIGELOW & SCHROEDER, 1962. Bulletin of the Museum of comparative Zoology, Harvard College, 128 (4) :217.

HETERODONTY

The dentition is gradient monognathic heterodont. Sexual heterodonty is shown in adults only by the presence of a cusp on teeth of males, whereas females have a transversal keel.

Only teeth of males present ontogenetic heterodonty by bearing a small cone without cutting edges in juveniles, which grows to a distinct cusp in maturing specimens.



Textfigure 2
Schroederobatis tooth : histological cross-section.

VASCULARIZATION

The teeth show an adapted kind of holaulacorhizy or secondary hemiaulacorhizy, with a large pulp cavity in the root area, from which the vascular tubes of the circumpulpar dentine radiate into crown and root part. Osteodentine was not observed, and inner lateral foramina are absent.

FEMALES

The crown base is semi-circular in occlusal view. Inner and outer faces are divided by a bluntly rounded transversal keel. Uvula, apron or ornamentation absent. The inner face is slightly concave, the outer one slightly convex.

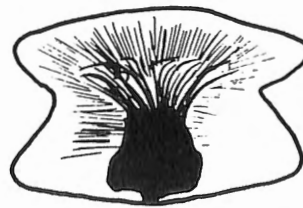
The root stem is very low and oval to almost circular in cross-section. Although the root base gradually widens in all directions, it is not bilobed, and the root base outer margin is weakly undulated. A basal groove is poorly developed, absent, or sometimes replaced by an inner and/or outer foramen. Root coating is absent.

MALES

The crown base of males is semi-circular to semi-quadrangular in occlusal view. The anterior teeth bear a well developed cusp at inner crown edge, which is directed inward, oblique distally, but with cutting edges curving upward.

Lateral teeth show a higher cusp, which is stronger oblique distally with cutting edges curving stronger upward. The commissural teeth possess a lower cusp, which is not directed distally but upright. Apron, uvula or ornamentation absent. The inner surface is concave, the outer one flat to slightly convex.

The root stem is very low and oval to almost circular in cross-section. Although the root base gradually widens in all directions, it is not bilobed, and the root base outer margin is weakly undulated. A basal groove is poorly developed, absent or sometimes replaced by inner and/or outer foramina. Root coating is absent.



Textfigure 3 – *Springeria* tooth : histological cross-section.

Subgenus : *Springeria* BIGELOW & SCHROEDER, 1951

Originally described as a genus for *S. folirostris*, the taxon was ranked as subgenus of *Anacanthobatis* by HULLEY (1973), who assigned two species : *A. folirostris* (BIGELOW & SCHROEDER, 1951) as type species and *A. longirostris* BIGELOW & SCHROEDER, 1962.

Anacanthobatis (Springeria) longirostris
BIGELOW & SCHROEDER, 1962
(Plates : 4, 5 & 6; textfigure 3)

Anacanthobatis longirostris BIGELOW & SCHROEDER, 1961. Bulletin of the Museum of comparative Zoology, Harvard College, 128 (4) : 223, figs 17 and 18.

HETERODONTY

The dentition is gradient monognathic heterodont. Sexual and ontogenetic heterodonty absent.

VASCULARIZATION

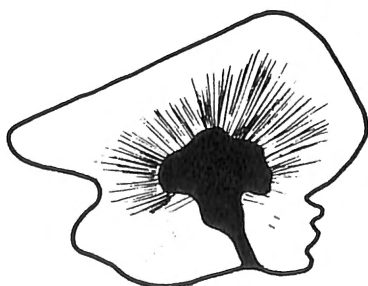
The teeth show an adapted kind of holaulacorhizy or secondary hemiaulacorhizy, with a large pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine was not observed, and inner lateral foramina are absent.

FEMALES AND MALES

The crown base is more or less oval in occlusal view. Anterior teeth bear a low cusp with mesial and distal cutting edges, which are replaced by a transversal keel on lateral and commissural teeth. The crown rim has a sharp, irregularly shaped ridge of costules around the outer face. The outer surface of the crown is slightly convex, the inner one is concave.

An apron or ornamentation are absent. However, a small, poorly developed uvula is present.

The root stem is low and is ovally shaped in cross-section. The root base gradually widens in all directions, is bilobed, and has a smooth root base edge. A well developed basal groove is present, which is deeper than wide and encloses one or two small central apertures. Some teeth even possess two basal grooves. Root coating is absent.



Textfigure 4 – *Breviraja* tooth : histological cross-section.

Genus : *Breviraja* BIGELOW & SCHROEDER, 1948

This genus comprises the following species : *B. claramaculata*, *B. colesi*, *B. markeli*, *B. nigriventralis*, *B. schroederi* and *B. spinosa*. The latter one is the type species.

Breviraja spinosa BIGELOW & SCHROEDER, 1950
(Plates : 7 to 11; textfigure 4)

Breviraja spinosa BIGELOW & SCHROEDER, 1950, Bulletin of the Museum of comparative Zoology, Harvard College, 103 (7) : 400.

HETERODONTY

The dentition is gradient monognathic heterodont. Sexual heterodonty is shown in adults only by the presence of a rather high cusp on anterior teeth of males, which becomes lower and broader on commissural teeth. Females have a lower cusp, with a small central cone. Ontogenetic heterodonty is documented by much lower cusps on teeth of juveniles.

VASCULARIZATION

The teeth of this genus have an adapted kind of holaulacorhizy, in that the vascular tubes of the circumpulpar dentine radiate into crown and root part from a large pulp cavity in the root. Osteodentine was not observed, and inner lateral foramina are absent.

FEMALES

The crown base of females is semi-triangular in occlusal view. Inner and outer faces are divided by blunt mesial and distal cutting edges. An apron or ornamentation are absent, but a poorly developed inner uvula is present. The inner face shows a slightly concave surface, the outer one is slightly convex.

The root stem is very low and is ovally to almost circularly shaped in cross-section. The root base strongly widens in all directions, is bilobed, and the root base edge is weakly undulated. A well developed basal groove is deep and encloses a rather large central aperture. Root coating is absent.

MALES

The crown base of males is semi-triangular in occlusal view. The anterior and lateral teeth bear a well developed cusp, which more or less directed inward and slightly oblique distally [see above]. Both mesial and distal cutting edges curve weakly [which way?]. The cusp is lower on teeth toward the commissure. An apron or ornamentation is absent, but a poorly developed inner uvula is present. The inner surface is concave, the outer one flat to slightly convex.

The root stem is very low and oval to almost circular in cross-section. The root base strongly widens in all directions, is bilobate, and shows a weakly undulated root base outer margin. A well developed basal groove is deep and encloses a large central aperture. Root coating is absent.

Genus : *Dactylobatus* BEAN & WEED, 1909

The genus is monotypic with the type species *Dactylobatus armatus*. MCEACHRAN & MIYAKE (1990b : 326) list *D. clarki* as a second species but give no explanation for the reallocation of *Raja clarki*.

Dactylobatus armatus BEAN & WEED, 1909
(Plates : 12 & 13; textfigure 5)

Dactylobatus armatus BEAN & WEED, 1909. Proceedings of the United States National Museum 36 : 459.

HETERODONTY

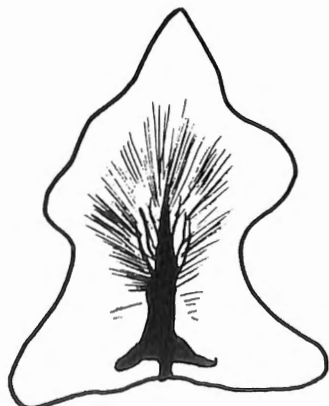
The dentition is gradient monognathic heterodont. Although an adult male is not known so far, the well developed cusp on teeth of the adult female, here described, makes it plausible, that sexual, as well as ontogenetic heterodonty is not to be expected.

VASCULARIZATION

The teeth of this genus show an adapted kind of holaulacorhizy or secondary hemiaulacorhizy, in that vascular strings penetrate the crown section from a rather high, narrow pulp cavity. Both, pulp cavity and vascular string have tubes of the circumpulpar dentine radiating into root and crown. Osteodentine was not observed, and inner lateral foramina are absent.

FEMALES

The crown base is more or less circular in occlusal view. The well developed, elongated crown is directed



Textfigure 5 – *Dactylobatus* tooth : histological cross-section.

inward, and the mesial and distal cutting edges are blunt and rounded. The outer surface is slightly convex, the inner one strongly concave.

An apron or ornamentation are absent. However, a well developed uvula is present on the inner crown part [? surface].

The root stem is moderately high and oval to semi-triangular in cross-section. The root base strongly widens in all directions, presenting a well developed bilobation with smooth or slightly undulating root base outer margin. A well developed, relatively broad but shallow basal groove encloses an extremely large central aperture. The basal groove may be closed on posterior teeth, so that only one or two large foramina remain. Root coating is present half way down the root stem.

Genus : *Gurgesiella* DE BUEN, 1959

This genus was subdivided into two subgenera *G. (Gurgesiella)* and *G. (Fenestraja)* by MCEACHRAN & COMPAGNO (1982)

Subgenus : *Fenestraja* MCEACHRAN & COMPAGNO, 1982

This subgenus comprises the species : *G. atripinna*, *G. cubensis*, *G. ishiyamai*, *G. mamillidens*, *G. plutonia* (type species), *G. sibogae* and *G. sinusmexicanus*.



Textfigure 6 – *Fenestraja* tooth : histological cross-section.

Gurgesiella (Fenestraja) plutonia (GARMAN, 1881)
(Plates : 14 to 17; textfigure 6)

Raja plutonia GARMAN, 1881. Bulletin of the Museum of comparative Zoology, Harvard College, 8 : 236.

HETERODONTY

The dentition is gradient monognathic heterodont. Sexual heterodonty is presented in adults only by a rather elongated cusp on anterior teeth of males, which becomes lower and broader and loses [do you mean that?] mesial and distal cutting edges on teeth toward the commissure. Females also have a well developed but lower cusp on anterior, lateral and commissural teeth, which gradually become lower [where ?] and

possess mesial and distal cutting edges. Ontogenetic heterodonty is only documented in juvenile males, teeth of which have a lower cusp with mesial and distal cutting edges.

VASCULARIZATION

The teeth show an adapted kind of holaulacorhizy in that semi-parallel tubes of the circumpulpar dentine radiate from the vascular string into crown and root from a large and high pulp cavity in the root. Osteodentine was not observed, and inner lateral foramina are absent.

FEMALES

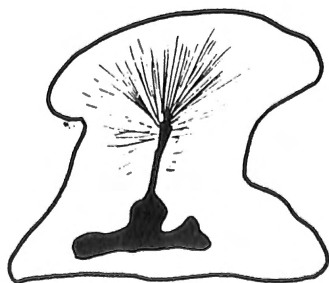
The crown base is semi-oval in occlusal view. Inner and outer faces are not strictly divided, and mesial and distal cutting edges are absent. A semi-central cone is present on the crown. An apron, uvula and ornamentation are absent. The inner face shows a slightly concave surface, the outer one is slightly convex.

The root stem is moderately high and more or less oval in cross-section. The root widens at the base [see above] but is not bilobed. The root base edge is weakly undulated. A basal groove is overgrown, and only enlarged outer and inner apertures remain. Root coating is only present on the crown-root junction.

MALES

The crown base is semi-circular to semi-triangular in occlusal view. The anterior teeth have a well developed, broad based but narrow and elongated cusp, more or less directed inward and slightly oblique distally [see above]. Lateral and commissural teeth have a much lower cusp. Both, mesial and distal cutting edges are absent in anterior but present in lateral and commissural teeth. The outer crown surface is strongly convex on anterior but rather plain on lateral and commissural teeth. An apron, uvula and ornamentation are absent.

The root stem is moderately high and oval to almost circular shaped in cross-section. The root base strongly widens in all directions but is not bilobed. A basal groove is overgrown, and only enlarged outer and inner apertures remain. Root coating is only present on the crown-root junction.



Textfigure 7 – *Gurgesiella* tooth : histological cross-section.

Subgenus : *Gurgesiella* DE BUEN, 1959

This subgenus comprises the species : *G. atlantica*, *G. dorsalifera* (type species) and *G. furvescens*.

Gurgesiella (*Gurgesiella*) *dorsalifera*

MCEACHRAN & COMPAGNO, 1980

(Plates : 18 to 21; textfigure 7)

Gurgesiella (*Gurgesiella*) *dorsalifera* MCEACHRAN & COMPAGNO, 1980. Archiv für Fischereiwissenschaft, 31 (1) : 1-14 figs. 1-8.

HETERODONTY

The dentition is gradient monognathic heterodont. Sexual heterodonty is present in adults only, in that males have a rather elongated cusp on anterior teeth, which becomes lower and broader on teeth toward the commissure. Females also have a well developed but lower cusp on anterior, lateral and commissural teeth, which gradually become lower. Ontogenetic heterodonty is only documented in juvenile males, teeth of which have a low cusp only.

VASCULARIZATION

The teeth show an adapted kind of holaulacorhizy, in that a broad canal runs vertically into the crown area from a large but low pulp cavity in the root. The semi-parallel tubes of the circumpulpar dentine spread out from this canal into crown and root. Osteodentine was not observed, and inner lateral foramina are absent.

FEMALES

The crown base is semi-oval in occlusal view. Inner and outer faces are divided by sharp mesial and distal cutting edges. An apron or ornamentation are absent, but a well developed inner uvula is present. The inner face shows a slightly concave surface, the outer one is slightly convex.

The broad root is moderately high and more or less oval in cross-section. The root widens at the base but is not bilobate. The root base edge is weakly waved [see above]. Only remains of a basal groove are one or two enlarged outer and inner apertures. Root coating is present on upper third of the root stem.

MALES

The crown base is semi-circular in occlusal view. The anterior and lateral teeth bear a well developed cusp, which is more or less directed inward and slightly oblique distally. Both, mesial and distal cutting edges curve weakly. A poorly developed outer cutting edge is present on the upper part of the outer crown surface.

The cusp is lower on posterior teeth but has well developed cutting edges. The outer crown surface is rather plain, and an outer cutting edge is absent. An apron or ornamentation are absent, but a well developed inner uvula is present.

The root stem is moderately high and oval to almost circular in cross-section. The root base strongly widens [see above] but is not bilobed. A basal groove is overgrown and only inner and outer apertures remain. Root coating is present on the upper third of the root stem.

Genus : *Malacoraja* STEHMANN, 1970

This genus comprises 3 species : *M. krefftii*, *M. senta* and *M. spinacidermis* (type species under junior synonym *Raja mollis*).

Malacoraja senta (GARMAN, 1885)
(Plates : 23 & 24; textfigure 8)

Raja senta GARMAN, 1885. Proceedings of the United States National Museum, 8 : 43.



Textfigure 8 – *Malacoraja* tooth : histological cross-section.

HETERODONTY

The dentition is gradient monognathic heterodont. Sexual heterodonty is present in adults only, in that teeth of males have a well developed, elongated cusp, which is a low, more or less central cone on teeth of females only.

Only males present ontogenetic heterodonty by a more ovally shaped crown in occlusal view, with a distinct cusp, which is still a small cone in juveniles, while in females only a more ovally shaped crown in occlusal view is significant for the ontogenetic heterodonty.

VASCULARIZATION

The teeth show an adapted kind of holaulacorhizy or secondary hemiaulacorhizy, in that the vascular tubes of the circumpulpar dentine radiate into crown and root from a large and high pulp cavity in the root. Osteodentine was not observed, and inner lateral foramina are absent.

FEMALES

The crown base is semi-circular in occlusal view. Inner and outer faces are not strictly divided. The poorly developed cusp is reduced to a cone, without mesial or distal cutting edges. The inner face is rather concave, the outer is convex. An apron or ornamentation are absent, but a poorly developed uvula is present.

The root stem is moderately high and more or less oval in cross-section. The root base gradually widens in all directions and is bilobed with weakly undulated root base outer margins. A basal groove is poorly developed, absent, or sometimes overgrown with only inner and/or outer foramina remaining. Root coating is present on the upper half of the root stem.

MALES

The crown base is semi-circular in occlusal view. The anterior teeth bear a well developed cusp, which is directed inward and slightly oblique distally but lacks true mesial or distal cutting edges.

The cusp is higher, less oblique distally on lateral teeth, and gradually becomes lower and more oblique on teeth closer to the commissure. The inner surface is concave, the outer one is flat to slightly convex, and both surfaces are not strictly divided. An apron or ornamentation are absent but a poorly developed uvula is present.

The root stem is moderately high and more or less oval in cross-section. The root base gradually widens in all directions and is bilobed with weakly undulated root base outer margins. A basal groove is poorly developed, absent or sometimes overgrown with only inner and/or outer foramina remaining. Root coating is present on the upper half of the root stem.



Textfigure 9 – *Neoraja* tooth : histological cross-section.

Genus : *Neoraja* MCEACHRAN & COMPAGNO, 1982

This genus comprises the species *N. africana*, *N. caerulea* (type species), *N. carolensis* and *N. stehmanni*.

Neoraja caerulea (STEHMANN, 1976)
(Plates : 25, 26 & 27; textfigure 9)

Breviraja caerulea STEHMANN, 1976. Archiv für Fischwissenschaft, 27 (2) : 97-114

HETERODONTY

The dentition is gradient monognathic heterodont. Sexual heterodonty is presented in adults only, in that males show a well developed, elongated cusp on teeth of the anterior and antero-lateral rows. The lateral and commissural teeth of males and females show a low, more or less central cone and hardly sexual heterodonty. Males present ontogenetic heterodonty in anterior teeth, which only have cusps with a small cone in juveniles.

VASCULARIZATION

The teeth present an adapted kind of holaulacorhizy, in that from a large, but low pulp cavity in the root section several vascular canals enter the crown section. From these canals the the vascular tubes of the circumpulpar dentine radiate into the crown section. Osteodentine was not observed, and inner lateral foramina are absent.

FEMALES

The crown base of anterior and commissural rows of females is semi-circular in occlusal view. The crowns in lateral rows are more ovaly-shaped in occlusal view. Inner and outer faces are not strictly divided. The poorly developed cusp is reduced to a cone, without mesial or distal cutting edges. The inner face shows a rather concave surface, while the outer one is convex. An apron, ornamentation, or a true uvula are absent (an uvula may develop on anterior teeth). The root stem is moderately high and more or less oval in cross-section. The root base gradually widens in all directions and is bilobed with multilobed root base outer margins. A extremely shallow, basal groove is poorly developed, absent, or sometimes overgrown with only inner and/or outer foramina remaining. Root coating is present on the upper part of the root stem.

MALES

The crown base of anterior and commissural teeth is semi-circular in occlusal view. Tooth crowns in lateral rows are more oval in occlusal view. The anterior teeth bear a well developed cusp, which is broad based with a narrow, elongated, inward directed cone lacking true mesial or distal cutting edges.

The cone of the cusp strongly reduces in height in lateral teeth and further gradually in commissural teeth. The inner surface is concave, the outer one is flat to slightly convex. They are not strictly divided. An apron or ornamentation are absent, but a poorly developed uvula is present.

The root stem is moderately high and more or less oval in cross-section. The root base gradually widens in all directions and is bilobed with multilobed root base outer margins. An extremely shallow, basal groove is poorly

developed, absent, or sometimes overgrown with only inner and/or outer foramina remaining. Root coating is present on the upper half of the root stem.

Genus : *Pavoraja* WHITLEY, 1939

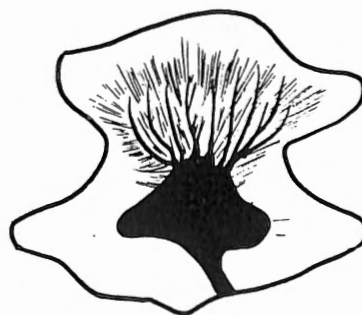
This genus was subdivided by MCEACHRAN (1984) into two subgenera *Pavoraja* (*Pavoraja*) and *Pavoraja* (A), the latter still unnamed. YEARSLEY & LAST (1992) introduced a third subgenus *P. (Insentiraja)*.

Subgenus : *Pavoraja* (A), *sensu* MCEACHRAN (1984)

This subgenus comprises the species *P. asperula* (type species) and *P. spinifera*.

Pavoraja asperula (GARRICK & PAUL, 1974)
(Plates : 28, 29 & 30; textfigure 10)

Bathyraja asperula GARRICK & PAUL, 1974. Journal of the Royal Society of New Zealand, 4 (3) : 363, figs 8 and 10.



Textfigure 10 – *Pavoraja* tooth : histological cross-section.

HETERODONTY

The dentition is gradient monognathic heterodont. Sexual heterodonty is presented in adults only, in that males bear an elongated cusp on anterior teeth, which becomes lower on teeth toward the commissure. Females only possess a low semi-central cone. Ontogenetic heterodonty is documented only in juvenile males, which have a low cusp.

VASCULARIZATION

The teeth show an adapted kind of holaulacorhizy or secondary hemiaulacorhizy, in that a large pulp cavity in the root section, from which semi-parallel tubes of the circumpulpar dentine radiate into crown and root part [see above]. Osteodentine was not observed, and inner lateral foramina are absent.

FEMALES

The crown base is semi-oval in occlusal view. Inner and outer faces are not strictly divided and, mesial and distal cutting edges are absent. An apron, uvula and ornamentation are absent. A semi-central cone is present on the cusp. The inner face shows a slightly concave surface, the outer one is slightly convex. The inner and outer basal crown rim is irregularly undulated.

The root stem is moderately high and more or less oval in cross-section. The root base gradually widens in all directions and is bilobed. The root base outer margin in weakly undulated. A wide, shallow, basal groove is poorly developed, absent, or sometimes overgrown with only inner and/or outer foramina remaining. Root coating is present on the upper quarter of the root stem.

MALES

The crown base is semi-circular in occlusal view. The anterior and lateral teeth bear a well developed, broad based, narrow and elongated cusp, which is more or less directed inward and slightly oblique distally. Mesial and distal cutting edges are absent. Inner and outer surfaces are convex, and the inner and outer basal crown rims are irregularly undulated. The cusp becomes lower on teeth toward the commissure, the outer crown surface plainer. An apron, uvula and ornamentation are absent.

The root stem is high and more or less circular in cross-section. The root base gradually widens in all directions and is bilobed. The root base outer margin in weakly undulated. A well developed basal groove encloses a large foramen. Root coating is present on the upper part of the root stem.

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Bibliography

BIGELOW, H.B. & SCHROEDER, W.C. - 1953. Sawfishes, Guiltarfishes, Skates and Rays (pp. 1-514). In : TEE-VAN, J. *et al.* (Eds). Fishes of the Western North Atlantic. *Memoir Sears Foundation for Marine Research*, 1 (2) : I-XV + 588 pp.

CLARK, R.S. - 1926. Rays and Skates, a revision of the European species. *Scientific Investigations of the Fishery Board of Scotland*, 1926 (1) (Text) : 1-66, figs 1-42, pls 1-36.

COMPAGNO, L.J.V. - 1984. FAO species catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes. *FAO Fisheries Synopsis No. 125*, vol. 4 (1) : iii-viii, 1-249.

COMPAGNO, L.J.V. - 1984. FAO species catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniformes. *FAO Fisheries Synopsis No. 125*, vol. 4 (2) : iii-x, 251-655.

COMPAGNO, L.J.V. - 1984. Sharks of the Order Carcharhiniformes. *Princeton University Press, Princeton, New Jersey* : vii-xxi, 3-486, figs 1.1-21.10, pls 1-35.

DIDIER, D.A. (in press). Phylogenetic systematics of extant chimaeroid fishes (Holocephali, Chimaeroidei). *Bulletin of the American Museum of Natural History*.

GARMAN, S.W. - 1913. The Plagiostomia (sharks, skates and rays). *Memoirs of the Museum of Comparative Zoology, Harvard College*, 36 : xiii + 515 pp., 75 pls.

HULLEY, P.A. - 1970. An investigation of the Rajidae of the west and south coasts of Southern Africa. *Annals of the South African Museum*, 55 (4) : 151-220, 21 figs, 13 pls.

HULLEY, P.A. - 1973. Interrelationships within the Anacanthobatidae (Chondrichthyes, Rajoidea), with a description of the lectotype of *Anacanthobatis marmoratus* VON BONDE & SWART, 1923. *Annals of the South African Museum*, 62 (4) : 131-158.

ISHIYAMA, R. - 1958. Studies on the Rajid Fishes (Rajidae) found in the Waters around Japan. *Journal of the Shimonoseki College of Fisheries*, 7 (2, 3) : 193-394.

MCEACHRAN, J.D. - 1984. Anatomical Investigations of the New Zealand Skates *Bathyraja asperula* and *B. spinifera*, With an Evaluation of Their Classification Within the Rajoid-ei (Chondrichthyes). *Copeia* 1984 (1) : 45-58.

MCEACHRAN, J.D. & COMPAGNO, L.J.V. - 1982. Interrelationships of and within *Breviraja* based on anatomical structures (Pisces : Rajoidei). *Bulletin of Marine Science*, 32 (2) : 399-425.

MCEACHRAN, J.D. & MIYAKE, T. - 1990a. Phylogenetic Interrelationships of Skates : A Working Hypothesis (Chondrichthyes Rajoidei). In Pratt Jr., H.L., Gruber, S.H. & Taniuchi, T. (Eds.) Elasmobranchs as Living Resources : Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries : Proceedings of the Second United States-Japan Workshop East-West Center. *NOAA Technical Report NMFS 90* : 285-304.

MCEACHRAN, J.D. & MIYAKE, T. - 1990b. Zoogeography and Bathymetry of Skates (Chondrichthyes, Rajoidei). In Pratt Jr., H. L., Gruber, S.H. & Taniuchi, T. (Eds.) Elasmobranchs as Living Resources : Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries : Proceedings of the Second United States-Japan Workshop East-West Center. *NOAA Technical Report NMFS 90* : 305-326.

NORMAN, J.R. - 1926. A Synopsis of the Rays of the Family Rhinobatidae, with a Revision of the Genus *Rhinobatus*. *Proceedings of the Zoological Society of London*, 1926 (4) : 941-982.

MENNI, R.C. - 1972. *Raja* (*Atlantoraja*) subgen. nov. y lista critica de los Rajidae Argentinos (Chondrichthyes, Rajiformes). *Revista del Museo de La Plata (N.S.) (Zoologia)*, 11 : 165-173.

MENNI, R.C. - 1973. Rajidae del Litoral Bonarense. I. Especies de los generos *Raja*, *Bathyrāja* y *Sympterygia* (Chondrichthyes). *Physis (A)*, 32 (85) : 413-439.

STEHMANN, M. - 1970. Vergleichend morphologische und anatomische Untersuchungen zur Neuordnung der Systematik der nordostatlantischen Rajidae (Chondrichthyes, Batoidei). *Archiv für Fischereiwissenschaft*, 21 (2) : 73-164.

STEHMANN, M. - 1986. Notes on the systematics of the Rajid genus *Bathyrāja* and its distribution in the World Ocean. In Uyeno, T. *et al.* (eds.): *Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes. Ichthyological Society of Japan*, Tokyo : 261-168.

WARD, D.J. - 1984. Additions to the fish fauna of the English Palaeogene. 5. A new species of *Raja* from the London Clay. *Tertiary Research*, Leiden 6 (2) : 65-68.

YEARSLEY, G. & LAST, P. - 1992. *Pavoraja* (Insentiraja) *laxipella*, a new subgenus and species of skate (Chondrichthyes : Rajoidei) from the western Pacific. *Copeia* 3 : 839-850.

General glossary

(applying to all previous issues of this series).

CONCERNING THE JAW

Anterior

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

Commissural

Tooth position near the end of jaw.

Dignathic

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

File

Tooth row from symphysis toward end of jaw.

Heterodonty

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

Homodonty

Uniform tooth morphology within a tooth file

Lateral

Tooth positions half way along the jaw.

Longitudinal

Symphysial/commissural direction of a tooth file.

Monognathic

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

Parasymphysial

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

Posterior

Tooth positions toward the angle of 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 vascularization, E. Casier (1947) recognised and described 4 phylogenetically significant root types within the orthodont histotypes of elasmobranch teeth.

Anaulacorhizid

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

Hemiaulacorhizid

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

Holaulacorhizid

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

Polyaulacorhizid

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

Apron

Expansion of the central part of the outer crown base.

Basal

Bottom face concerned.

Costules

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

Crown

Enamelated tooth part.

Distal

Tooth edge or part toward angle of jaws.

Histotype

Type of internal tooth vascularization.

Inner face

Viewed from inside the mouth.

Longitudinally

Apico-basally directed structuring on a tooth.

Median groove

Groove running from the inner root base to the inner crown-root junction, dividing a holaulacorhizid type

- of root into two root lobes. It includes the main foramina of the vascularization system.
- 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-holaulacorhizy**
Modification of the holaulacorhizid type of root, combining a shallow median groove and an extremely expanded pulp cavity.
- Orthodont**
Histotype of vascularization, by which a tooth is supplied primarily by an internal pulp cavity radiating into numerous tiny canals penetrating the orthodontine layer.
- Osteodont**
Histotype of vascularization, by which a tooth is supplied without any pulp cavity by scattered tiny cavities and canals penetrating the osteodontine layer of the root and the internal crown material.
- Outer face**
Viewed from outside the mouth.
- Pseudo-apron**
Apron-like vertical ridges that appear sometimes on lateral and posterior teeth.
- Pseudo-osteodont**
The former pulp cavity of an originally orthodont histotype of tooth being filled secondarily with osteodontine.
- Pulp cavity**
Cavity inside the tooth from which the vascularization is spread via canaliculi.
- Root**
Non-enamelled tooth part, that forms the junction with the jaw and provides vascularization of the tooth.
- Root coating**
Coating on the upper part of the root (probably enameliod)
- Root stem**
Root part between the crown base and root lobe section.
- Secondarily anaulacorhizid**
Median groove of a holaulacorhizid type of anaulacorhizid root totally overgrown to form a closed tube internally connected or merged with the pulp cavity
- Secondarily**
Median groove of holaulacorhizid type of hemiaulacorhizid root overgrown to various extent, but
- Striae**
Vertical ridges running from crown base toward apex.
Terminally groove or pores still open.

Sulcus

Groove developed by the primary vascularization 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 poly-aulacorhizid 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 plates of isolated teeth of one juvenile (male or female) and of both male and female adults are presented for each supraspecific taxa.

The plates have a consistent composition : upper teeth are presented with their cusps downward and lower teeth with their cusps upward.

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

Legend

a = anterior position
l = lateral position

p = posterior position
c = commissural position

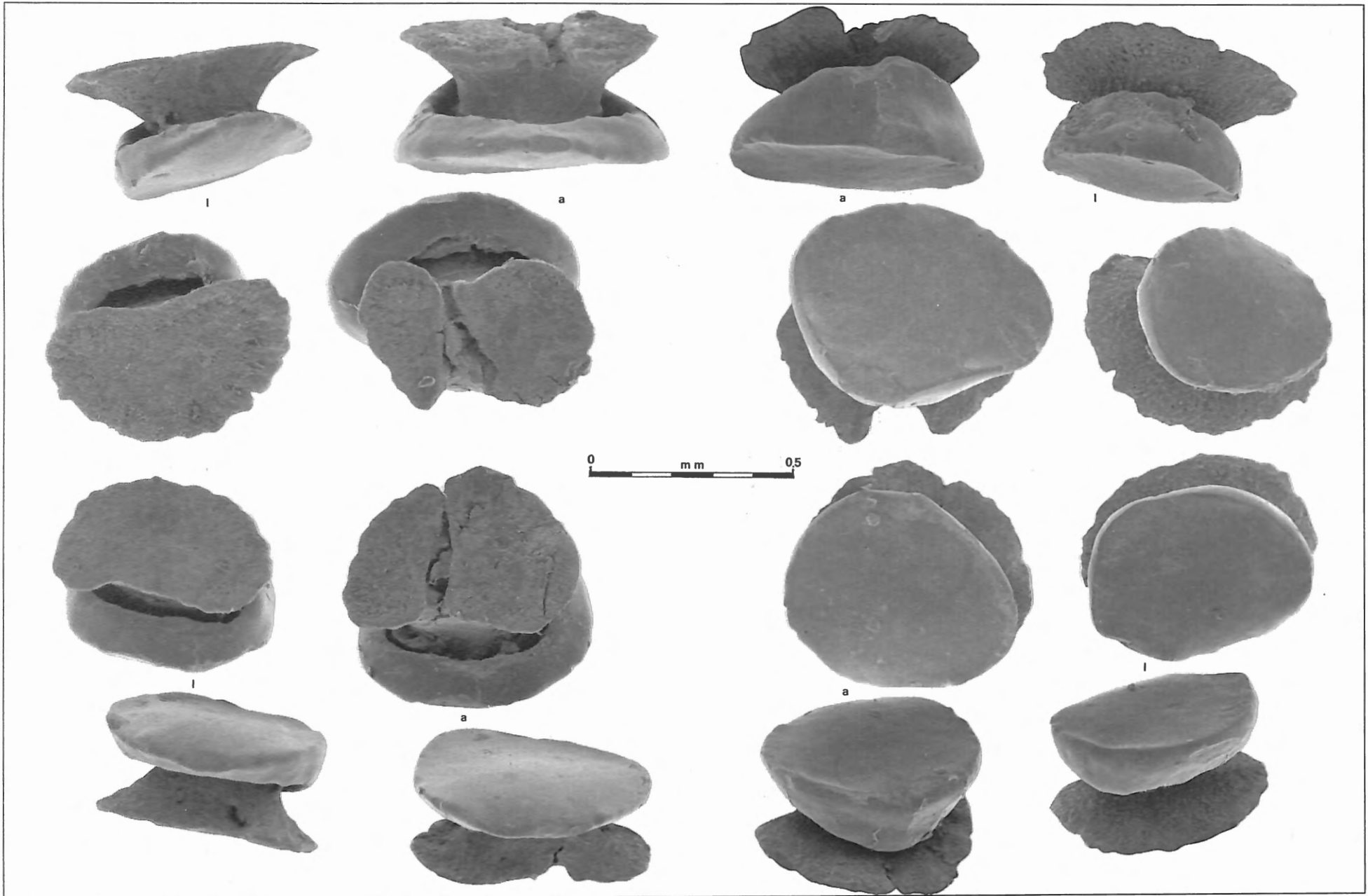


Plate 1 – *Anacanthobatis (Schroederobatis) americanus* BIGELOW & SCHROEDER, 1962. Adult ♀ ISH 260-1981, 353 mm tl., Suriname.

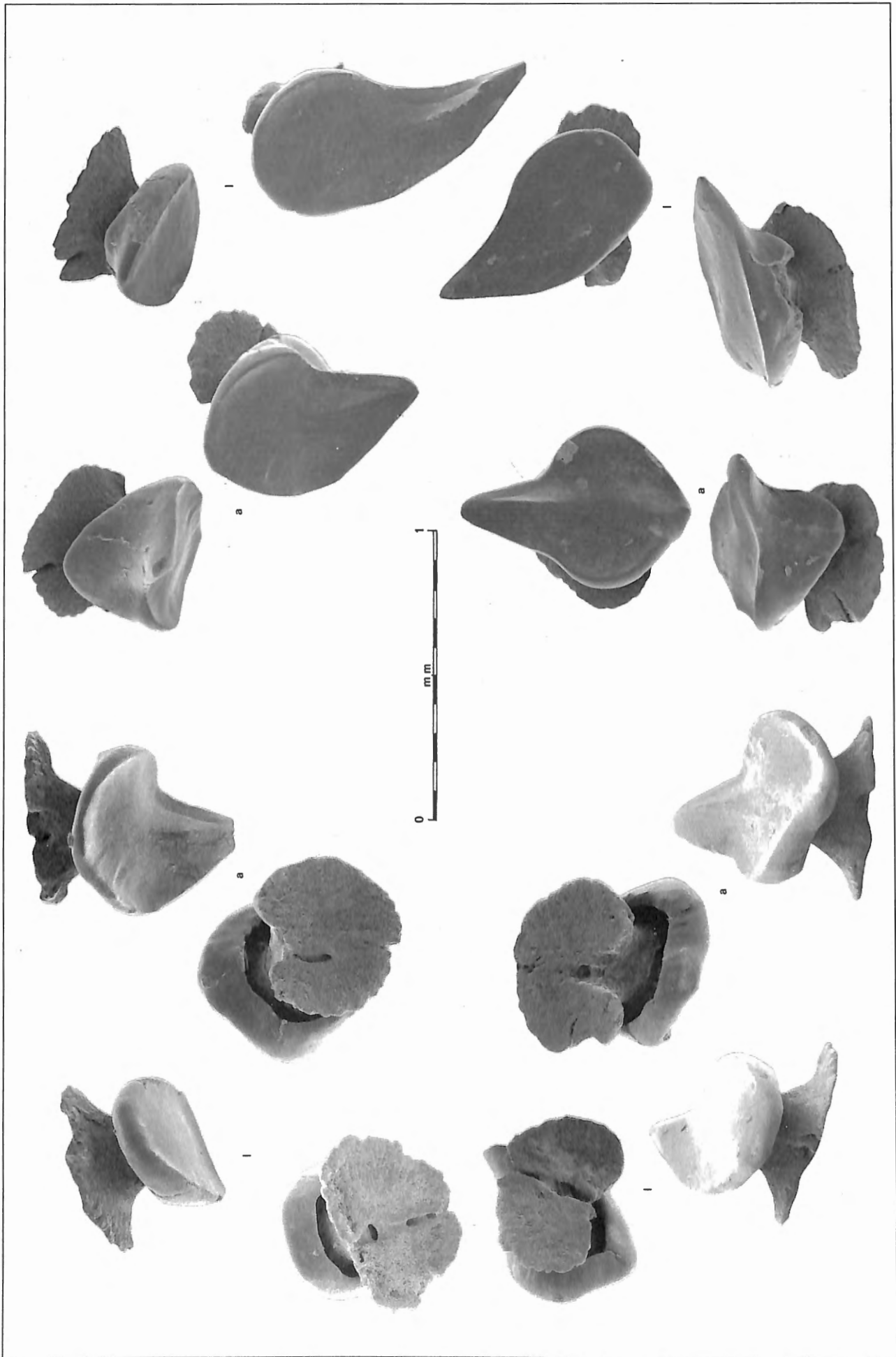


Plate 2 - *Anacanthobatis (Schroederobatis) americanus* BIGELOW & SCHROEDER, 1962. Adult ♂ ISH 256-1981, 314 mm tl., Suriname.

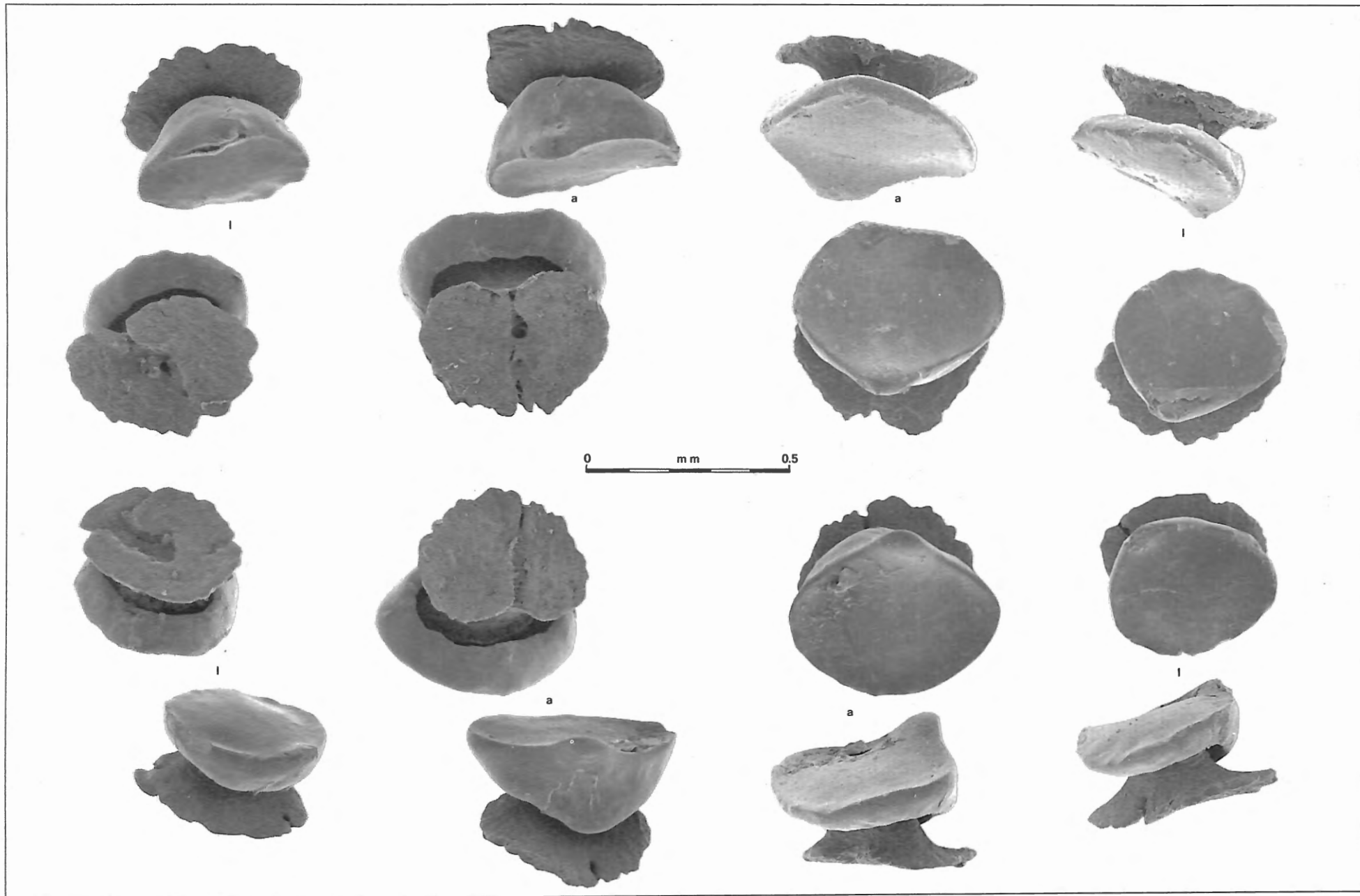


Plate 3 – *Anacanthobatis (Schroederobatis) americanus* BIGELOW & SCHROEDER, 1962. Juvenile ♂ ISH 260-1981, 273 mm tl., Suriname.

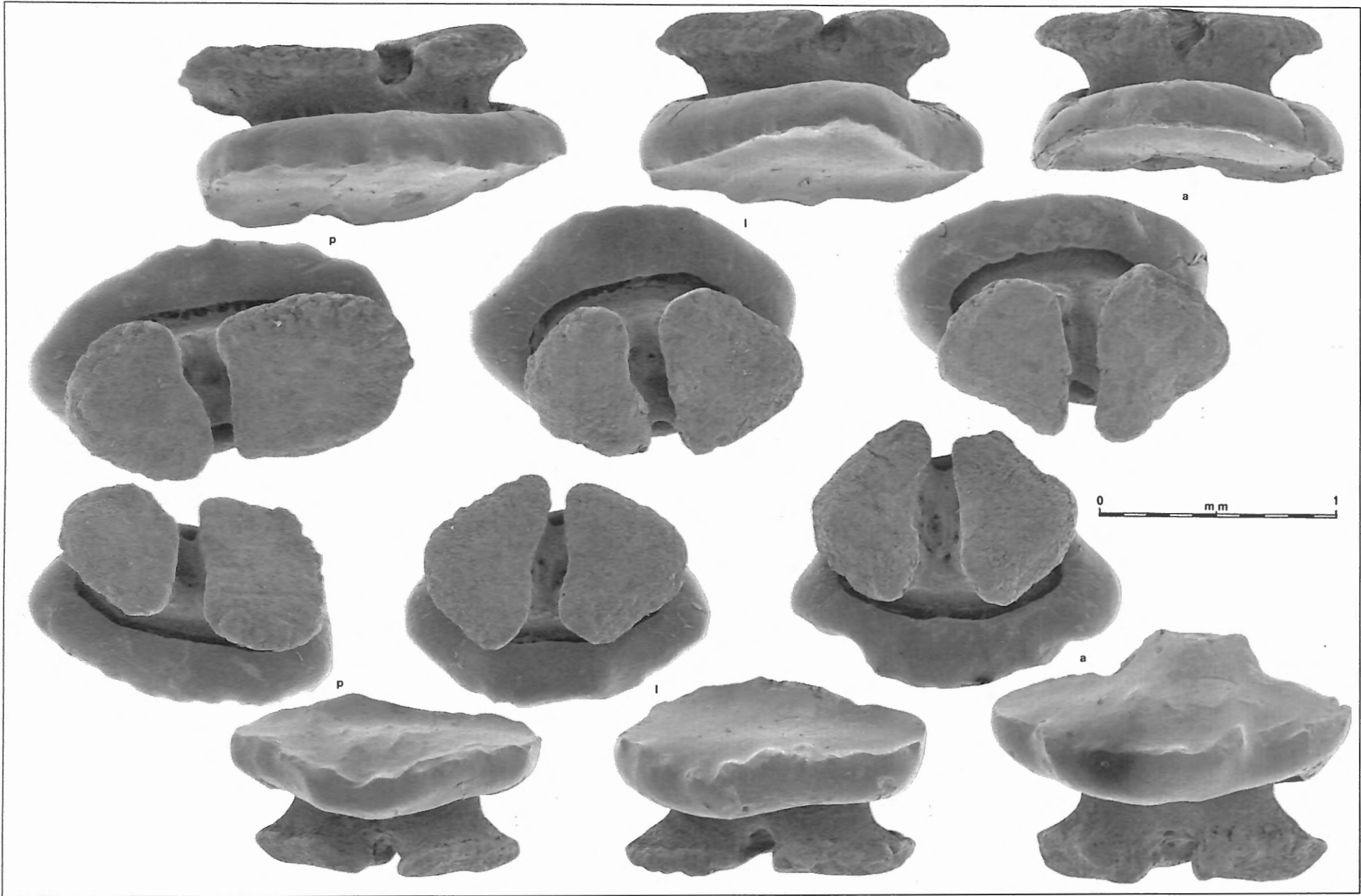


Plate 4 – *Anacanthobatis (Springeria) longirostris* BIGELOW & SCHROEDER, 1962. Adult ♀ ISH 3570-1979, 660 mm tl., Florida.

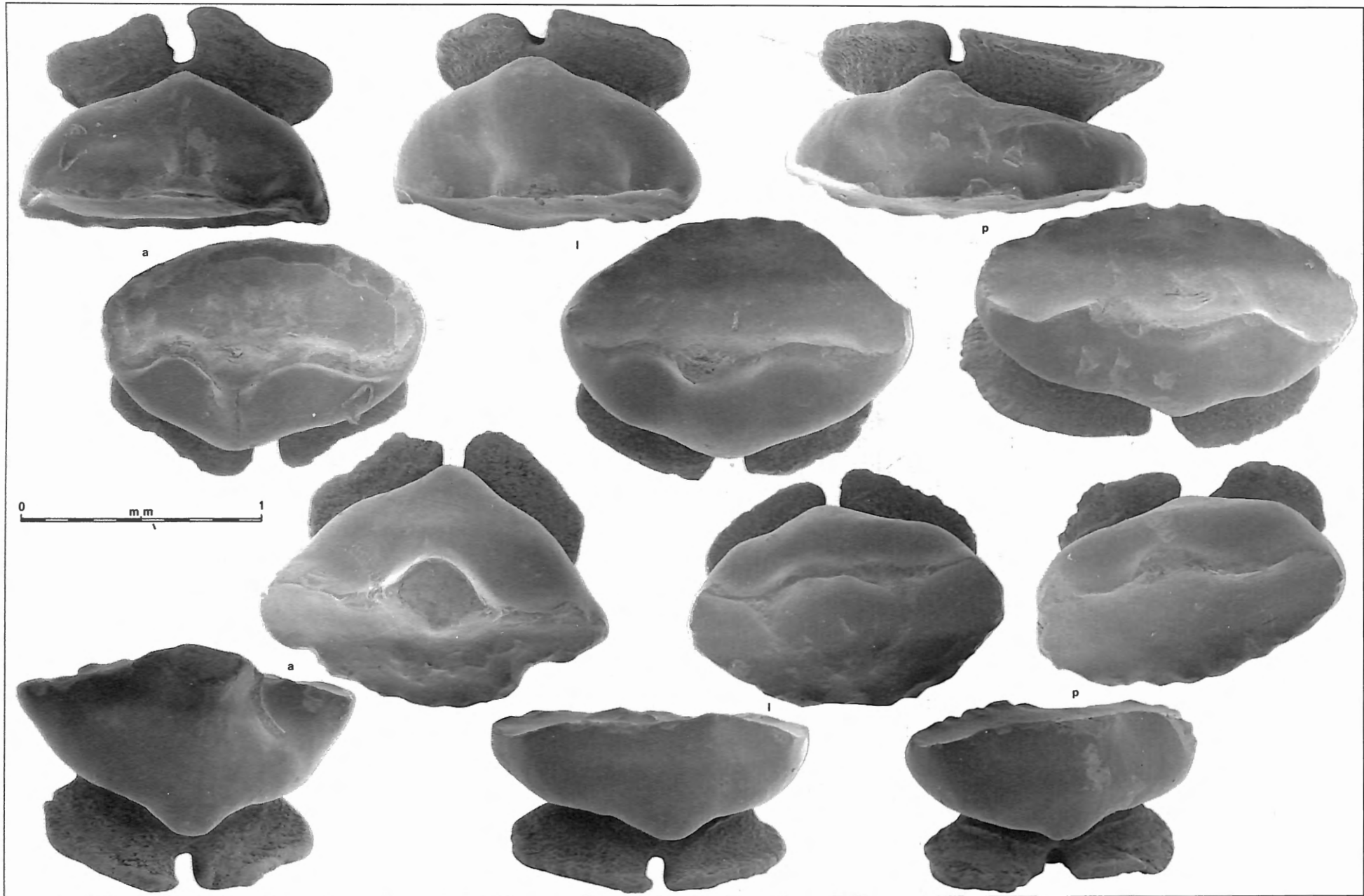


Plate 5 – *Anacanthobatis (Springeria) longirostris* BIGELOW & SCHROEDER, 1962. Adult ♂ ISH 256-1981, 514 mm tl., Florida.

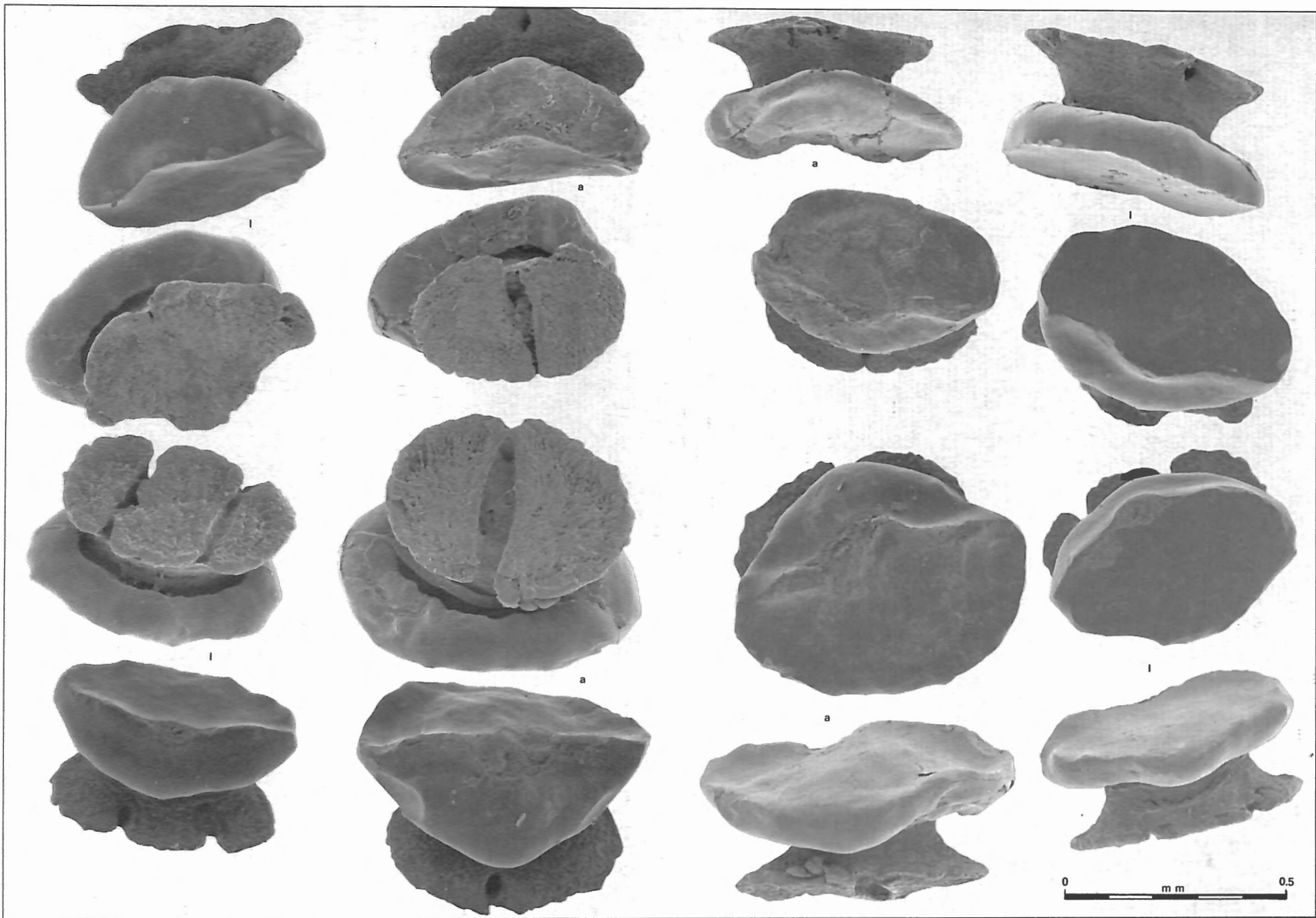


Plate 6 – *Anacanthobatis (Springeria) longirostris* BIGELOW & SCHROEDER, 1962. Juvenile ♀ ISH 3583-1979, 308 mm tl., Florida.

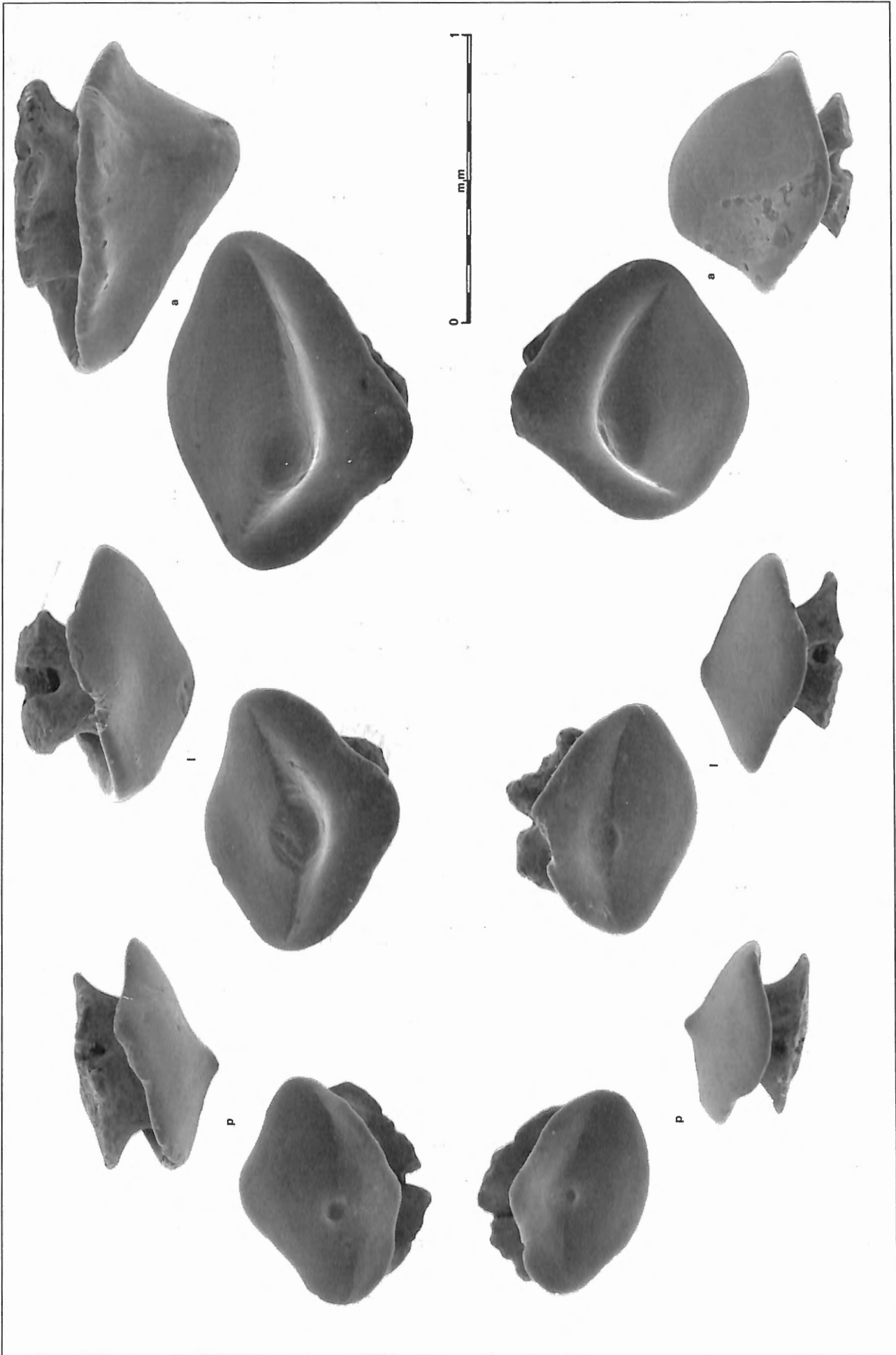


Plate 7 - *Breviraja spinosa* BIGELOW & SCHROEDER, 1950. Adult ♀ ISH 3595-1979, 305 mm tl., N.W. Atlantic.

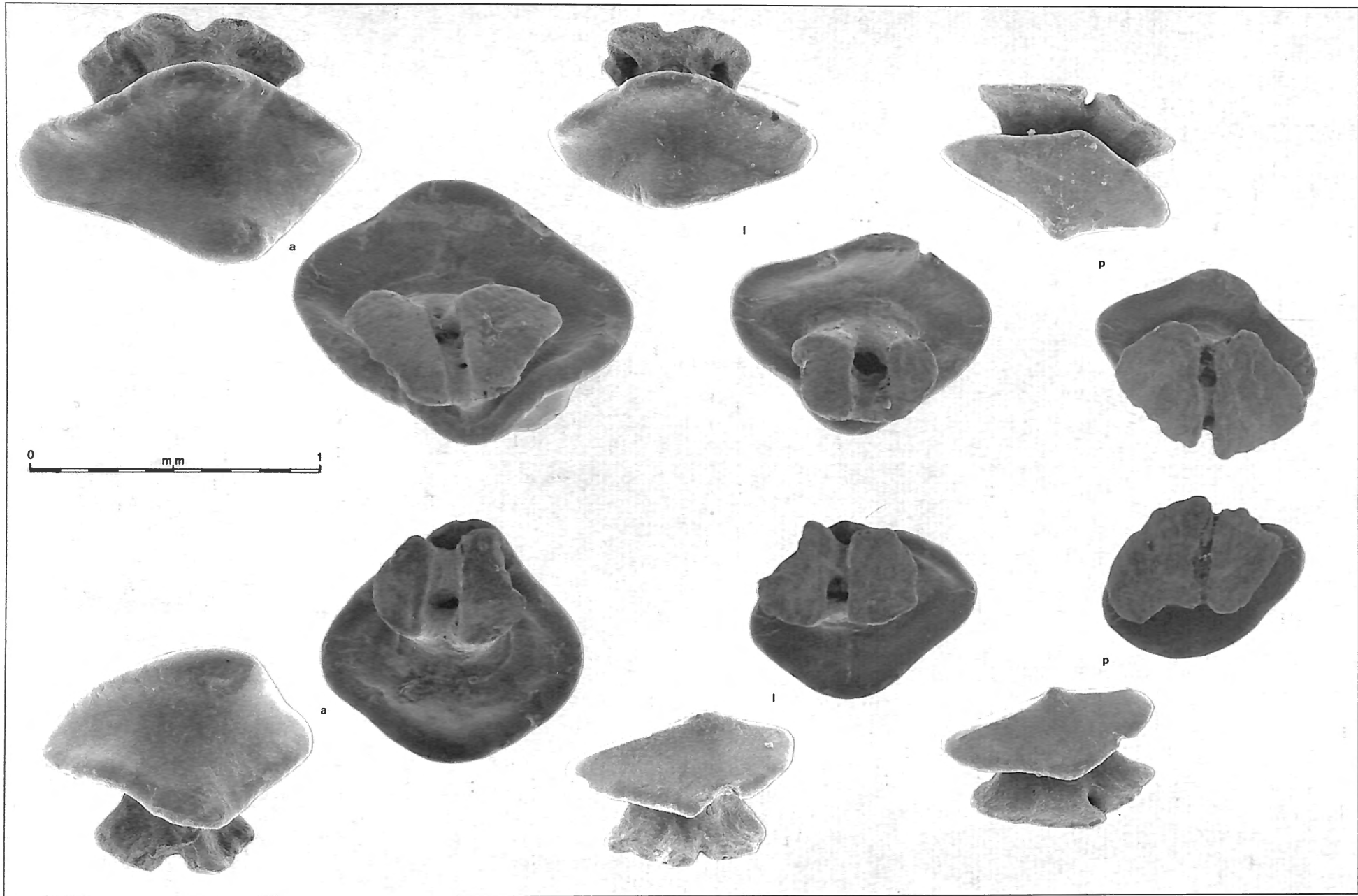


Plate 8 - *Breviraja spinosa* BIGELOW & SCHROEDER, 1950. Adult ♀ ISH 3595-1979, 305 mm tl., N.W. Atlantic.

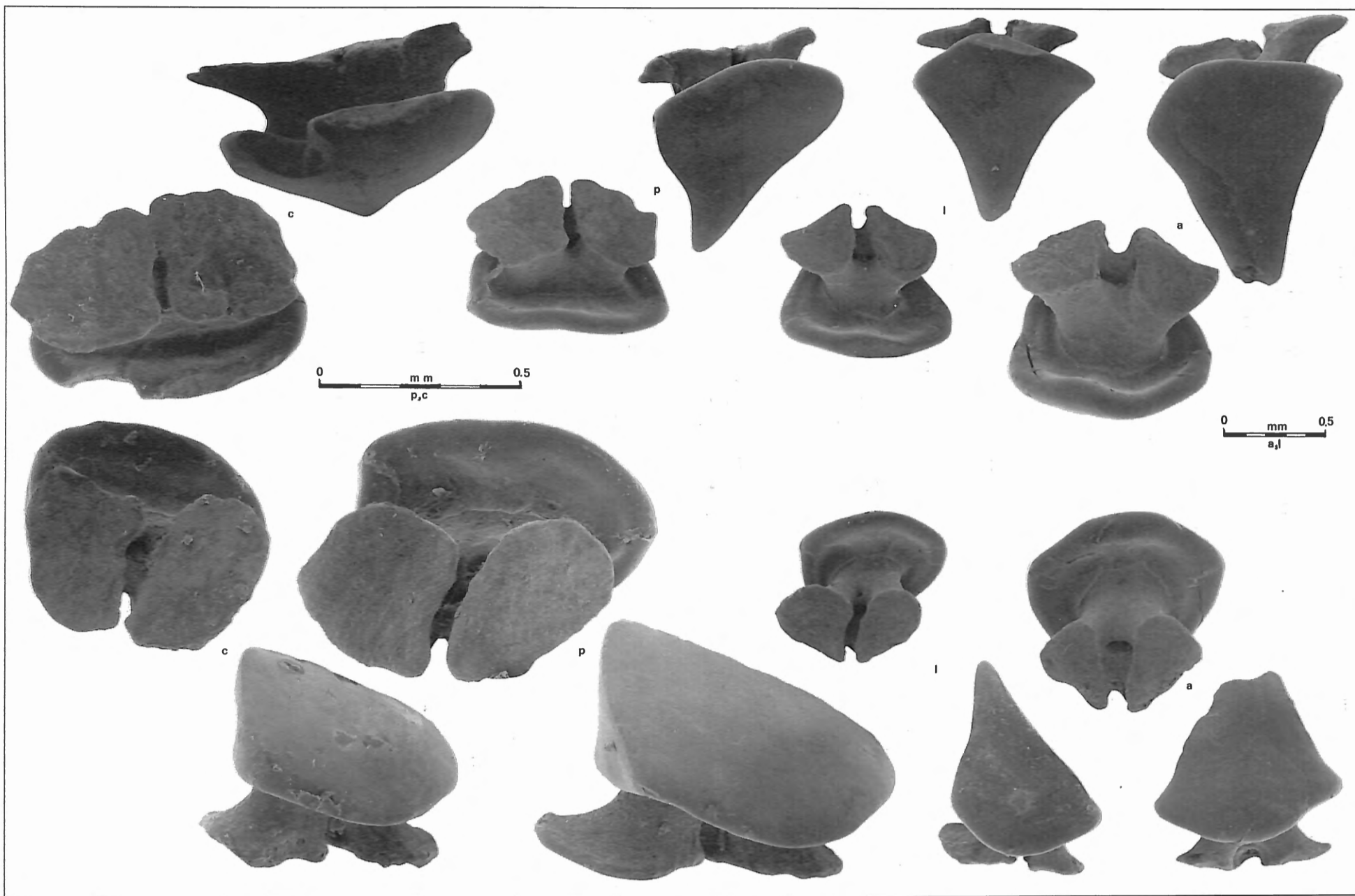


Plate 9 – *Breviraja spinosa* BIGELOW & SCHROEDER, 1950. Adult ♂ ISH 3600-1979, 300 mm tl., N.W. Atlantic.

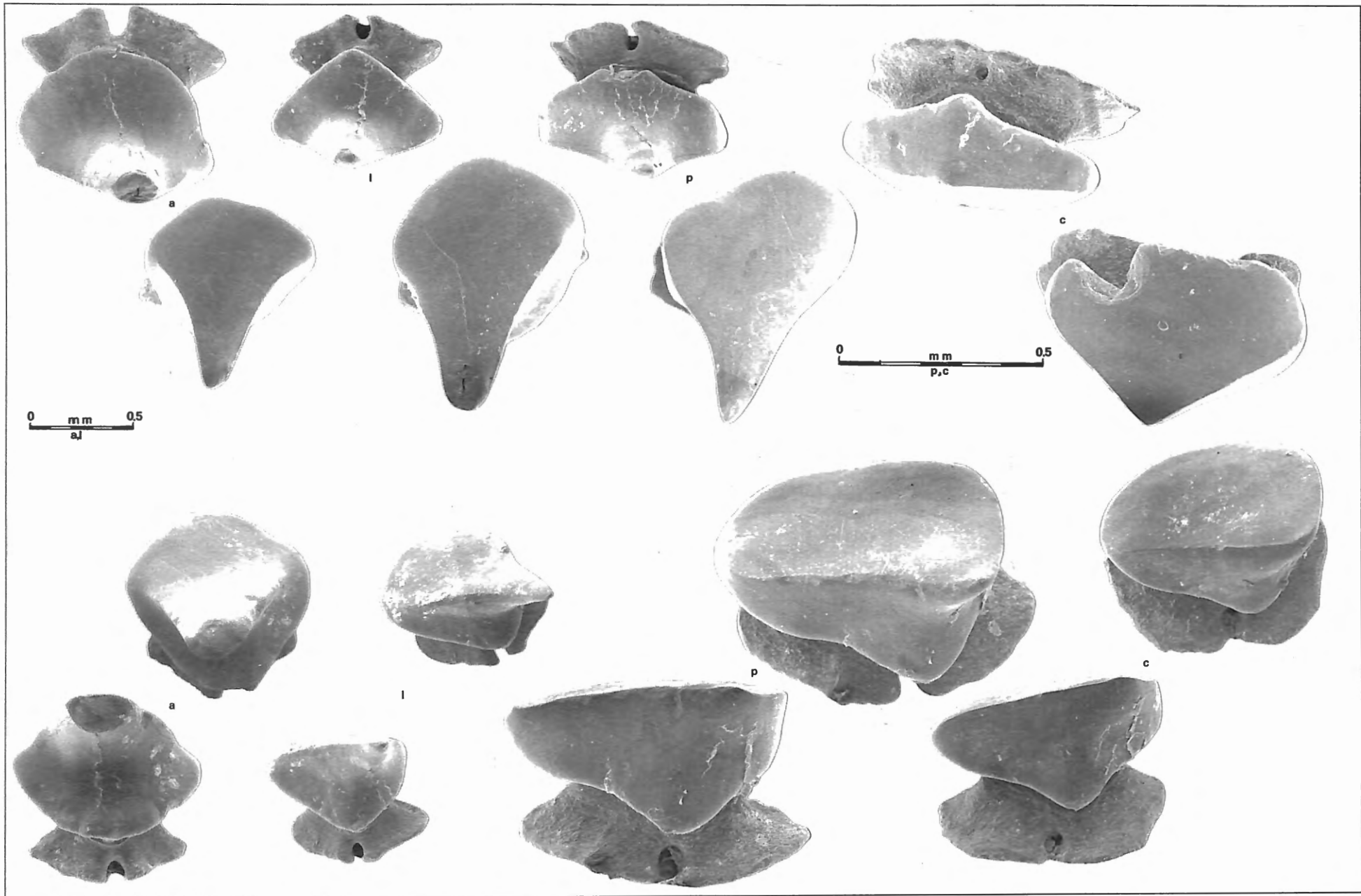


Plate 10 – *Breviraja spinosa* BIGELOW & SCHROEDER, 1950. Adult ♂ ISH 3600-1979, 300 mm tl., N.W. Atlantic.

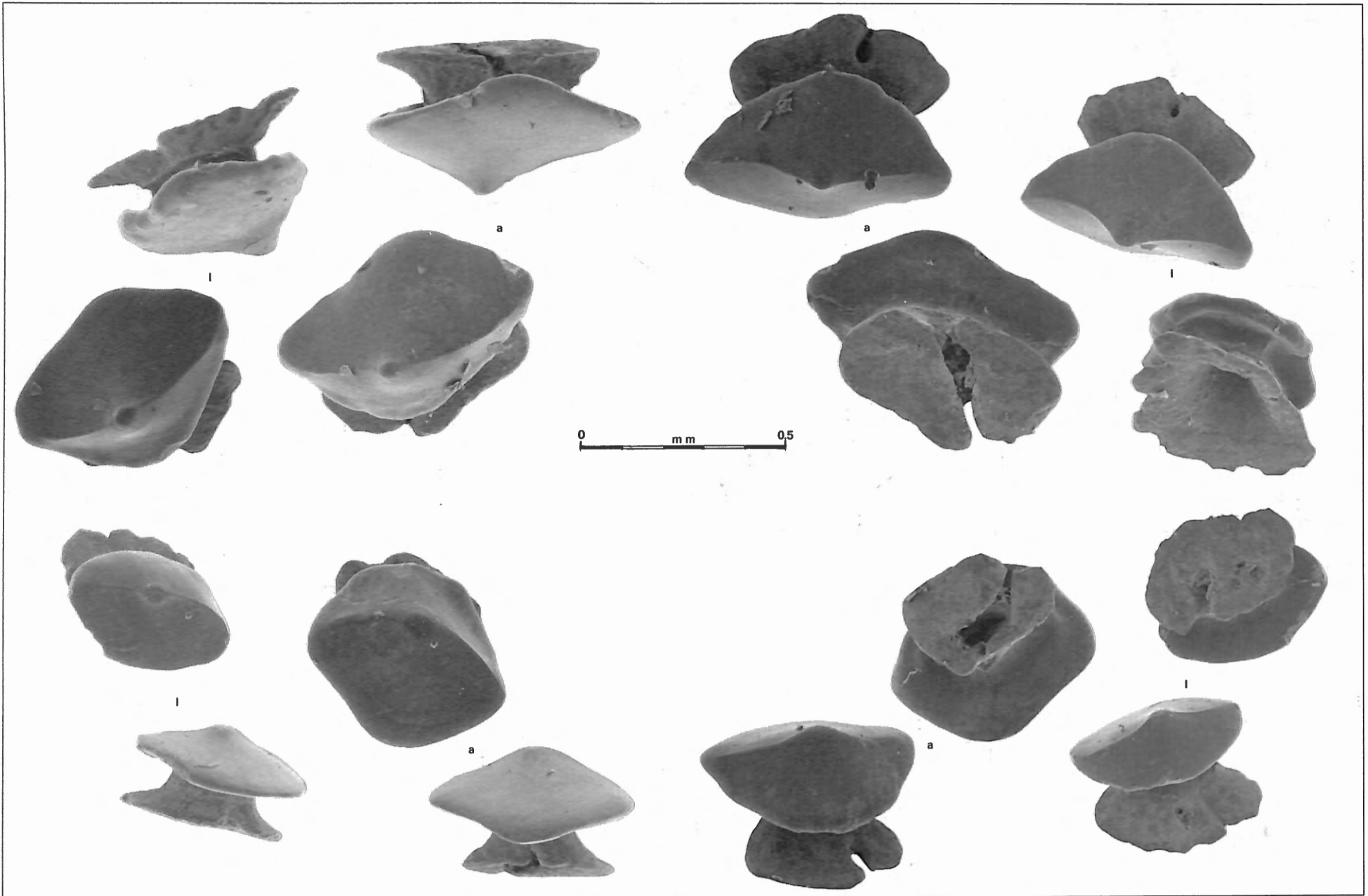


Plate 11 – *Breviraja spinosa* BIGELOW & SCHROEDER, 1950. Juvenile ♂ ISH 3657-1979, 200 mm tl., N.W. Atlantic.

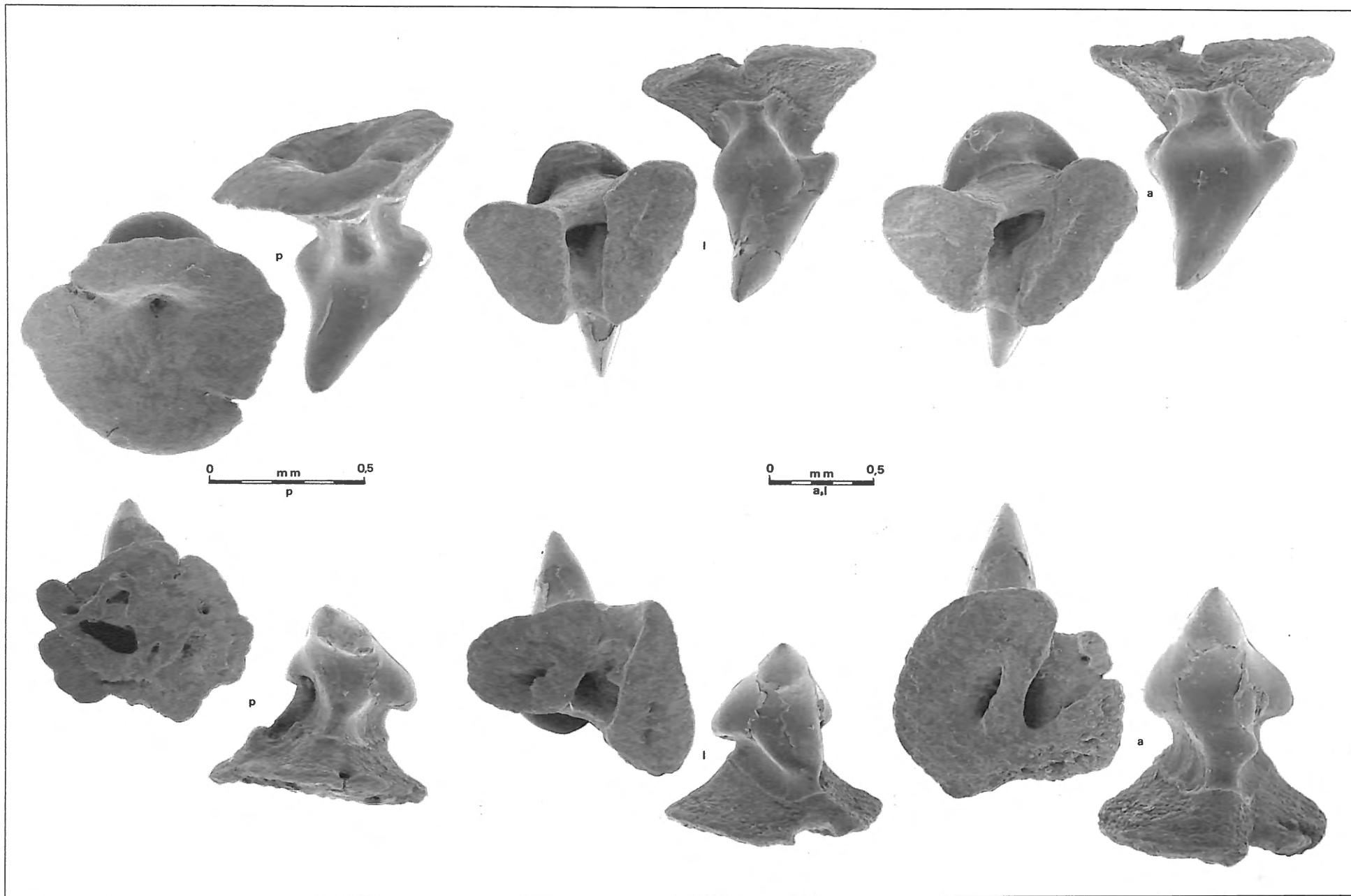


Plate 12 – *Dactylobatus armatus* BEAN & WEED, 1909. Adult ♀ ISH 3582-1979, 685 mm tl., Florida.

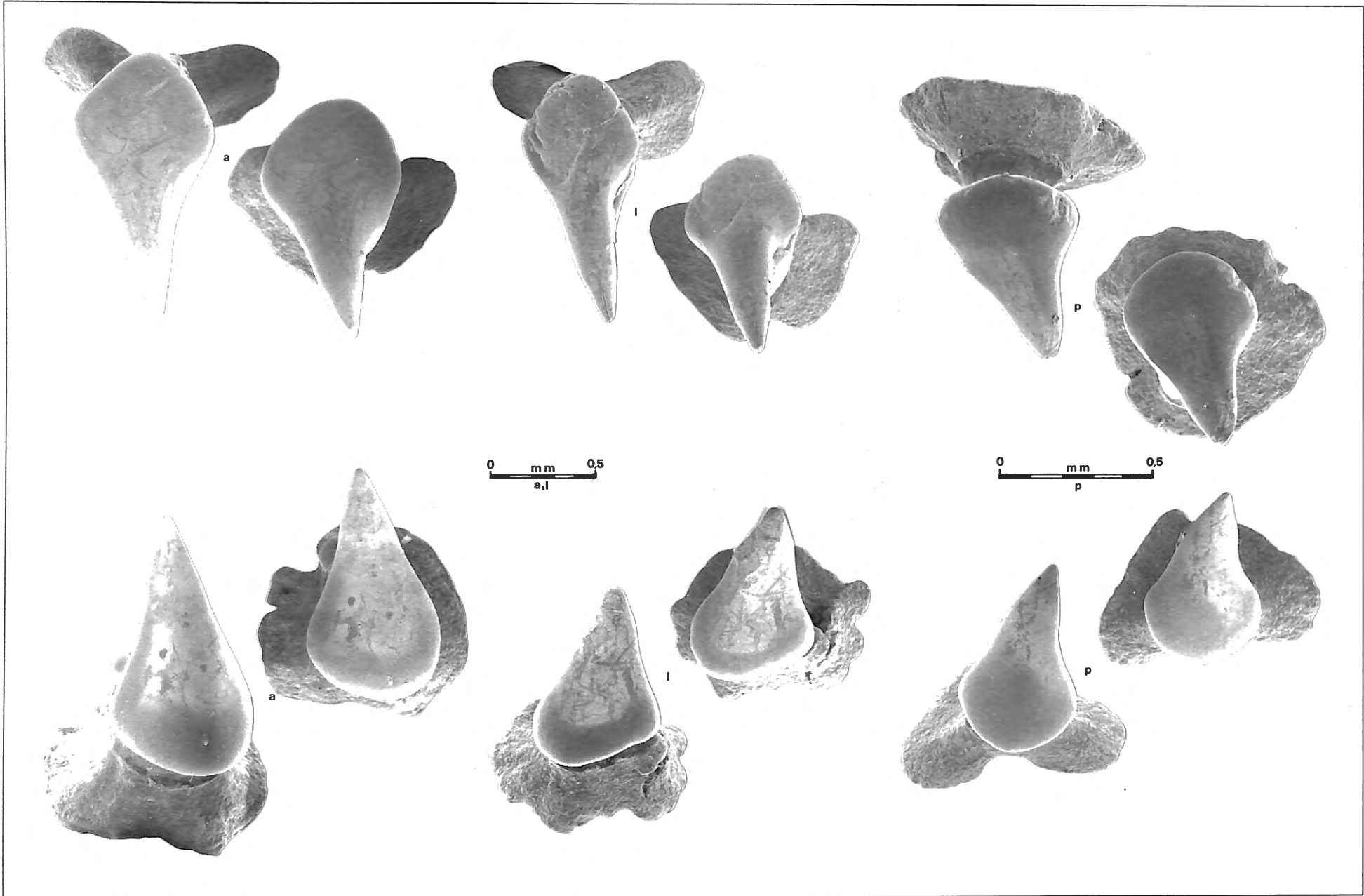


Plate 13 – *Dactylobatus armatus* BEAN & WEED, 1909. Adult ♀ ISH 3582-1979, 685 mm tl., Florida.

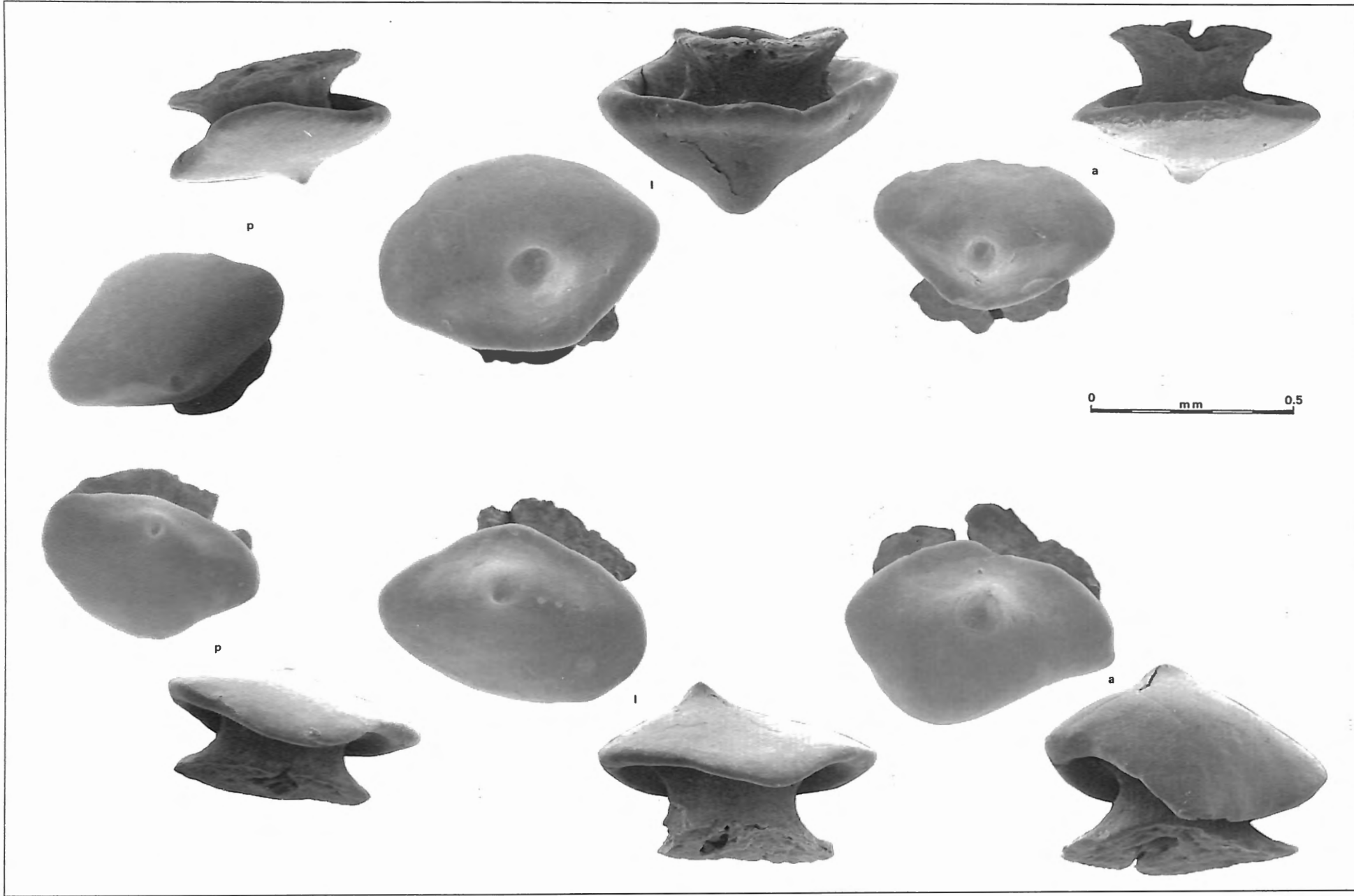


Plate 14 – *Gurgesiella (Fenestraja) plutonia* GARMAN, 1881. Adult ♀ ISH 3542-1979, 267 mm tl., Florida.

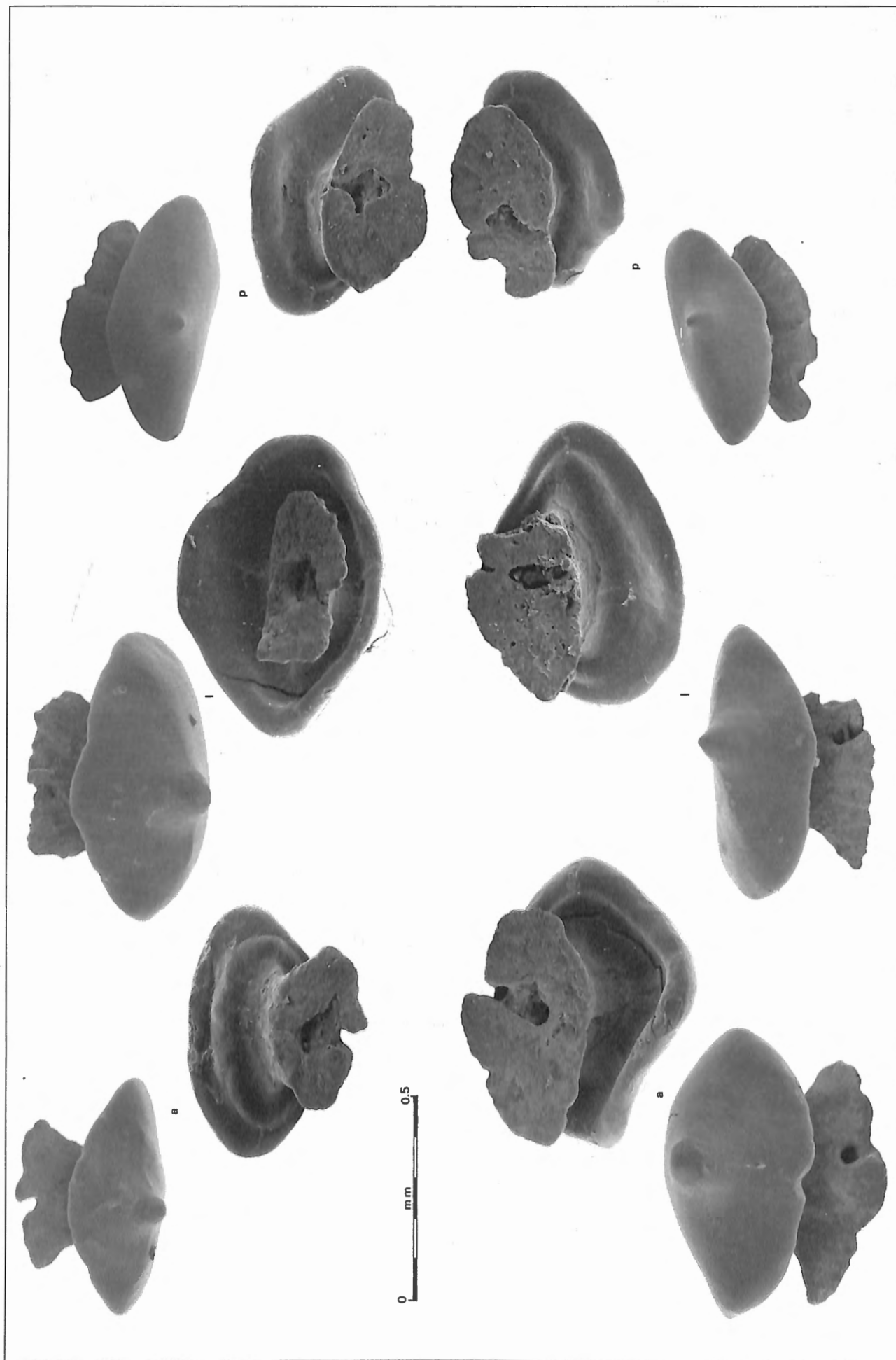


Plate 15 - Gurgesiella (Fenestraja) plutonia GARMAN, 1881. Adult ♀ ISH 3542-1979, 267 mm tl., Florida.

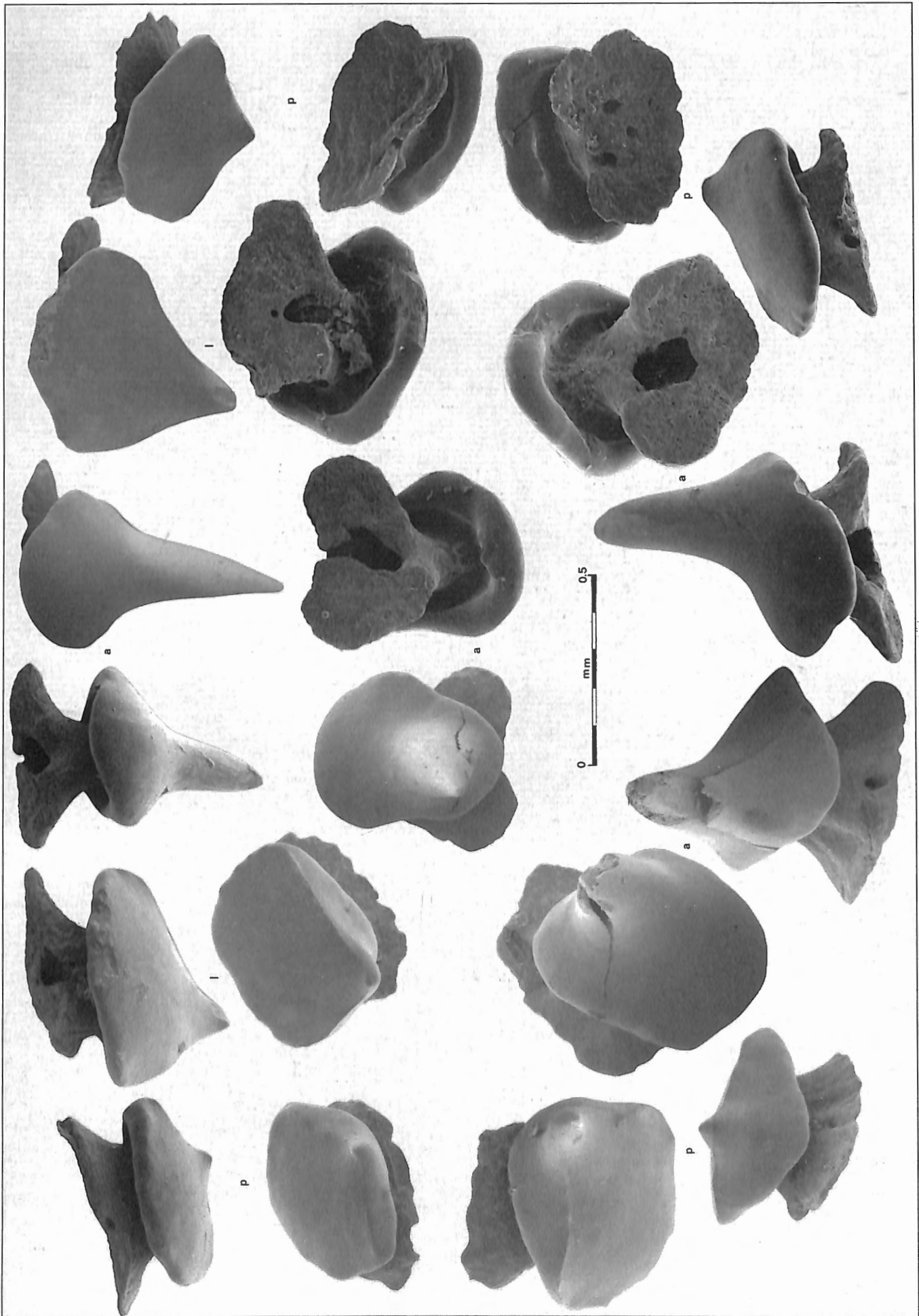


Plate 16 - Gurgesiella (Fenestraja) plutonia GARMAN, 1881. Adult ♂ ISH 3522-1979, 232 mm tl., N.W. Atlantic.

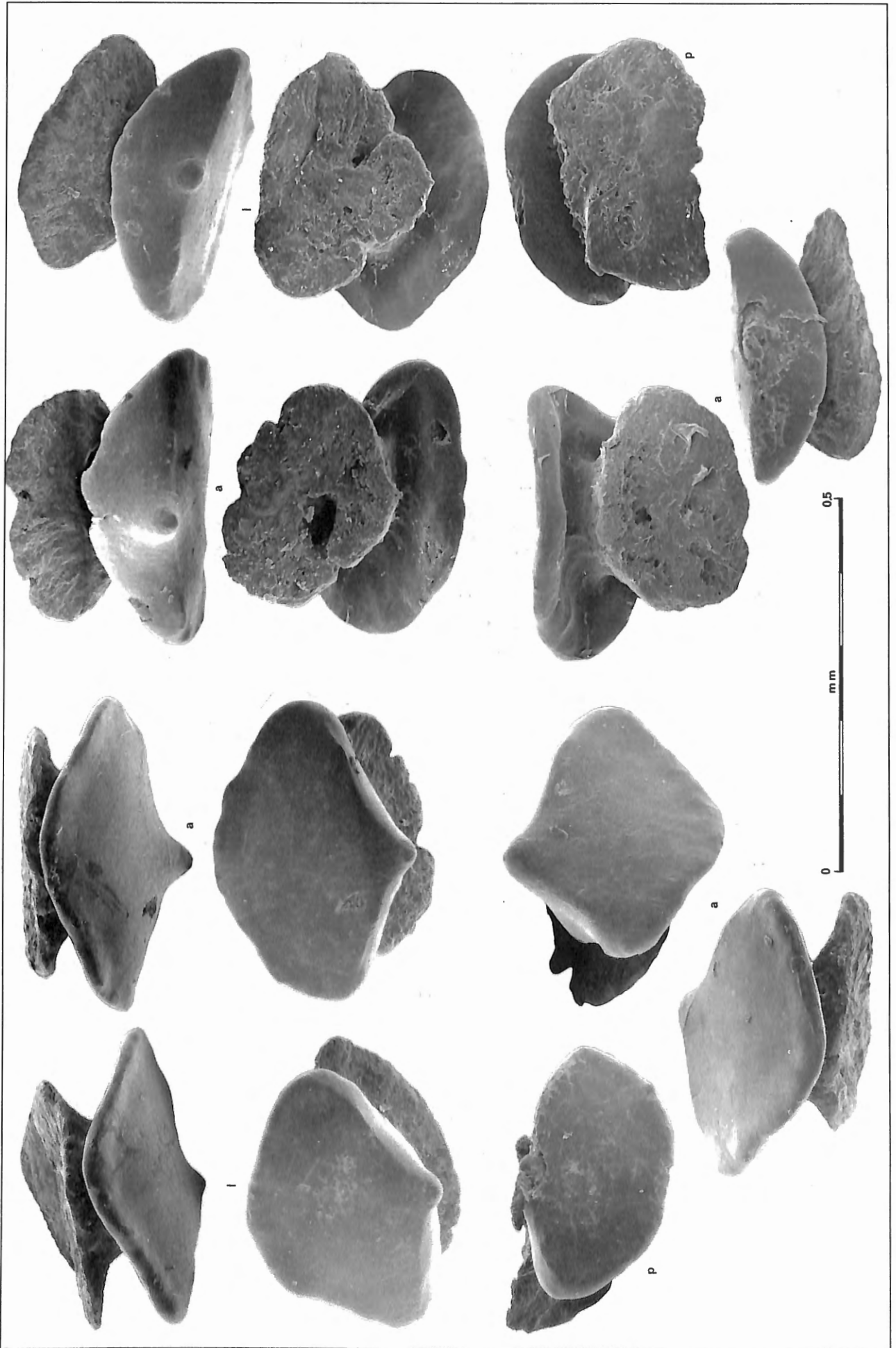


Plate 17 - *Gurgesiella (Fenestraja) plutonia* GARMAN, 1881. Juvenile ♀ ISH 3580-1979, 147 mm tl., Florida.

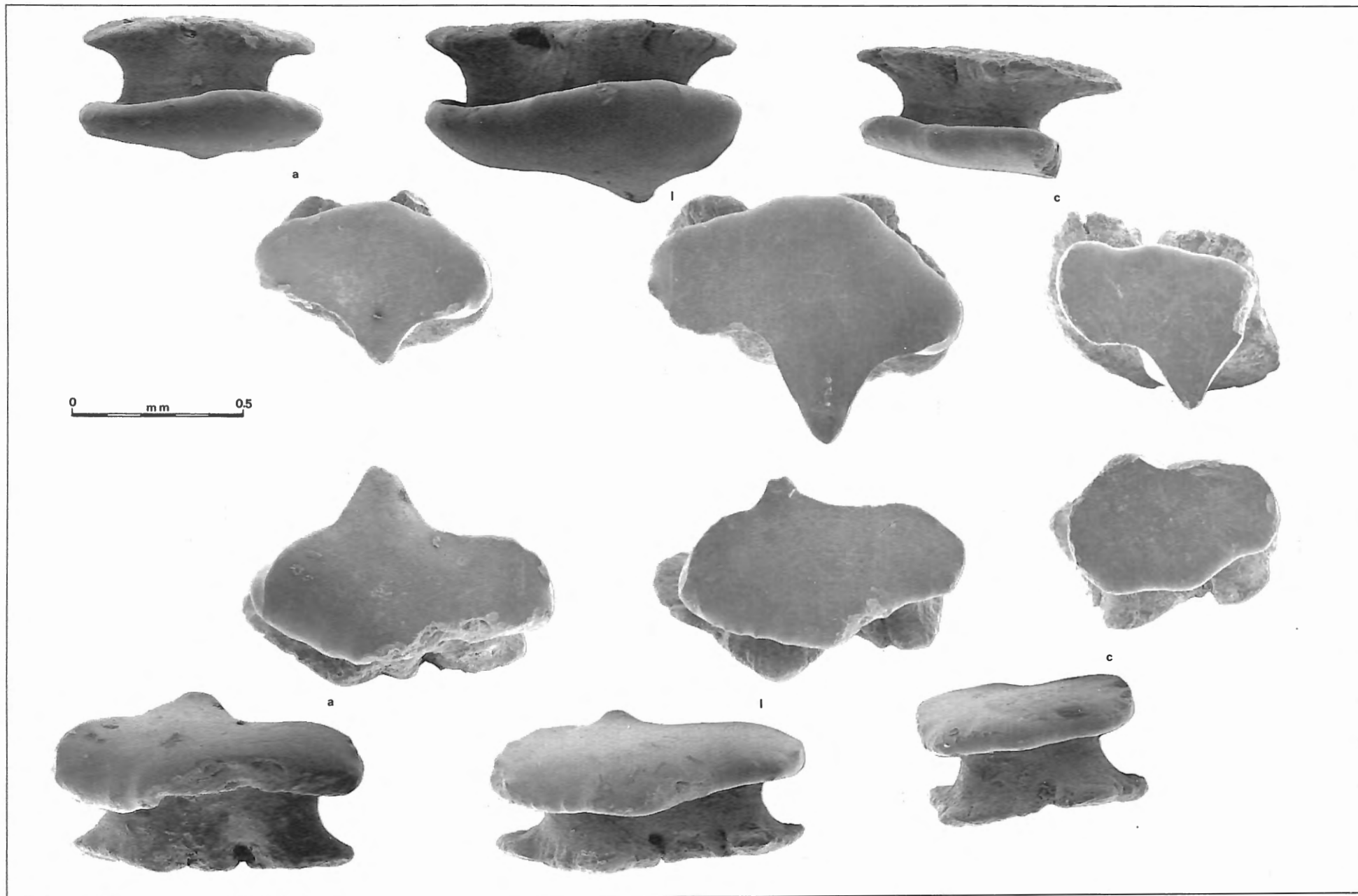


Plate 18 – *Gurgesiella (Gurgesiella) dorsalifera* MCEACHRAN & COMPAGNO, 1980. Adult ♀ ISH 1931-1968, 526 mm tl., Brasil.

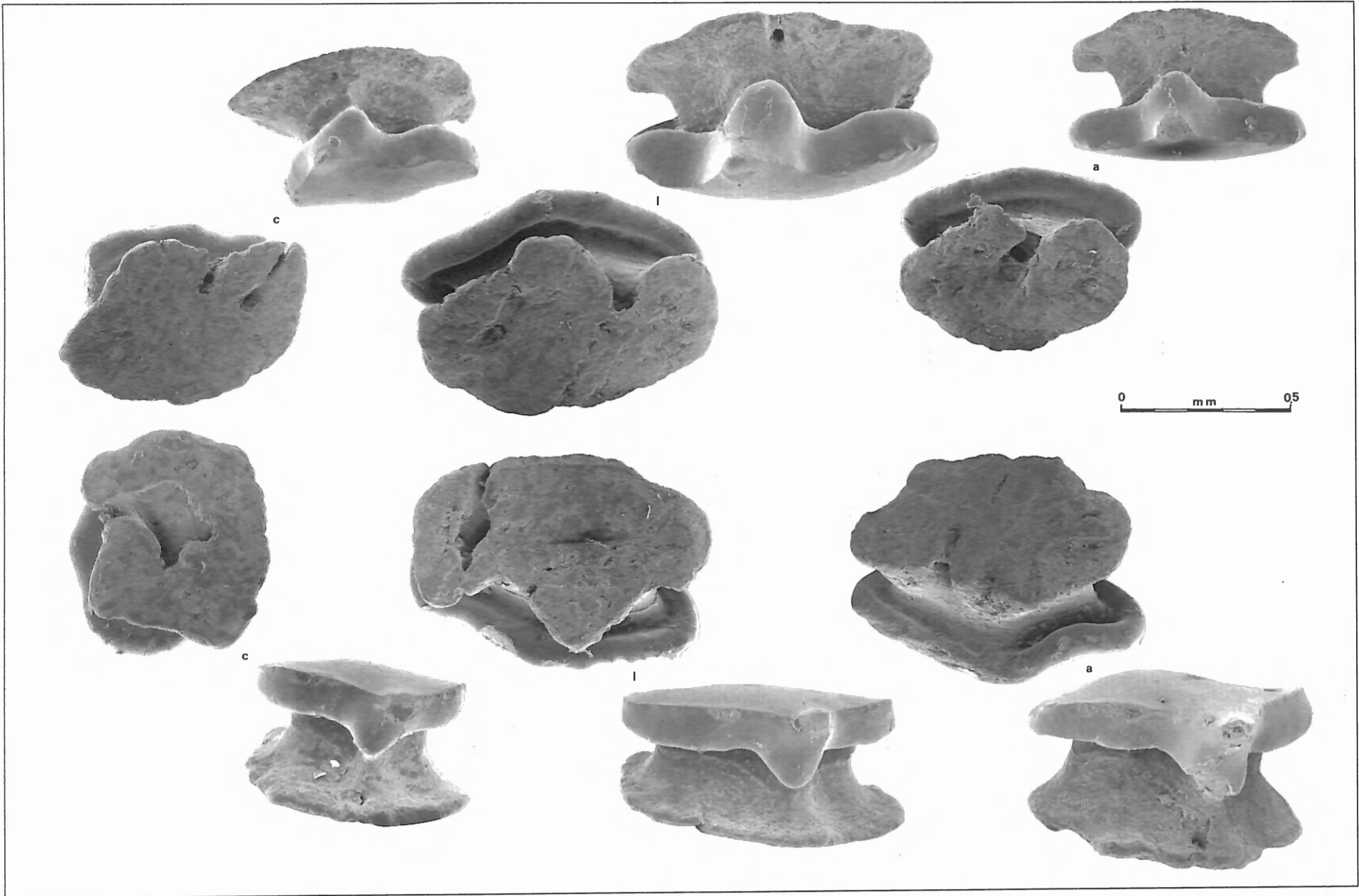


Plate 19 – *Gurgesiella (Gurgesiella) dorsalifera* MCEACHRAN & COMPAGNO, 1980. Adult ♀ ISH 1931-1968, 526 mm tl., Brasil.

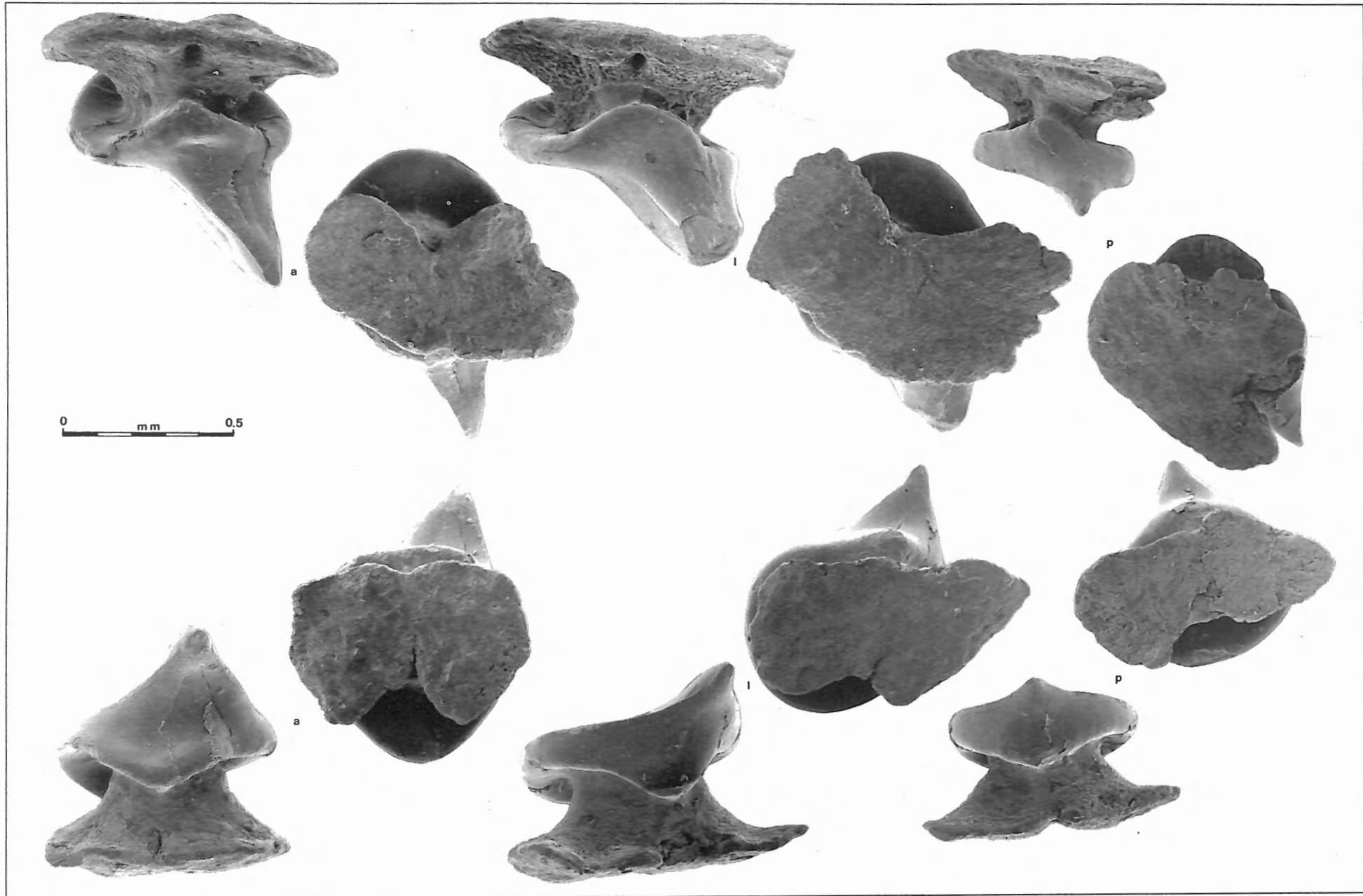


Plate 20 – *Gurgesiella (Gurgesiella) dorsalifera* MCEACHRAN & COMPAGNO, 1980. Adult ♂ ISH 1948-1968, 417 mm tl., Brasil.

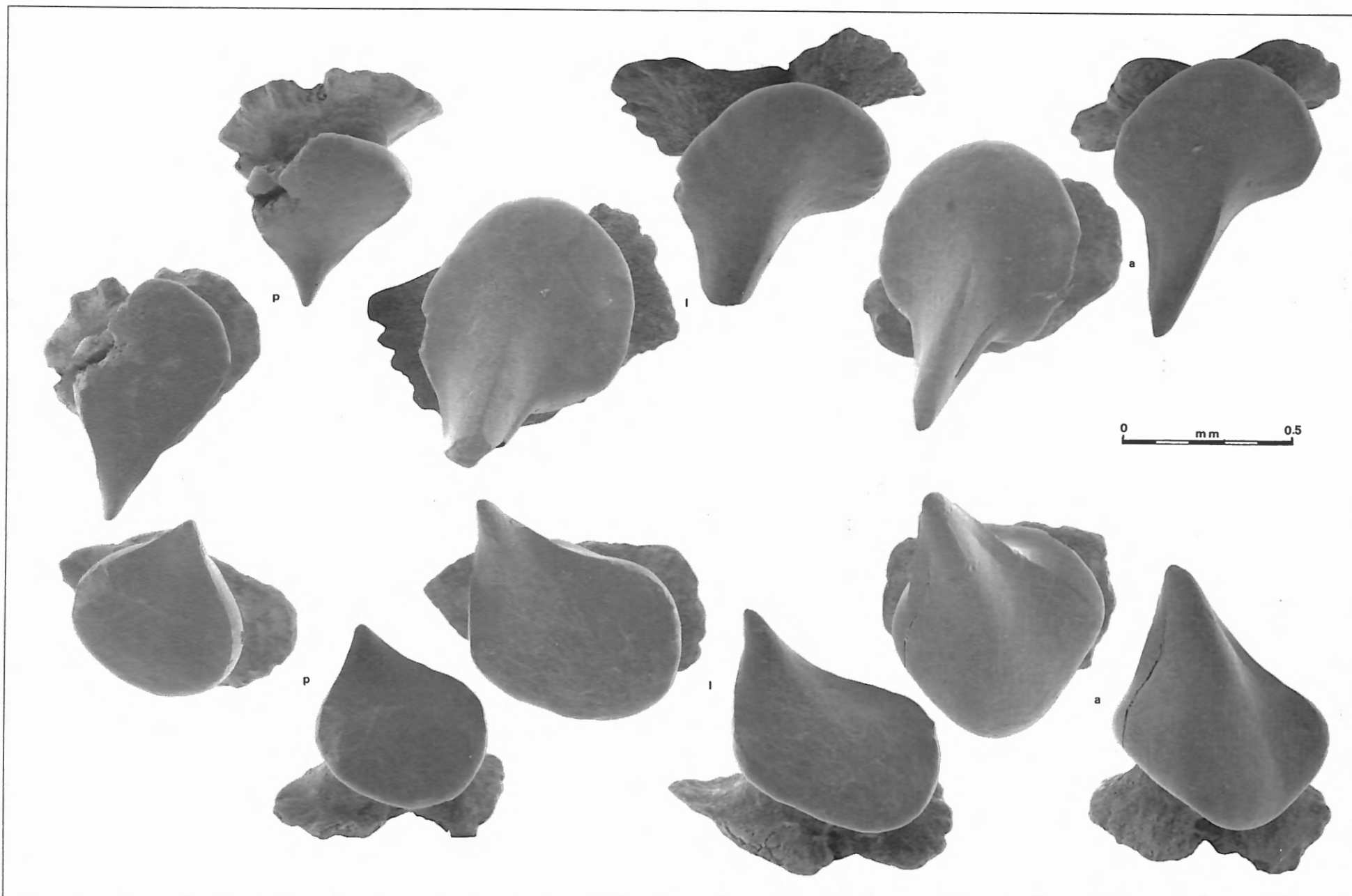


Plate 21 – *Gurgesiella (Gurgesiella) dorsalifera* MCEACHRAN & COMPAGNO, 1980. Adult ♂ ISH 1948-1968, 417 mm tl., Brasil.



Plate 22 - *Malacoraja senta* (GARMAN, 1885). Adult ♀ ISH 251-1985, 571 mm tl., Labrador.

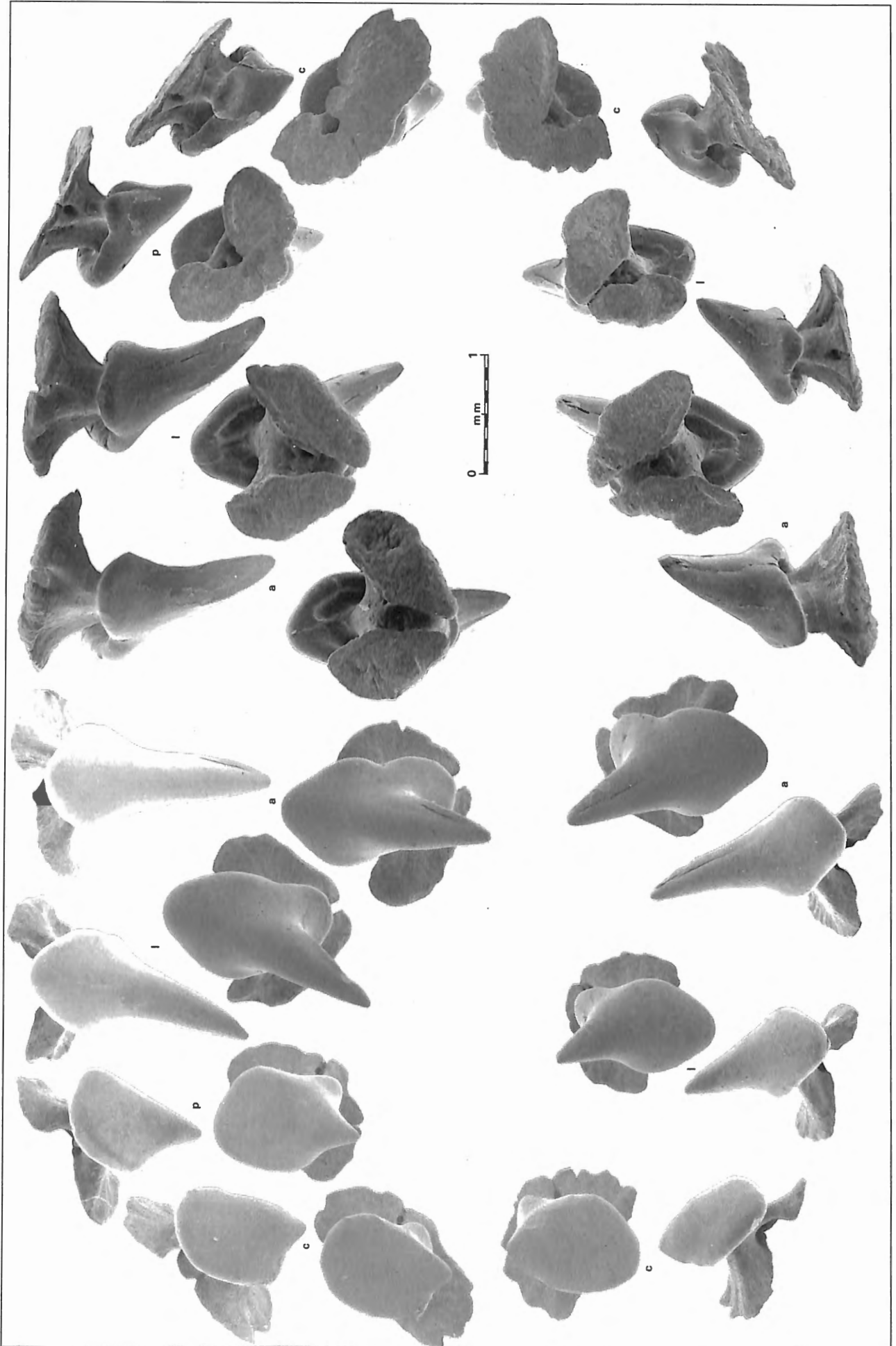


Plate 23 - *Malacoraja senta* (GARMAN, 1885). Adult ♂ ISH 1029-1982, 570 mm tl., Labrador.

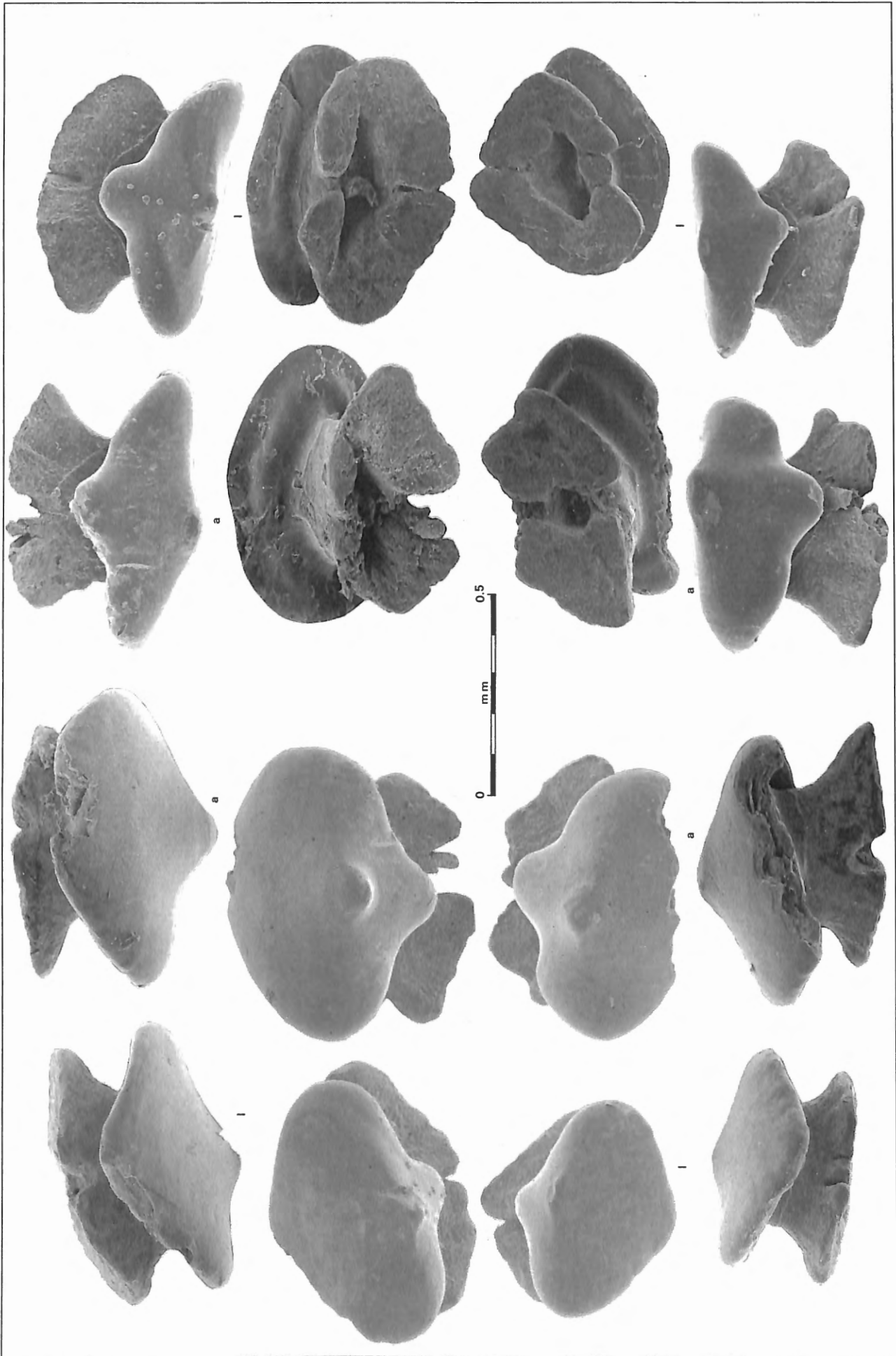


Plate 24 - *Malacoraja senta* (GARMAN, 1885). Juvenile ♀ ISH 8-1969, 291 mm tl., N.W. Atlantic.

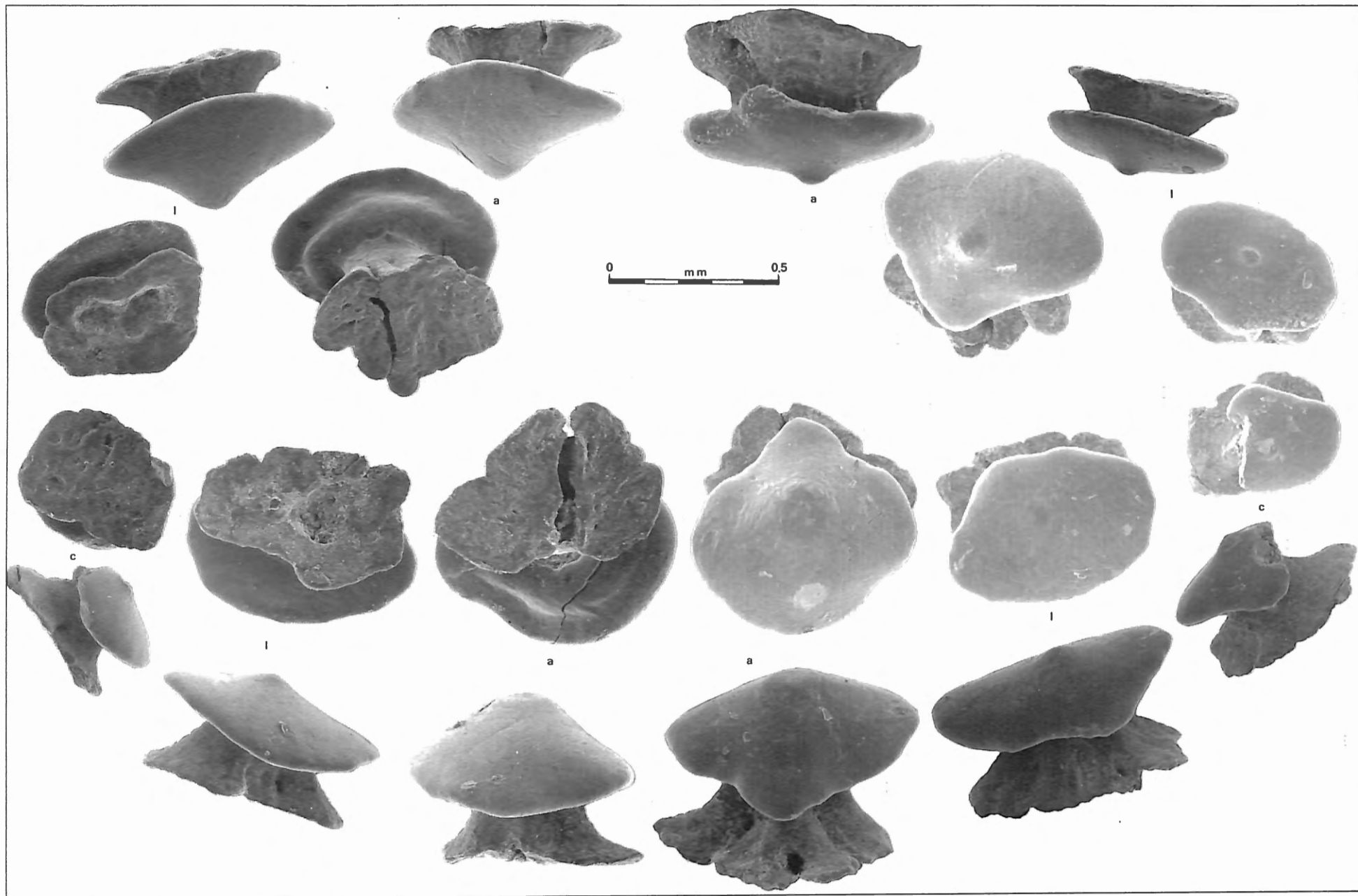


Plate 25 – *Neoraja caerulea* (STEHMANN, 1976). Adult ♀ ISH 175-1983, 277 mm tl., E. Rockall.



Plate 26 - *Neoraja caerulea* (STEHMANN, 1976). Adult ♂ ISH 641-1986, 277 mm tl., Hatton-bank.

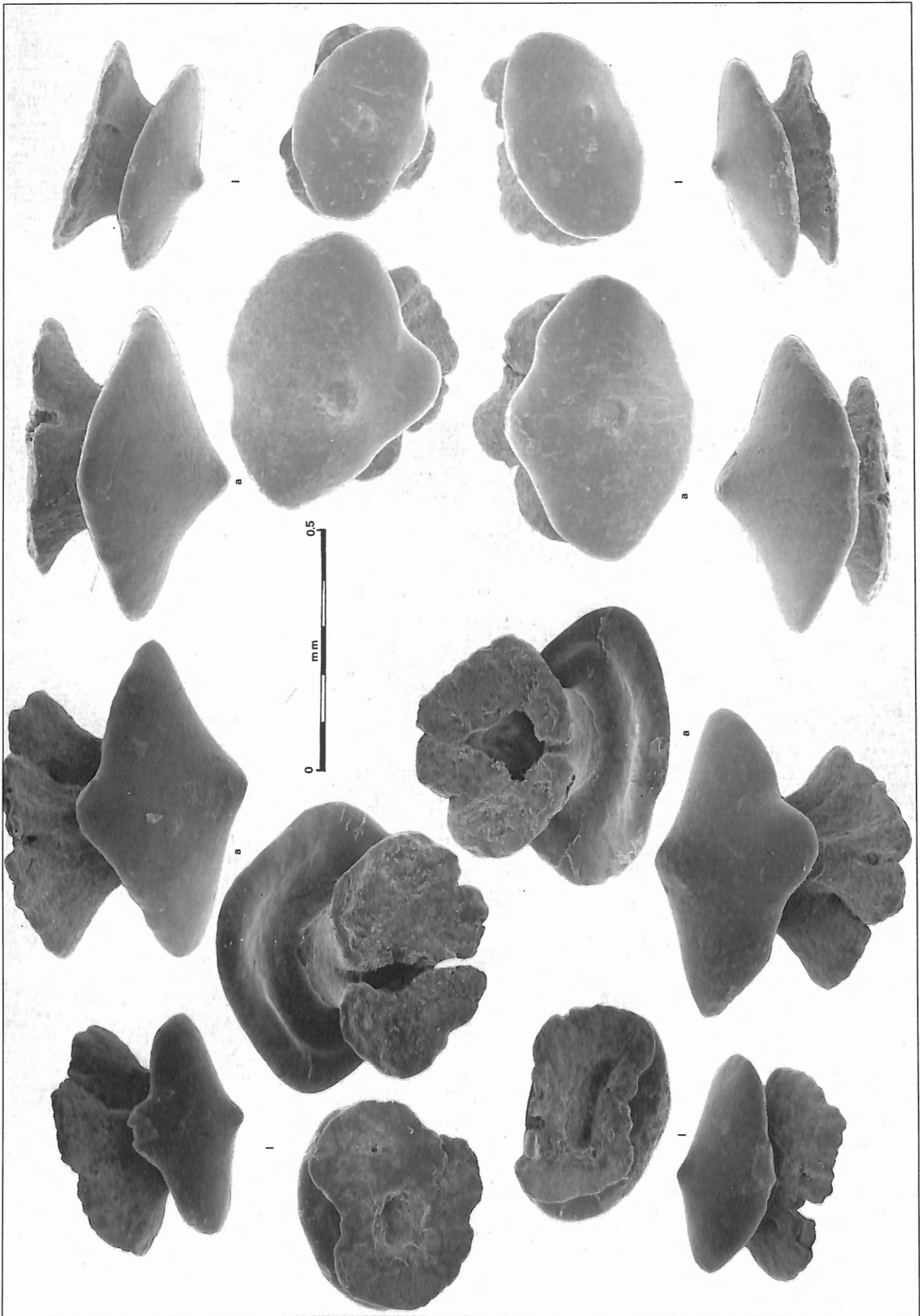


Plate 27 - *Neoraja caerulea* (STEHMANN, 1976). Juvenile ♀ ISH 647-1986, 239 mm tl., Hatton-bank.

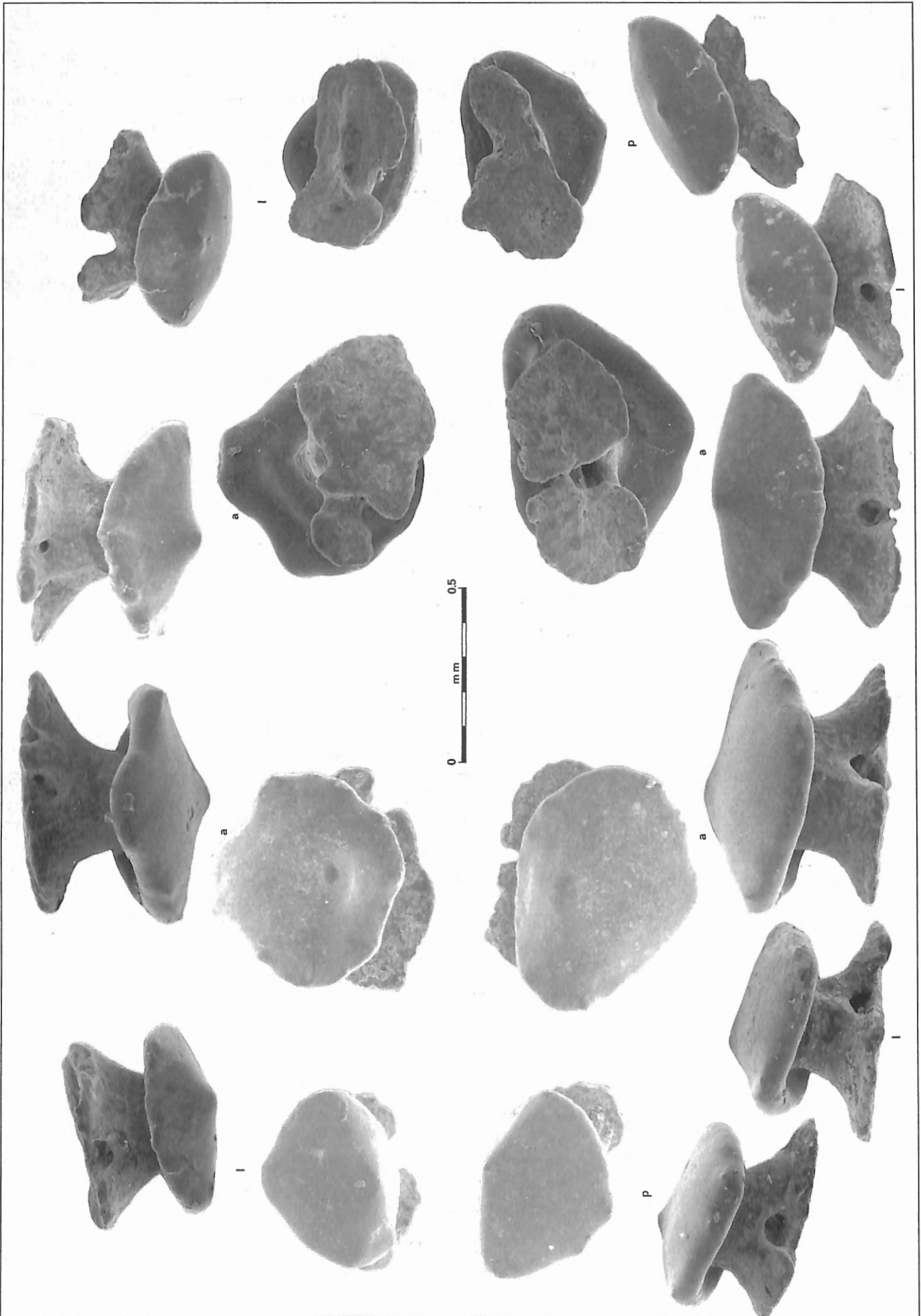


Plate 28 — *Pavoraja asperula* (GARRICK & PAUL, 1974). Adult ♀ ISH uncatalogued specimen 520 mm tl., New Zealand.



Plate 29 – *Pavoraja asperula* (GARRICK & PAUL, 1974). Adult ♂ ISH uncatalogued specimen 527 mm tl., New Zealand.



Plate 30 - *Pavoraja asperula* (GARRICK & PAUL, 1974). Juvenile ♂ ISH uncatalogued specimen 339 mm tl., New Zealand.