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BULLETIN VAN HET KONINKLIJK BELGISCH INSTITUUT VOOR NATUURWETENSCHAPPEN, BIOLOGIE, 66: 179-236, 1996

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. 1c: Order Rajiformes - Suborder Rajoidei - Family: Rajidae - Genera and Subgenera: *Arhynchobatis, Bathyraja richardsoni*-type, *Cruriraja, Irolita, Notoraja, Pavoraja (Insentiraja), Pavoraja (Pavoraja), Pseudoraja, Raja (Atlantoraja), Raja (Okamejei)* and *Rhinoraja.*

by J.HERMAN, M. HOVESTADT-EULER, D.C. HOVESTADT and M. STEHMANN

Abstract

Part B, Nos. 1a and 1b of this series, comprising of the Batomorphii the first and second sections on the Rajoidei, is continued with the last group of rajoid taxa as far as material was available. The tooth morphology of representatives of eleven more genera and subgenera, namely *Arhynchobatis, Bathyraja richardsoni*-type, *Cruriraja, Irolita, Notoraja, Pavoraja (Insentiraja), Pavoraja (Pavoraja), Pseudoraja, Raja (Atlantoraja), Raja (Okamejei)* and *Rhinoraja*, is described and illustrated by SEM-photographs. Differential diagnoses and systematic interpretations are presented as a result of the odontological examinations described here and in the previous two issues 1a and 1b for the supraspecific taxa of the Rajoidei.
Key-words: Elasmobranchii - Batomorphii - Rajoidei - Odontology - Systematics.

Résumé

Ce fascicule constitue le troisième et dernier volet de l'étude odontologique des Rajoidei. La morphologie dentaire des représentants de onze autre genres et sous-genres, *Arhynchobatis, Bathyraja richardsoni*-type, *Cruriraja, Irolita, Notoraja, Pavoraja (Insentiraja), Pavoraja (Pavoraja), Pseudoraja, Raja (Atlantoraja), Raja (Okamejei)* and *Rhinoraja*, est décrité et illustrée (clichés MEB). Diagnose différentielle et interprétations systématiques de tous les taxa supraspécifiques de Rajoidei examinés dans les trois fascicules (1a, 1b et le présent 1c) sont présentées.
Mots-clés: Elasmobranchii - Batomorphii - Rajoidei - Odontologie - Systematique.

Kurzfassung

Teil B, Nr. 1a and 1b dieser Serie, die für die Batomorphii mit den Rajoidei begannen, wird fortgesetzt mit Beschreibungen und Abbildungen durch REM-Photos der Zahnmorphologie elf weiterer Rajoidentaxa: *Arhynchobatis, Bathyraja richardsoni*-type, *Cruriraja, Irolita, Notoraja, Pavoraja (Insentiraja), Pavoraja (Pavoraja), Pseudoraja, Raja (Atlantoraja), Raja (Okamejei)* und *Rhinoraja*. Differentialdiagnosen und systematische Bewertungen werden präsentiert, die sich aus den odontologischen Untersuchungen dieses Teils und beider vorgehenden 1a und 1b für die supraspezifischen Taxa der Rajoidei ergeben haben.
Schlüsselwörter: Elasmobranchii - Batomorphii - Rajoidei - Odontologie - Systematik.

Part B: Batomorphii - Order: Rajiformes - Suborder: Rajoidei

Introduction

This issue continues the previous contributions of part B, Nos. 1a and 1b of this series comprising of the Batomorphii the first and second section on the Rajoidei, with the last group of rajoid taxa as far as material was available. The tooth morphology of representatives of eleven more genera and subgenera, namely *Arhynchobatis asperrimus, Bathyraja richardsoni, Cruriraja parcomaculata, Irolita waitii, Notoraja tobitukai, Pavoraja (Insentiraja) laxipella, Pavoraja (Pavoraja) nitida, Pseudoraja fischeri, Raja (Atlantoraja) cyclophora, Raja (Okamejei) kenojei* and *Rhinoraja longicauda,* is described and illustrated.

The subgenus *Pavoraja (Insentiraja)* could only be investigated with a female of *P. laxipella*. As the holotype

is the only male known, no male teeth were available. *Pseudoraja fischeri* is presented by a juvenile male only, because adult males unknown so far. With the exception of a juvenile male of *Raja (Okamejei) kenojei*, all available teeth of *Notoraja tobitukai, Raja (Okamejei) kenojei* and *Rhinoraja longicauda* were badly affected by formaldehyde. Their teeth are illustrated in their present state and described as far as possible.

Numbers of the nominal and yet undescribed species and their generic assignment based on MIYAKE & MCEACHRAN (1990b), except where more recent information available and referred to.

A differential diagnosis of the taxa described and illustrated in the issues 1a, 1b and the present one is given, with systematic conclusions from the odontological point of view.

Due to the complexity of rajoid odontological characters, the elaboration of an odontological key was not possible.

Additional to the previous issue of Part B no.1b the illustration of the teeth of a female of *Raja (Rajella) fyllae* will be given here (see plate 41).

The last group of rajoid genera and subgenera investigated for their tooth morphology is listed below under **Material**.

Material

The following 31 specimens of 11 species were examined for this issue:

Arhynchobatis asperrimus
ISH uncatalogued: WE05, sta. 9580-1979 ♂ 600 mm TL
ISH uncatalogued: WE05, sta. 958-1978 ♂ 425 mm TL
Bathyraja richardsoni
ISH 69-1973 ♂ 1800 mm TL
BMNH uncatalogued: R/V CHALLENGER sta. 51613≠1, 22.VII.1982 ♂ 383 mm TL
BMNH uncatalogued: R/V CHALLENGER sta. 51011, 3.V.1981 ♀ 449 mm TL
Cruriraja parcomaculata
SAM uncatalogued: R/V AFRICANA sta. A4384 cr. 046 ♂ 465 mm TL
SAM uncatalogued: R/V AFRICANA sta. A4329 cr. 046 ♀ 480 mm TL
Irolita waitii
CSIRO H 123 -01 ♂ 221 mm TL
CSIRO H 124 -01 ♀ 252 mm TL
Notoraja tobitukai
ISH 30-1984 ♂ 366 mm TL
MTUF 21869 ♀ 390+ mm TL
MTUF 25087 ♀ ? mm TL (tail missing)
ZMH 8409 ♂ 430 mm TL
Pavoraja (Insentiraja) laxipella
CSIRO H 716-01 ♀ 402 mm TL Paratype
Pavoraja (Pavoraja) nitida
CSIRO H 3507-05 ♂ 350 mm TL
CSIRO H 3524-03 ♀ 370 mm TL
Pseudoraja fischeri
TCWC 7466.01 ? 180 mm DW
MCZ 41851 ♀ 365 mm TL
MCZ 52241 ♂ 238 mm TL
Raja (Atlantoraja) cyclophora
ISH 1562-1966 ♂ 547 mm TL
ISH 1082-1966 ♂ 333 mm TL
ISH 1095-1966 ♀ 286 mm TL
Raja (Okamejei) kenojei
ZMH 8410 ♂ 315 mm TL
ZMH 8408 ♂ 295 mm TL
ZMH 8407 ♀ 270 mm TL
ZMH 8406 ♀ 465 mm TL
RMNH 7434 ♂ 300 mm TL (juv.)
Rhinoraja longicauda
ISH 327-1978 ♂ 433 mm TL
MTUF 23958 ♂ 355 mm TL (juv.)
HUMZ 34923 ♂ 580 mm TLHUMZ 49128 ♂ 370 mm TL

Description of the odontological characters

Genus: *Arhynchobatis* WAITE, 1909

This genus is monotypic with *A. asperrimus.*

Arhynchobatis asperrimus WAITE, 1909
(Plates: 1 to 4; textfigure 1)

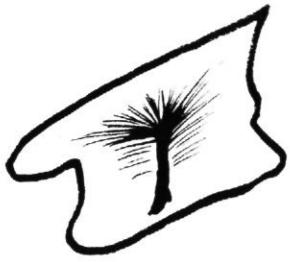
Arhynchobatis asperrimus WAITE, 1909. Records of the Canterbury Museum, 1 (2): 20.

HETERODONTY

The dentition is gradient monognathic heterodont. Although an adult female was not available for examination, sexual heterodonty appears to be absent. The adult male and the juvenile male examined have a similar tooth morphology, which makes it plausible that it is alike in the female. Ontogenetic heterodonty is also absent.

VASCULARIZATION

The teeth show an adapted holaulacorhizid root type with a narrow, elongated pulp cavity in the root area, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine was not observed, and inner lateral foramina are absent.
(See textfigure 1)



Textfigure 1.
Arhynchobatis asperrimus *histological tooth cross-section.*

FEMALES AND MALES

The crown base is oval-shaped in occlusal view. The principal cusp is vertically erect in anterior, lateral and posterior teeth and triangle-shaped, lowering toward the commissural teeth. Uvula, apron or ornamentation are absent. The inner face is convex, the outer one flat to slightly convex.
The root stem is low and oval to almost circular in cross-section. The root widens in all directions, forming a large base with two well developed root lobes. Both have flat basal surfaces, and are separated by a broad and deep median groove with a large central foramen. Root coating is absent.

Genus: *Bathyraja* ISHIYAMA, 1958

The listing of taxa of this genus was given in Part B, 1b of this series.

Bathyraja richardsoni (GARRICK, 1961)
(Plates: 5 to 8; textfigure 2)

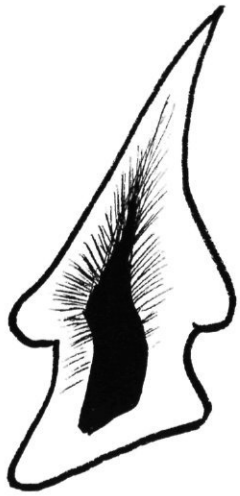
Bathyraja richardsoni GARRICK, 1961. Transactions of the royal Society of New Zealand, 88: 743.

HETERODONTY

The dentition is gradient monognathic heterodont. Although an adult female was not available for examination, sexual heterodonty is not to be expected, considering the absence of sexual heterodonty in both, *B. spinicauda* and *B. albomaculata.*
Ontogenetic heterodonty is also absent.

VASCULARIZATION

The teeth show an adapted holaulacorhizid root type 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. (See textfigure 2)



Textfigure 2.
Bathyraja richardsoni *tooth histological cross-section.*

FEMALES AND MALES

The crown base is more or less oval in occlusal view, with an inner extension due to an uvula. The elongated, slender principal cusp of anterior, lateral and posterior teeth is vertically erect and constricted just above the base. Lateralteeth slightly incline toward the commissure. An apron or ornamentation are absent, but a well developed uvula is present. The inner and outer faces are both strongly convex.
The broad root stem is rather high and oval to almost circular in cross-section. The root is extremely high, widens in all directions downward and forms a large base with two well developed root lobes. Both have more or less flat basal surfaces, and are separated by a broad and deep median groove with one large central foramen. Root coating is absent.

Genus: *Cruriraja* BIGELOW & SCHROEDER, 1948

This genus comprises eight species: *C. andamanica, C. atlantis* (type species), *C. cadenati, C. durbanensis, C. parcomaculata, C. poeyi, C. rugosa* and *C. triangularis.* Teeth of the type species were not available for examination and, therefore, teeth of *C. parcomaculata* were used instead.

Cruriraja parcomaculata (VON BONDE & SWART, 1923)
(Plates: 9 to 14; textfigure 3)

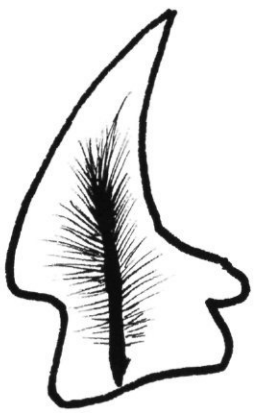
Raja parcomaculata VON BONDE & SWART, 1923. Rep. Fish. mar. biol. Surv. Un. S. Afr. (Spec. Rep. No. 5): 9.

HETERODONTY

The dentition is gradient monognathic heterodont. Sexual heterodonty is presented by teeth with a triangular, low crown in adult females versus teeth with narrower, elongated cusp in males. Ontogenetic heterodonty is demonstrated by low crowns in juveniles and elongated cusps in adult males.

VASCULARIZATION

The teeth show an adapted kind of holaulacorhizy or secondary hemiaulacorhizy, with a narrow, elongated 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.



Textfigure 3.
Cruriraja parcomaculata *tooth histological cross-section.*

FEMALES

The crown base is more or less oval in occlusal view, with the inner face more triangle-shaped and with a rounded, central angle. The teeth have a low, broad based triangular cusp. The inner surface of the crown is convex, the outer one is flat to slightly convex.
An apron, uvula or ornamentation are absent. However, a small, poorly developed uvula is present.
The root stem is relatively high and oval-shaped in cross-section. The root base gradually widens in all directions downward, is bilobed, and has a smooth root base edge. A deep basal groove is present, but tends to close by merging of both root base surfaces, including a large central foramen. Root coating is absent.

MALES

The crown base is more or less oval in occlusal view, with a rounded inner extension. The elongated, slender principal cusp of anterior, lateral and posterior teeth is vertically erect and constricted just above the base. Lateral teeth slightly incline toward the commissure. An apron, uvula or ornamentation are absent. The inner and outer faces are both strongly convex.
The broad root stem is rather high and oval to almost circular in cross-section. The root is extremely high, widens in all directions downward, forming a large base with two well developed root lobes. Both have more or less flat basal surfaces. A median groove has disappeared, leaving only an outer central foramen and sometimes a small inner central foramen. A small band of root coating is present near the crown-root junction.

Genus: *Irolita,* WHITLEY, 1931

This genus is presently monotypic with *I. waitii* (McCULLOCH, 1911), but another not yet described species was discovered in NW Australian waters (LAST & STEVENS, 1994).

Irolita waitii (McCULLOCH, 1911)
(Plates: 15 to 18; textfigure 4)

Raja waitii McCULLOCH, 1911. Rep. Fish. obtained by R/V 'Endeavour' , part 1, 1: 87.

HETERODONTY

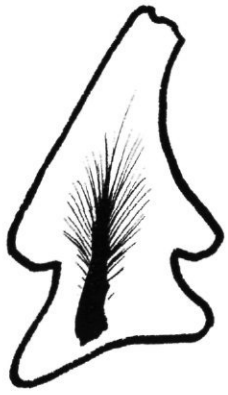
The dentition is gradient monognathic heterodont. Indistinct sexual heterodonty present in adults only, in that females show a low crown, in which the cusp is replaced by a median keel, and a broader crown base. In contrast, males exhibit a true cusp, that is erect and elongated in anterior teeth. Due to lack of a juvenile, ontogenetic heterodonty could not be examined, but juvenile teeth may very likely be similar to the female type of dentition.

VASCULARIZATION

The teeth show an adapted holaulacorhizid root type with a large, elongated pulp cavity in the root area, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine was not observed, and inner lateral foramina are absent. (See textfigure 4)

FEMALES

The crown base is semi-oval in occlusal view, with the outer part more or less forming an angle in the mid-section. Mesial and distal cutting edges of the crown are convexly arched and form a medial keel. Apron, uvula, inner and outer ornamentation are absent.



Textfigure 4.
Irolita waitii *tooth histological cross-section.*

The inner surface is flat to slightly concave, and the outer one is concave.
The broad root stem is relatively high and oval-shaped in cross-section. The bilobed root strongly widens in all directions and forms a large base. A deep basal groove encloses a rather large central aperture. Root coating is absent.

MALES

The crown base is more or less oval in occlusal view, with a rounded inner extension. The elongated, rather massive principal cusp of anterior teeth is vertically erect and constricted just above the base. Lateral and posterior teeth become asymmetrical posteriorly closer toward the commissure. Apron, uvula or ornamentation are absent, but the inner crown base is angled in the mid-section. The outer face is flat, whereas the outer one is slightly convex. The broad root stem is relatively high and oval in cross-section. The root widens in all directions downward to form a large base with two well developed root lobes. Both have more or less flat basal surfaces. A deep median groove encloses a large central aperture. Root coating is absent.

Genus: *Notoraja* ISHIYAMA, 1958

The genus comprises the three described species *N. ochroderma, N. subtilispinosa* and *N. tobitukai* (type species) and three further undescribed species in Australian waters (LAST & STEVENS, 1994, MCEACHRAN & LAST, 1994).

Notoraja tobitukai (HIYAMA, 1940)
(Plates: 19 & 20; textfigure 5)

Raja tobitukai, HIYAMA, 1940. Japanese Journal of Zoology, 9(1): 169.

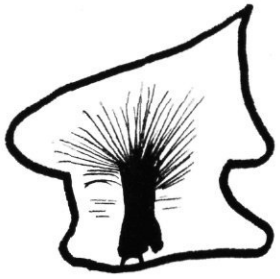
Note: Only an adult male was well preserved, with tooth structures being intact. Teeth of the only available adult female were badly affected by formaldehyde and did not reveal all odontological characters. However, as far as could be observed, the female seems to exhibit a tooth morphology similar to that of the male.

HETERODONTY

The dentition is gradient monognathic heterodont. Sexual heterodonty appears to be absent. A juvenile was not available for examination, and therefore ontogenetic heterodonty could not be examined.

VASCULARIZATION

The teeth show an adapted holaulacorhizid or secondary hemiaulacorhizid root type with a large, elongated pulp cavity in the root area, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine was not observed, and inner lateral foramina are absent. (See textfigure 5)



Textfigure 5.
Notoraja tobitukai *tooth histological cross-section.*

MALES AND FEMALES

The crown base is more or less quadrangular in occlusal view, with both outer and inner edges bluntly angled medially. The well developed, massive and low crown is slightly pointed inward, and mesial and distal cutting edges are concavely arched. The outer surface is slightly convex. The arched outer crown base overhangs the crown-root junction and is shaped like a very broad apron on anterior teeth. Apron, uvula and inner or outer ornamentation are absent.
The root stem is relatively high and oval in cross-section. The root strongly widens in all directions, forming a large base with slightly undulated margins. A median groove is absent, but outer and inner foramina reveal a secondarily hemiaulacorhizid type of root. Root coating is absent.

Genus: *Pavoraja* WHITLEY, 1939

The listing of taxa of this genus was given in Part B, 1b of this series.

Subgenus: *Insentiraja* YEARSLEY & LAST, 1992

This subgenus is presently monotypic with *P. laxipella*, but another yet undescribed species is mentioned by LAST & STEVENS (1994) from Australian waters.

Pavoraja (Insentiraja) laxipella YEARSLEY & LAST, 1992
(Plates 21 & 22; textfigure 6)

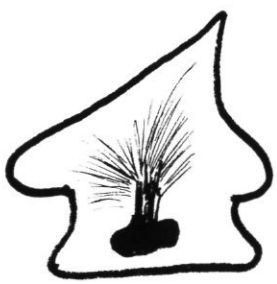
Pavoraja (Insentiraja) laxipella YEARSLEY & LAST, 1992. Copeia 1992(3): 839.

HETERODONTY

The dentition is gradient monognathic heterodont. The lack of an adult male made it impossible to observe sexual and ontogenetic heterodonty. Females possess a low semi-central cone.

VASCULARIZATION

The teeth show an adapted kind of holaulacorhizy with a low, large pulp cavity in the root section, with vertical strings of vascular canals from which semi-parallel tubes of the circumpulpar dentine radiate into crown and root. Osteodentine was not observed, and inner lateral foramina are absent. (See textfigure 6)



Textfigure 6.
Pavoraja (Insentiraja) laxipella *tooth histological cross-section.*

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. Apron, uvula and ornamentation are absent. A semi-central cone is present on the cusp on the crown. The inner face shows a slightly concave surface, the outer one is slightly convex. The inner and outer basal crown rims are 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 outer margin of the root base is weakly undulated. A basal groove is absent, an outer foramen present. Root coating is absent.

Subgenus: *Pavoraja* MCEACHRAN, 1994

The subgenus comprises after MCEACHRAN & MIYAKE, (1990b) the species *P. alleni* and *P. nitida* (type species) and four undescribed ones, which are mentioned and illustrated in LAST & STEVENS (1994).

Pavoraja (Pavoraja) nitida (GÜNTHER, 1880)
(Plates: 23 to 26; textfigure 7)

Raja nitida GÜNTHER, 1880. Report on the shore fishes collected by H.M.S. Challenger, Part 6: 27, London.
Chemical reaction during the cleaning process of the teeth. This "ornamented" appearance should not be misunderstood as an odontological character. In fact, the tooth surfaces are completely smooth.

HETERODONTY

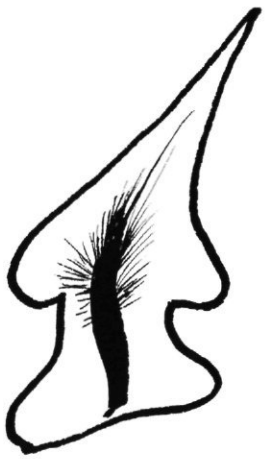
The dentition is gradient monognathic heterodont. Sexual heterodonty is presented in adults only, in that males bear on anterior teeth an elongated cusp, which becomes lower on teeth toward the commissure. Females only possess a low semi-central cone. Ontogenetic heterodonty is documented only in juvenile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

VASCULARIZATION

The teeth show an adapted kind of holaulacorhizy or secondary hemiaulacorhizy, with relatively narrow and elongted pulp cavity in the root section, from which semi-parallel tubes of the circumpulpar dentine radiate into crown and root part. Osteodentine was not observed, and inner lateral foramina are absent. (See textfigure 7)

FEMALES

The crown base is semi-oval in occlusal view. Inner and outer faces are not always strictly divided, and mesial and



Textfigure 7.
Pavoraja (Pavoraja) nitida *tooth histological cross-section.*

distal cutting edges are only present in anterior teeth. Apron, uvula and ornamentation are absent. A semi-central cone is present on the crown. The anterior teeth have non-arched cutting edges, forming a triangular shape of the crown. The inner face shows a slightly concave surface, the outer one is slightly convex. Inner and outer basal crown rims are smooth.
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 outer margin of the root base is weakly undulated. A wide, shallow, basal groove may be 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, narrowly elongated, erect cusp. Mesial and distal cutting edges are absent. Inner and outer surfaces are convex, and the inner and outer basal crown rims are smooth. The cusp becomes lower and the outer crown surface plainer on teeth toward the commissure. 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 outer margin of the root base is weakly undulated. A basal groove is absent in most of the teeth but a large outer foramen always present. Roots are coated is present on the upper part of the root stem.

Genus: *Pseudoraja* BIGELOW & SCHROEDER, 1954

The genus is monotypic with *P. fischeri.*

Pseudoraja fischeri BIGELOW & SCHROEDER, 1954
(Plates: 27 to 30; textfigure 8)

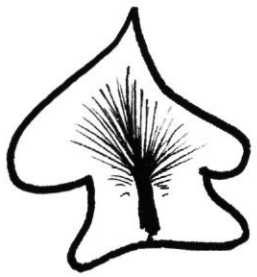
Pseudoraja fischeri BIGELOW & SCHROEDER, 1954. Breviora, 24: 4.

HETERODONTY

The dentition is gradient monognathic heterodont. The lack of an adult male made it impossible to establish sexual and ontogenetic heterodonty. However, a subadult male reveals a dentition similar to that of an adult female examined, which possesses a low semi-central tooth cone.

VASCULARIZATION

The teeth show an adapted holaulacorhizid or secondary hemiaulacorhizid root type with a narrow, elongated pulp cavity in the root area, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine was not observed, and inner lateral foramina are absent. The inner and outer foramina could not be made visible. (See textfigure 8)



Textfigure 8.
Pseudoraja fischeri *tooth histological cross-section.*

FEMALES AND MALES

The crown base is semi-oval in occlusal view, with an arched outer edge and an inner one with a medial protuberation. The crown bears a well developed, centrally situated cone. Mesial and distal cutting edges are absent. Apron, uvula, inner and outer ornamentation are absent. The inner surface is weakly convex, the outer one is flat. The root stem is relatively low and more or less oval in cross-section. The root widens in all directions to form a large base with weakly multilobed inner face. A basal groove is poorly developed, often partly closed in lateral, and completely closed in posterior teeth, corresponding to secondary hemiaulacorhizy and secondary anaulacorhizy, respectively. Root coating is absent.

Genus: *Raja* LINNAEUS, 1758

The listing of the taxa of this genus is given in the previous issue B, 1b.

Subgenus: *Atlantoraja* MENNI, 1972

This subgenus comprises the species *R. castelnaui, R. cyclophora* (type species) and *R. platana.*

Raja (Atlantoraja) cyclophora REGAN, 1903
(Plates: 31 to 34; textfigure 9)

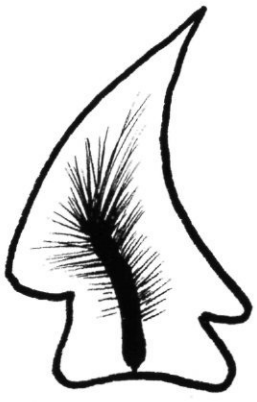
Raja cyclophora REGAN, 1903. Proceedings of the Zoological Society, London, 2: 60.

HETERODONTY

The dentition is gradient monognathic heterodont, but with a significant difference in the morphology between anterior teeth on the one, and lateral and posterior teeth on the other hand. The anterior teeth have an elongated principal cusp arising from a broad crown base. The lateral and posterior teeth have a low principal cusp. An adult female was not available for examination, but the low tooth cusps of a juvenile male indicate sexual heterodonty. Ontogenetic heterodonty is documented by female-like characters in the juvenile male.

VASCULARIZATION

The teeth show an adapted holaulacorhizid root type with a narrow, elongated pulp cavity in the root area, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine was not observed, and inner lateral foramina are absent. The inner and outer foramina could not be made visible.
(See textfigure 9)



Textfigure 9.
Raja (Atlantoraja) cyclophora *tooth histological cross-section.*

MALES

The crown base is semi-circular in occlusal view. The anterior teeth bear a well developed, broad-based cusp with a narrowly elongated, inward directed cone without mesial and distal cutting edges but an outer cutting edge. Lateral and posterior teeth exhibit a flat crown, with convexly arched mesial and distal cutting edges, which almost form a transversal keel becoming gradually lower and asymmetrical on teeth closer toward the commissure. The inner surface is concave, the outer one flat to slightly convex, showing an indistinct, finely reticulated ornamentation. Apron, uvula and inner ornamentation are absent. The root stem is relatively low and more or less oval in cross-section. The root base widens in all directions to form a large base. A deep basal groove encloses one or two central foramina. Root coating is present on the upper part of the root stem.

Subgenus: *Raja (Okamejei)* ISHIYAMA, 1958

The subgenus comprises the following 13 species: *R. acutispina, R. australensis, R. boesemani, R. cerva, R. dentata, R. heemstrai, R. hollandi, R. kenojei* (type species as senior synonym of originally designated *R. fusca*), *R. lemprieri, R. meerdervoortii, R. polyommata, R. powelli and R. schmidti.* Judging from descriptive texts and illustrations by LAST & STEVENS (1994) of further undescribed species in Australian waters, apparently more species of this subgenus are existing.

Raja (Okamejei) kenojei MÜLLER & HENLE, 1841
(Plates: 37 to 39; textfigure 10)

Raja kenojei MÜLLER & HENLE, 1841. Systematische Beschreibungen der Plagiostomen: 149.

HETERODONTY

The dentition is gradient monognathic heterodont. Due to the lack of an adult male it is impossible to establish sexual and ontogenetic heterodonty. However, a sub-adult male reveals a dentition similar to that of the adult female examined, which possesses a low, semi-central tooth cone.

VASCULARIZATION

The teeth show an adapted holaulacorhizid to secondary hemiaulacorhizid root type with a broad, elongated pulp cavity in the root area, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine was not observed, and inner lateral foramina are absent. (See textfigure 10)

Textfigure 10.
Raja (Okamejei) kenojei *tooth histological cross-section.*

FEMALES AND FEMALES

The crown base is semi-oval in occlusal view, with an arched outer edge and an inner one with a medial protuberation. The crown bears a well developed, centrally situated cone. Mesial and distal cutting edges are convexly arched. Apron, uvula, inner and outer ornamentation are absent. The inner surface is weakly convex, the outer one is flat.
The root stem is relatively high and more or less oval in cross-section. The root widens in all directions to form a large base. A basal groove is poorly developed and completely closed in posterior teeth. Root coating is present at the upper part of the root stem.

Genus: *Rhinoraja* ISHIYAMA, 1952

The genus comprises the species *R. kujiensis* (type species), *R. longicauda, R. odai* and *R. taranetzi.*

Rhinoraja longicauda ISHIYAMA, 1952
(Plate: 40; textfigure 11)

Rhinoraja longicauda ISHIYAMA, 1952. Journal of the Shimonoseki College of Fisheries, 2(1): 25.

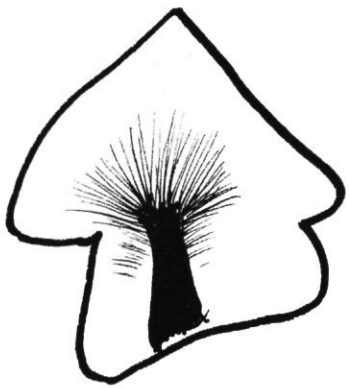
Note: The poor condition of the available teeth has limited the odontological examination, and the plates are a selection of their best possible illustration. Their description is given with all reservation only.

HETERODONTY

The dentition is gradient monognathic heterodont, but with a significant difference in the morphology between anterior teeth on the one, and lateral and posterior teeth on the other hand. The anterior teeth have an elongated principal cusp arising from a broad crown base. The lateral and posterior teeth have a low principal cusp. Sexual heterodonty is documented by lower and broader crowns of all female teeth. Although a juvenile was not available for examination, ontogenetic heterodonty is to be expected, because juveniles use to exhibit female-like characters.

VASCULARIZATION

The teeth show an holaulacorhizid root type with a large, elongated pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine is present in the inner part of the root. Inner lateral foramina are absent. (See textfigure 11)



Textfigure 11.
Rhinoraja longicauda *tooth histological cross-section.*

FEMALES

The crowns of anterior teeth are broad and oval-shaped, becoming semi-circular closer toward the commissure. The outer edge is arched, and the inner one exhibits a medial protuberation due to the presence of an uvula. A cusp or cone are absent. A transverse keel separates inner and outer parts of the crown. An apron, inner and outer ornamentation are absent, but a small, well developed uvula is present at the inner crown base. The root stem seems to be moderately high. Root lobes are branched, exhibiting a deep median groove. Root coating is absent.

MALES

The crown base is semi-circular in occlusal view. The anterior teeth bear a well developed broad-based cusp with a triangularly, elongated, inward directed cone, mesial and distal cutting edges of which are non-arched. Lateral and posterior teeth exhibit a flat crown, the more or less convexly arched mesial and distal cutting edges of which almost merge to a low cusp becoming gradually lower and asymmetrical in teeth closer toward the com-

missure. The inner surface is concave, the outer one flat to slightly convex. Apron,inner and outer ornamentation are absent. A well developed uvula seems to be present. The root stem is relatively low and more or less oval in cross-section. Vertically, the root base widens in all directions to form a large base. A deep basal groove encloses a large foramen. Root coating seems to be absent.

Differential diagnosis

Teeth of representatives of the following supraspecific taxa of the Rajoidei were so far examined, described and illustrated in issues 1a, 1b and the present one of part B of this series: *Anacanthobatis (Schroederobatis), Anacanthobatis (Springeria), Arhynchobatis, Bathyraja, Breviraja, Cruriraja, Dactylobatus, Gurgesiella (Fenestraja), Gurgesiella (Gurgesiella), Irolita, Malacoraja, Neoraja, Notoraja, Pavoraja (A), Pavoraja (Insentiraja), Pavoraja (Pavoraja), Psammobatis, Pseudoraja, Raja (Amblyraja), Raja (Atlantoraja), Raja (Dipturus), Raja (Leucoraja), Raja (Okamejei), Raja (Raja), Raja (Rajella), Raja (Rostroraja), Raja (Rioraja), Rhinoraja* and *Sympterygia*. Three morphotypes of the genus *Bathyraja* were examined, described and illustrated, with the examples *B. albomaculata, B. richardsoni* and *B. spinicauda* representing the shallow water, deep water and transitional morphotype, respectively (STEHMANN, 1986). Both, *Raja (Rajella) fyllae* and *R. (Rajella) bathyphila* were examined, described and illustrated, representing two intrasubgeneric morphotypes (STEHMANN, unpublished data). The teeth of *Raja lintea* were also described.

Selection of the odontological characters

The odontological characters of living Rajoidei were never defined with regard to their phylogenetic significance. The following odontological characters were observed during the examinations:

1. Two types of monognathic heterodonty:
1a.1 All teeth are morphological identical, and only their height is reduced closer toward the commissure. Their principal cusp is not oblique toward the commissure but is always vertically erect.
1a.2 As 1a.1, but some morphological characters modified in lateral and posterior teeth.
1b.1 All teeth morphologically identical, but: principal cusp of anterior teeth symmetrical, whereas in lateral teeth gradually becoming asymmetrical closer toward the commissure through a more oblique principal cusp, and in posterior teeth with an extremely oblique or even a vertically erect cusp.
1b.2 Same as 1b.1, but with some morphological characters modified in lateral and posterior teeth.
2. Principal cusp may be low, sometimes only appearing as a transverse keel, or may show a narrow, elongated cusp, placed concentrically or eccentrically on the crown base.
3. The root shape and height.
4. The development of an uvula. Some taxa have developed a distinct uvula supported by a protuberation of the inner root part.
5. The development of an apron. Some taxa have developed an apron, which is always involved in interlocking of the teeth in a row.
6. The development of mesial and distal cutting edges. Some taxa have concavely arched cutting edges, whereas others have convexly arched ones. Several taxa show only partly developed cutting edges, or these are even absent.
7. The presence of an outer cutting edge.
8. The presence of root coating.
9. Multilobation of the root.
10. Sexual heterodonty.

See also textfigure 1 of Part B, 1a of this series.

Analysis of the odontological characters resulted in a grouping of primary and secondary features.

Primary odontological characters

The development of the principal cusp in relation to the jaw position of teeth concerned divides the Rajoidei into two suprageneric groups. In the one group, the principal cusp is always vertically erect in teeth at all jaw positions, or sometimes slightly inclining (1a.1). This condition applies to the following supraspecific taxa: *Anacanthobatis (Springeria), Arhynchobatis, Bathyraja, Cruriraja, Dactylobatus, Neoraja, Notoraja*, Pavoraja (A), Pavoraja (Insentiraja)*, Pavoraja (Pavoraja), Pseudoraja*, Raja (Amblyraja), Raja (Dipturus), Raja (Okamejei)*, Raja (Leucoraja), Raja (Raja), Raja (Rajella)*, and *Raja (Rostroraja)*. However, the lateral and posterior teeth show flattening outer crown surfaces (1a.2) in some taxa, which condition is considered as a variation of odontological character 1a.1 defined above. This phenomenon is found in *Neoraja*.

In the other group, the principal cusp is oblique toward the commissure from the antero-lateral positions to the posterior ones (1b.1). This is the case in the following supraspecific taxa: *Anacanthobatis (Schroederobatis), Breviraja, Gurgesiella (Fenestraja), Gurgesiella (Gurgesiella), Irolita, Malacoraja, Raja (Atlantoraja), Psammobatis, Raja (Rioraja), Rhinoraja** and *Sympterygia*. This group exhibits a variation, in that some taxa have lateral and commissural teeth with outer crown surfaces becoming flatter, and commissural teeth with the principal cusp becoming vertically erect again (1b.2). This phenomenon is found in the taxa: *Gurgesiella (Fenestraja), Malacoraja, Raja (Atlantoraja), Raja (Rioraja)*, and *Sympterygia*.

The bad condition of the teeth of *Notoraja, Raja (Okamejei)* and *Rhinoraja* and the lack of adult males of *Pseudoraja* and *Pavoraja (Insentiraja)* made several important odontological features impossible to examine. They are therefore tentatively assigned to their group and marked with*. Their odontological comparison with the other supraspecific taxa is with all reservation only.

Both groups are defined by character complexes of supraspecific significance, i.e. by the shape of the principal cusp combined with the root shape, in some cases even more specific by the presence or absence of an apron and/or uvula and by the root height.

Secondary odontological characters

Some taxa of both groups have an outer, third cutting edge, which is present in teeth of the following genera and subgenera: *Raja (Amblyraja) radiata*-type, *Raja (Rioraja), Sympterygia, Anacanthobatis (Schroederobatis)* and more or less also in *Gurgesiella (Gurgesiella)*.
In most genera and subgenera both, mesial and distal cutting edges of the teeth are concavely arched. However, they have convexly arched mesial and distal cutting edges in the following genera and subgenera: *Breviraja, Irolita, Rhinoraja, Sympterygia, Anacanthobatis (Schroederobatis), Arhynchobatis, Raja (Raja)*, only in lateral and posterior teeth of *Raja (Atlantoraja)* and in posterior teeth of *Bathyraja albomaculata*-type and *Malacoraja*.
Root coating is observed on upper part of the root stem of the following taxa: *Dactylobatus, Raja (Rajella), Pavoraja (A), Pavoraja (Pavoraja), Raja (Leucoraja), Gurgesiella (Gurgesiella), Malacoraja* and *Notoraja*.
Multilobation of the root is mostly occurring in juvenile specimens of some taxa. In several taxa, some adults present a weak root lobation of lateral and posterior teeth, namely in: *Anacanthobatis (Schroederobatis), Gurgesiella (Fenestraja)* and *Gurgesiella (Gurgesiella)*.

Sexual heterodonty

Roughly half of the genera and subgenera of the Rajoidei exhibit sexual heterodonty, as shown in the following list.

Sexual heterodonty:	Sexual homodonty:
Anacanthobatis (Schroederobatis)	*Anacanthobatis (Springeria)*
Cruriraja	*Arhynchobatis*
Gurgesiella (Gurgesiella)	*Dactylobatus*
Gurgesiella (Fenestraja)	*Bathyraja spinicauda*-type
Irolita	*Bathyraja richardsoni*-type
Malacoraja	*Pseudoraja**
Neoraja	*Raja (Amblyraja) radiata*-type
Pavoraja (A)	*Raja (Dipturus)*
*Pavoraja (Insentiraja)**	*Raja (Leucoraja)*
Pavoraja (Pavoraja)	*Raja (Okamejei)*
Psammobatis	*Raja (Rioraja)*
Raja (Atlantoraja)	*Raja (Rostroraja)*
Raja (Raja)	*Notoraja*
Rhinoraja	
Sympterygia	

Only weak sexual heterodonty is exhibited in *Breviraja*.

Sexual heterodonty is demonstrated by the tooth morphology of females, which is more or less intermediate between the rather flat crowns of juveniles and the high, elongated crowns of mature males.
There are two types of tooth morphology in case of sexual homodonty: the principal cusp is either low or high.A low principal cusp is exhibited in teeth of the following genera and subgenera:
Anacanthobatis (Springeria), Notoraja, Pseudoraja, Raja (Dipturus), Raja (Okamejei), Raja (Rostroraja), Rhinoraja* and *Arhynchobatis*.
In contrast, a high, more or less elongated principal cusp is exhibited in the genera and subgenera:
Dactylobatus, Bathyraja spinicauda, Cruriraja, Raja (Amblyraja), Raja (Leucoraja), Raja (Rioraja) and *Bathyraja richardsoni*-type.
Very likely, sexual heterodonty is an intermediate stage of evolutionary development only and should therefore not be used as an odontological distinctive character.

Both rajoid groups are further separated by primary character complexes like the shape of the principal cusp, combined with the root shape and height, and in some cases the presence or absence of an apron and/or uvula offer more specific distinctions. To exclude influence of sexual heterodonty, only males are used for the division of taxa by odontological characters.

Group 1

Neoraja is separated from the other genera and subgenera of this group by having low, little branched root lobes. Of the remaining taxa, *Anacanthobatis (Springeria), Arhynchobatis, Bathyraja, Cruriraja, Dactylobatus, Pavoraja (A.), Pavoraja (Insentiraja), Pavoraja (Pavoraja), Raja (Amblyraja), Raja (Leucoraja), Raja (Rajella)* and *Raja (Rostroraja)* have widely branched root lobes. *Raja (Raja)* and *Raja (Dipturus)*, in contrast, have a triangle-shaped principal cusp and a short and massive root. The teeth of *Raja (Raja)* are narrower based than those of *Raja (Dipturus)*, and teeth of the latter have a more or less apron-shaped outer crown base.
Investigation of further species of the subgenus *R. (Dipturus)* revealed a second species-group within this subgenus with a very different tooth morphology. Examples of the latter are *R. (Dipturus) nidarosiensis* and *R. (Dipturus) doutrei*. They can easily be distinguished by their elongated, relatively narrow-based principal tooth cusp exhibiting a well developed outer ornamentation (see plates: 35 and 36)

Anacanthobatis (Springeria), Arhynchobatis, Notoraja, Raja (Okamejei) and *Pseudoraja** possess teeth with an extremely low principal cusps and a low root. Teeth of *Arhynchobatis* still show a triangle-shaped principal cusp, whereas only a transverse ridge is existing in *Anacanthobatis (Springeria)*. Insufficient information about the odontological characters of *Notoraja, Raja (Okamejei)* and *Pseudoraja* does not allow to make further distinctions.

Cruriraja and all three morphotypes of *Bathyraja* can easily be distinguished by an extremely high tooth root. *Cruriraja*, however, has a holaulacorhizid type of root, with a narrow median groove or even a secondary hemiaulacorhizid one, whereas the root in *Bathyraja* is strictly holaulacorhizid, with a deep and broad median groove.

The three different morphotypes of *Bathyraja* can also be distinguished by their tooth morphology. All share the character of an elongated principal tooth cusp and a very high root. However, the *B. richardsoni*- and *B. spinicauda*-types share a principal cusp constricted just above its base, resulting in concavely arched cutting edges, whereas the principal cusp is more or less triangle-shaped in the *B. albomaculata*-type. The principal cusp in *B. richardsoni* is significantly narrower based than *B. spinicauda*.

Raja (Leucoraja) and *Raja (Rostroraja)* are characterized by the presence of an apron. They can easily be separated by a broad crown base in the latter taxon but a narrow one in *Raja (Leucoraja)*.

Pavoraja (A.), Pavoraja (Insentiraja), Pavoraja (Pavoraja) and *Raja (Rajella) fyllae*-type differ from *Dactylobatus, Raja (Amblyraja)* and *Raja (Rajella) bathyphila*-type by the presence of an uvula at the crown base of the latter three. *Pavoraja (A.), Pavoraja (Insentiraja)* and *Pavoraja (Pavoraja)* are odontologically similar, whereas *Raja (Rajella) fyllae*-type is different in having a broader based cusp. *Dactylobatus* and *Raja (Amblyraja)* differ from eachother by a shorter principal cusp of *Dactylobatus*, and both differ from *Raja (Rajella) fyllae*-type by the strongly convex outer face of the crown of the latter one, appearing like an outer cutting edge.

Group 2

Anacanthobatis (Schroederobatis), Sympterygia and *Raja (Rioraja)* are distinguished from all other taxa of this group by having a principal cusp of anterior teeth, that is eccentrically situated on its base. *Sympterygia* has a holaulacorhizid type of root, with a well developed median groove, whereas *Anacanthobatis (Schroederobatis)* and *Raja (Rioraja)* have a secondary hemiaulacorhizid type of root. The tooth morphology of species of *Anacanthobatis (Schroederobatis)* and *Raja (Rioraja)* is very similar.

Malacoraja and *Raja (Atlantoraja)* can be separated from the other taxa of their group by having a narrow and elongated principal cusp on anterior teeth and low, little branched root lobes. *Malacoraja* has a narrower based, more elongated principal cusp than *Raja (Atlantoraja)*. *Psammobatis, Pseudoraja* and *Breviraja* differ from the other group taxa by having a low triangular cusp. *Pseudoraja* has a much lower principal cusp than *Psammobatis* and *Breviraja*. The latter two are difficult to separate, because of their very similar odontological characters.

Gurgesiella (Fenestraja) and *Gurgesiella (Gurgesiella)* can be separated by a secondary hemiaulacorhizid type of root. However, *G. (Gurgesiella)* possesses an uvula, which is absent on teeth of *G. (Fenestraja)*.

From the odontological point of view, *Raja lintea* shares many characters with *Bathyraja*, particularly with the *Bathyraja spinicauda*-type, by having a very high root and broad based principal cusp, that is constricted just above the its base, with a well developed uvula.

Conclusions

Considering the low number of rajoid species known from the Cretaceous up to the upper Miocene and, in contrast the great specific diversity of living rajoid taxa, it is very likely that we are witnessing a possible explosive evolutionary development being still in progress to date. Examples of such phenomenon are well known to palaeontologists through other early developments in various groups of chondrichthyans. These were often characterized by taxa, which rapidly developed new specific or generic characters, as well as by taxa, in which these characters changed only slowly.

Odontologically, the large number of living taxa of Rajoidei shows relatively little intergeneric differentiation but many intergrades of development, as revealed in the differential diagnosis above. The ongoing evolutionary process of speciation likewise affects many other character complexes of external and internal body morphology and explains the difficulty of establishing an indisputable systematic classification for the Rajoidei.

The suborder Rajoidei may thus be split into two suprageneric groups eventually at family level, based on odontological characters specified above.

A comparison of the primary odontological characters found in the Rajoidei with the well known and distinctive odontological characters of the Selachii (see Part A of this series) results in subdividing the rajoid groups 1 and 2 into four and three subgroups, respectively, of which some exhibit a more specific subdivision as shown below (see also textfigure 12):

Group 1 (Principal cusp laterals posteriors vertically erect)

Subgroup 1
Cusp narrow and elongated,
Root lobes branched:
Root low:Apron absent:

Uvula present:	Uvula absent:
Raja(Rajella) bathyphila	*Pavoraja (Subgenus A)*
Dactylobatus	*Pavoraja (Pavoraja)*
Raja (Amblyraja) radiata	*Pavoraja (Insentiraja)*
	Raja (Rajella) fyllae-**type**

Apron present:
Raja (Leucoraja)
Raja (Rostroraja)

Root high:
Bathyraja
Cruriraja

Rootlobes unbranched:

Principal cusp triangular	Principal cusp anteriors narrow & elongated
Root massive:	Root low:
Raja (Raja)	*Neoraja*
Raja (Dipturus)	

Principal cusp low,
Root low:
Anacanthobatis (Springeria)
Arhynchobatis
Notoraja
*Pseudoraja**
Raja (Okamejei)

Group 2 (Principal cusp laterals & posteriors oblique)

Subgroup 1
Principal cusp eccentrical:

Root hemiaulacorhizid	Root secondary hemiaulacorhizid
Anacanthobatis (Schroederobatis)	*Gurgesiella (Fenestraja)*
Sympterygia	*Gurgesiella (Gurgesiella)*
Raja (Rioraja)	

Principal cusp anteriors elongated	Principal cusp triangular
Irolita	*Breviraja*
Malacoraja	*Psammobatis*
Raja (Atlantoraja)	
Rhinoraja?	

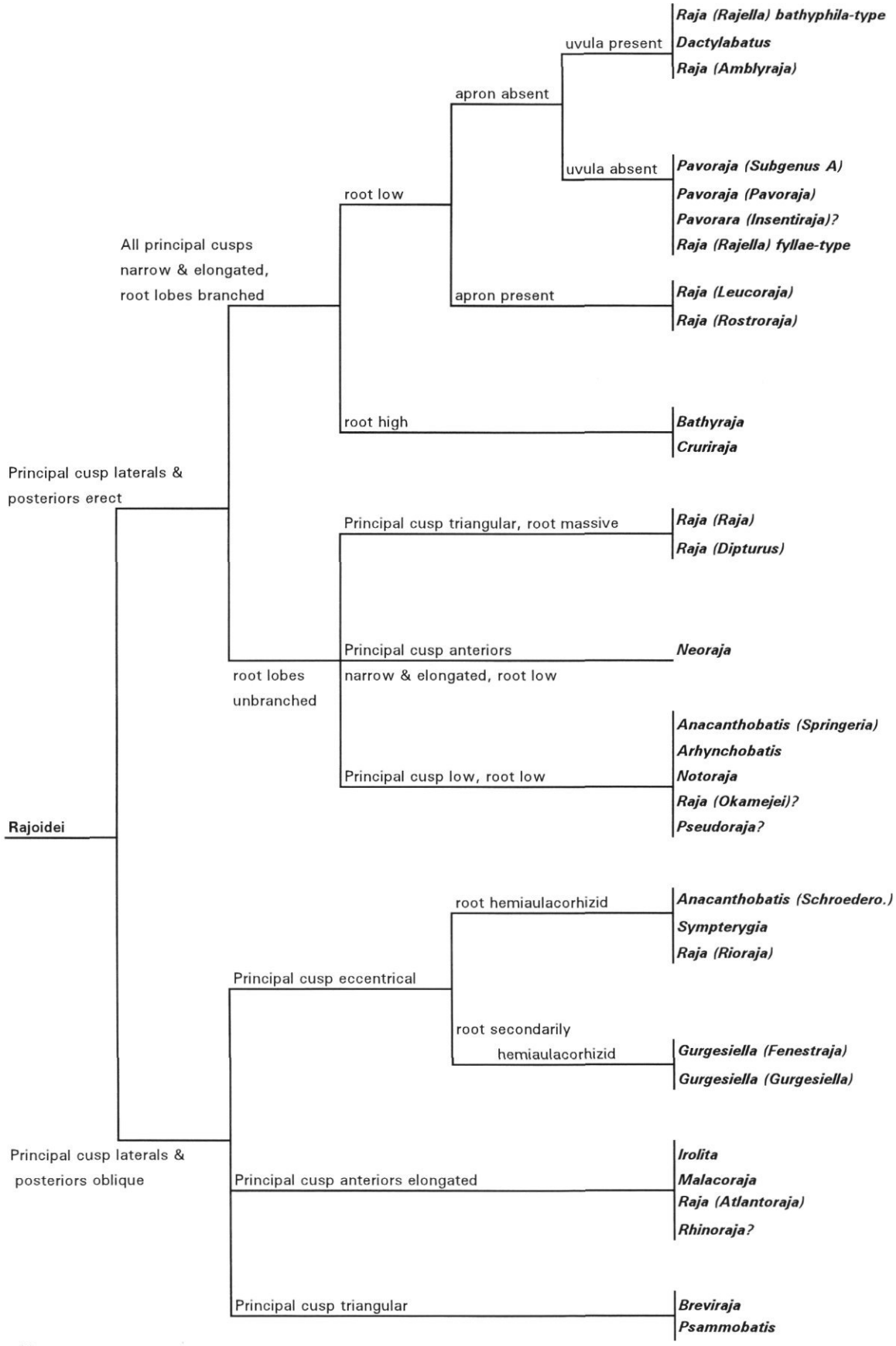
Like conclusions drawn from odontological characters of the Selachii, each of these rajoid subgroups may well represent generic level, supporting to lump the taxa within each group to one genus.
The three morphotypes of *Bathyraja* can be distinguished also by odontological characters. However, a comparison based only on one representative of each morphotype is not sufficient to ascertain a subdivision within the genus. *Raja lintea* is odontologically very similar to the *Bathyraja spinicauda*-morphotype.

The bad condition of teeth available of *Raja (Okamejei)*, *Notoraja* and *Rhinoraja*, and the lack of adult males of *Pseudoraja* and *Pavoraja (Insentiraja)* allowed a tentative positioning only within their groups, respectively.

Secondary odontological characters, like the development of cutting edges, root coating, crown ornamentation and basal root ornamentation, will be of use only interspecifically.
Multilobated tooth roots are mostly observed in immature specimens and therefore considered as a juvenile character. Half grown specimens, often misdetermined as sexually mature, may still show a weakening multilobation.
Sexual heterodonty may very likely be an intermediate stage between a dentition with a low principal cusp and the one with a high, elongated principal cusp and seems not to be depending on certain taxa. It is observed in taxa of both groups.

Type of vascularization

The tooth vascularization system of all taxa was also examined, described and illustrated. All vascularization types showed the same principle: a more or less large pulp cavity situated in the root centre, which is connected to apertures that are mostly found in the centre of a median groove in case of a holaulacorhizid types of root, or on the inner and/or outer faces of the root in case of secondary hemiaulacorhizy (HOVESTADT & HOVESTADT, 1993). One or two additional inner and/or outer foramina may be present sometimes just above the median groove, and these are connected to the pulp cavity too. In a few cases, foramina directly connected to the pulp cavity are present in the folds of multilobated roots. They are probably the remains of mesial and distal inner foramina. The pulp cavity is always surrounded by orthodentine, even in the root area, from which the vascular capillary tubes of the orthodentine radiate from the pulp cavity into root and crown. Large teeth have some osteodentine in the root base. Although all teeth examined were strictly orthodont and almost all showed a median groove at their base, their roots are not strictly holaulacorhizid (*sensu* CASIER, 1947c). Mesial and distal inner foramina, an important character for holaulacorhizy, are lacking and are probably got lost through the dominance of the orthodentine in the root. However, generally all further characters of a holaulacorhizid type of root (or secondary hemiaulacorhizy, which is a modification of holaulacorhizy) are present. Although numerous differences in their external and internal morphology have led in the past to the subdivision of the Rajoidei into numerous supraspecific taxonomic units, the very similar root vascularization of all rajoid taxa may indicate their still very close interrelationship.
Previous issues on sharks of this series have provided odontological keys for identification of the different genera and subgenera of an order or a family by their



Textfigure 12.
Odontological characteristics of the Rajoidei taxa examined.

tooth morphology only. Such keys cannot be given for the Rajoidei due to the strong sexual heterodonty existing in about half of the rajoid taxa, because their odontological characters were based on male specimens only, and because of significant morphological differences between anterior, lateral and posterior teeth found in several taxa.

The results of this study, as far as taxonomic conclusions are concerned, appear similar to those of the classification by MCEACHRAN & MIYAKE, (1990a), based on a wide scope of characters other than odontology. Although their grouping of taxa is concurrent to some degree with ours, based only on odontological characters, the group-assignment of taxa differs considerably with regards to the interpretation of phylogenetic interrelationships of the individual taxa.

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Bibliography

CASIER, E., 1947c. Constitution et evolution de la racine dentaire des Euselachii III. Evolution des principaux des Euselachii. *Bulletin de Musée royal d'Histoire naturelle de Belgique*, 23 (15): 45.

HERMAN, J., HOVESTADT-EULER, M., HOVESTADT, D. & STEHMANN, M., 1994. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes. Part B Batomorphii No. 1a: Order Rajiformes - Suborder Rajoidei - Family: Rajidae Genera and Subgenera: *Anacanthobatis (Schroederobatis), Anacanthobatis (Springeria), Breviraja, Dactylobatus, Gurgesiella (Gurgesiella), Gurgesiella (Fenestraja), Malacoraja, Neoraja* and *Pavoraja*. Ed. Stehmann, M. *Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Biologie*, **64**: 165-207.

HERMAN, J., HOVESTADT-EULER, M., HOVESTADT, D. & STEHMANN, M., 1995. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes. Part B Batomorphii No. 1b Order Rajiformes - Suborder Rajoidei - Family: Rajidae Genera and Subgenera: *Bathyraja* (with a deep-water, shallow-water and transitional morphotypes), *Psammobatis, Raja (Amblyraja), Raja (Dipturus), Raja (Leucoraja), Raja (Raja), Raja (Rajella)* (with two morphotypes), *Raja (Rioraja), Raja (Rostroraja), Raja lintea* and *Sympterygia*. Ed. Stehmann, M. *Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Biologie*, **65**: 237-307.

HOVESTADT, D.C. & HOVESTADT-EULER, M., 1993. Vascularization in Selachii. In: Elasmobranches et Stratigraphie. Herman, J. & Van Waes, H. (eds.) *Service Géologique de Belgique, Professional Paper* 1993/**6**, 264: VIII + 260 pp.

LAST, P.R. & STEVENS, J.D., 1994. Sharks and Rays of Australia. *CSIRO* Australia: 513 pp. 84 pls.

MCEACHRAN, J.D. & LAST, P.R., 1994. New Species of Skates, *Notoraja ochroderma*, from off Queensland, Australia, with Comments on the Taxonomic Limits of *Notoraja* (Chondrichthyes, Rajoidei). *Copeia* 1994 (2): 413-421).

MCEACHRAN, J.D. & MIYAKE, T., 1990a. Phylogenetic Interrelationships of Skates: A Working Hypothesis (Chondrichthyes, Rajoidei). In: Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries (Eds. Pratt, H.L. Jr., Gruber, S.H. & Taniuchi, T.), NOAA techn. Rep. NMFS **90**:285-304.

MCEACHRAN, J.D. & MIYAKE, T., 1990b. Zoogeography and Bathymetry of Skates (Chondrichthyes, Rajoidei). In: Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries (Eds. Pratt, H.L. Jr., Gruber, S.H. & Taniuchi, T.), NOAA techn. Rep. NMFS **90**: 305326.

General glossary (applying to all previous issues of this series).

CONCERNING THE JAW

Anterior
Tooth position close to junction of left and right jaw 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 jaws.
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.
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 orthodentine layer.
Osteodont
Histotype of vascularization, by which a tooth is supplied without any pulp cavity by scattered tiny cavities and canals penetrating the osteodentine layer of the root and the internal crown material.
Outer face
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 osteodentine.
Pulp cavity
Cavity inside the tooth from which the vascularization is spread via canaliculi.

Root
Non-enamelated tooth part, that forms the junction with the jaw gum 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 root totally overgrown to form a closed tube internally connected or merged with the pulp cavity.
Secondarily hemiaulacorhizid
Median groove of holaulacorhizid type of root overgrown to various extent, converting the median groove to an internal tube, which is merged with the pulp cavity.
Striae
Vertical ridges running from crown base toward apex.
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 polyaulacorhizid root type, respectively, in that a sulcus lacks foramina.
Transversal
Mesio-distally directed.
Transverse keel
Transverse ridge dividing the crown into inner and outer face.
Uvula
Lobate extension of the inner crown base.

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 taxon.
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

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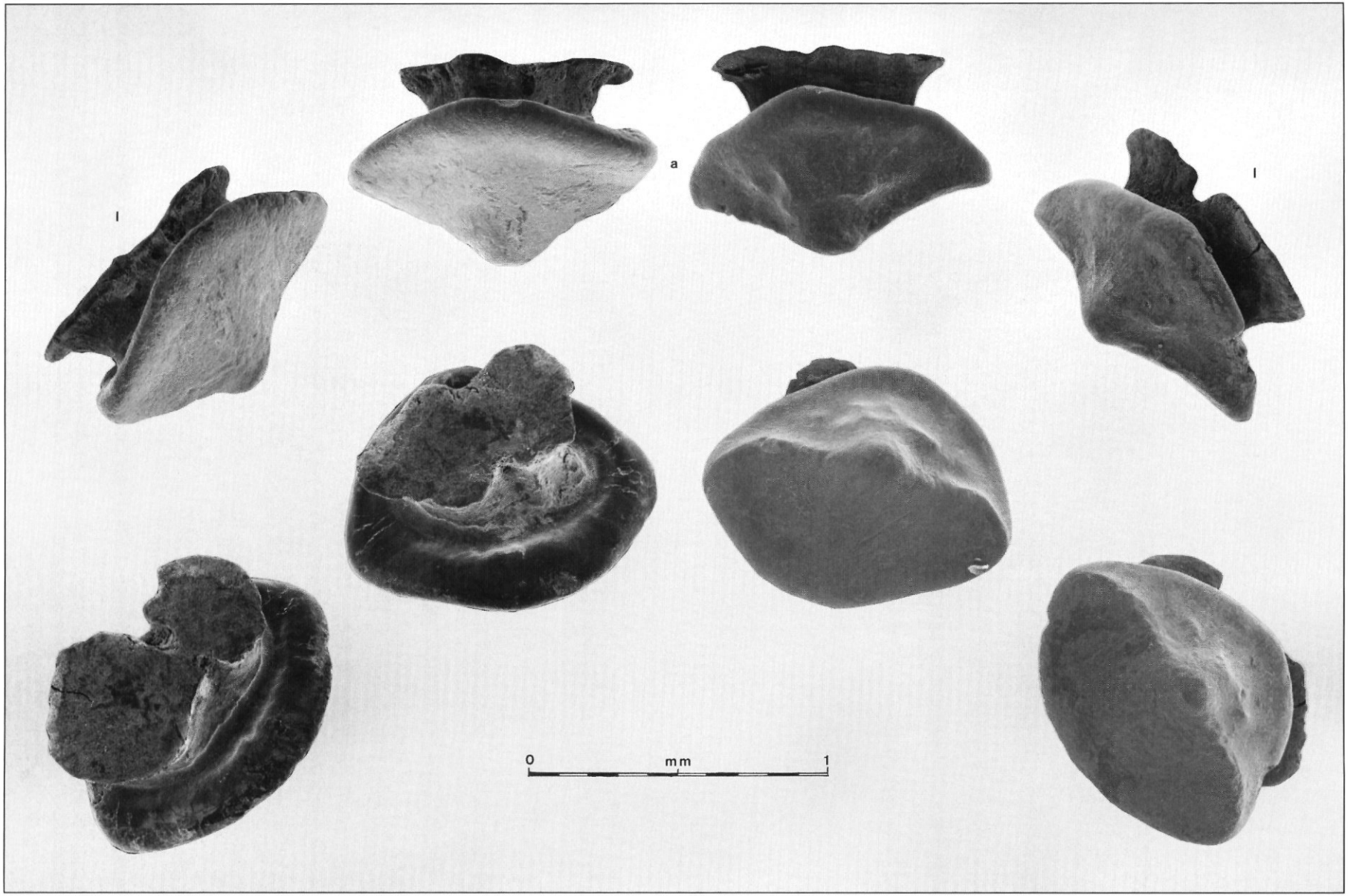

Plate 1. – Arhynchobatis asperrimus *WAITE, 1909. Male juvenile 42.5 cm (t.l.) ISH WE05 ST.958-1979, off New Zealand. Upper teeth.*

Plate 2. – Arhynchobatis asperrimus *Waite, 1909. Male juvenile 42.5 cm (t.l.) ISH WE05 ST.958-1979, off New Zealand. Lower teeth.*

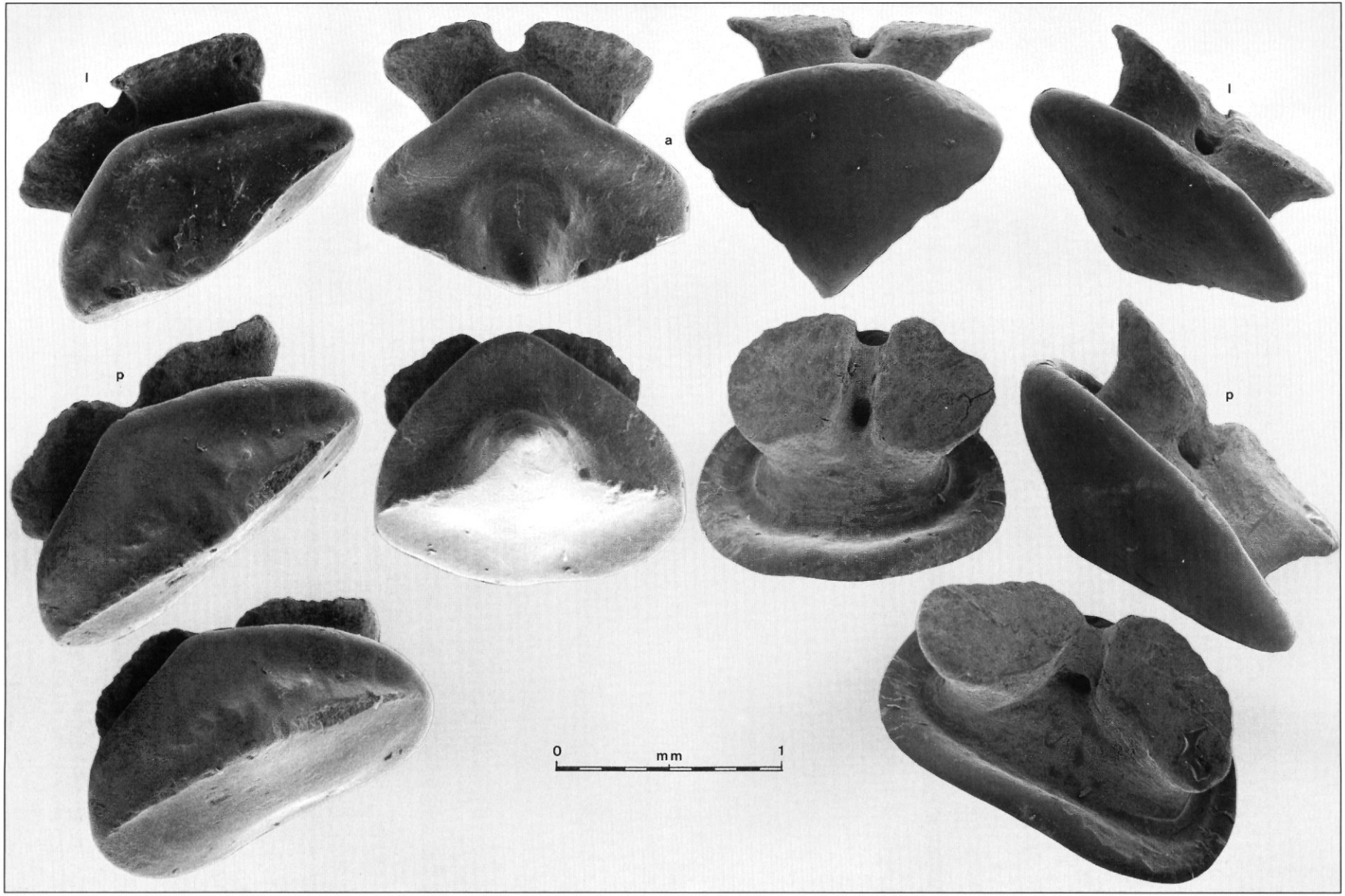

Plate 3. – Arhynchobatis asperrimus *WAITE, 1909. Male adult 60 cm (t.l.) ISH WE05 ST.958-1979, off New Zealand. Upper teeth.*

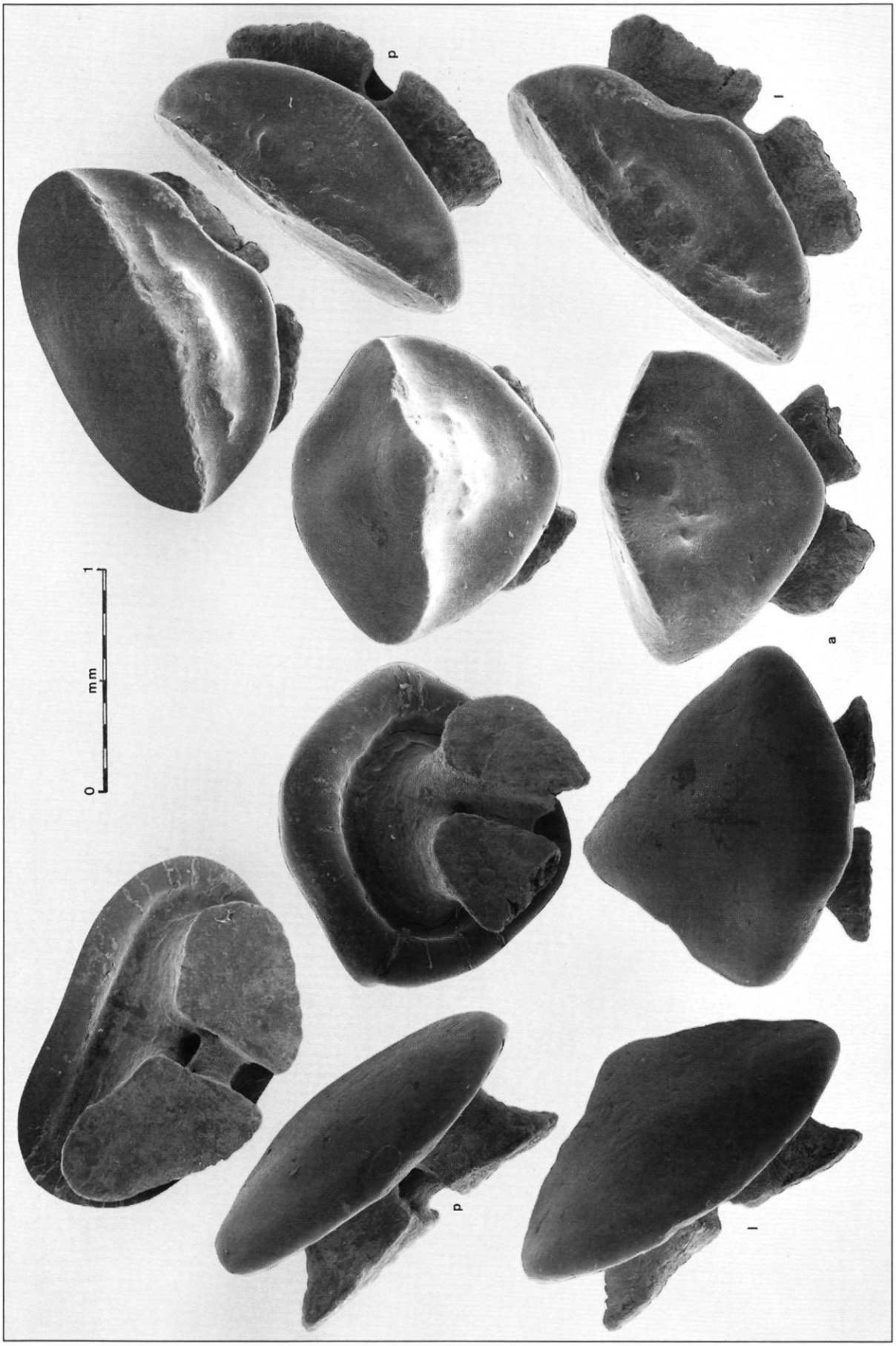

Plate 4. – Arhynchobatis asperrimus *Waite, 1909. Male adult 60 cm (t.l.) ISH WE05 ST.958-1979, off New Zealand. Lower teeth.*

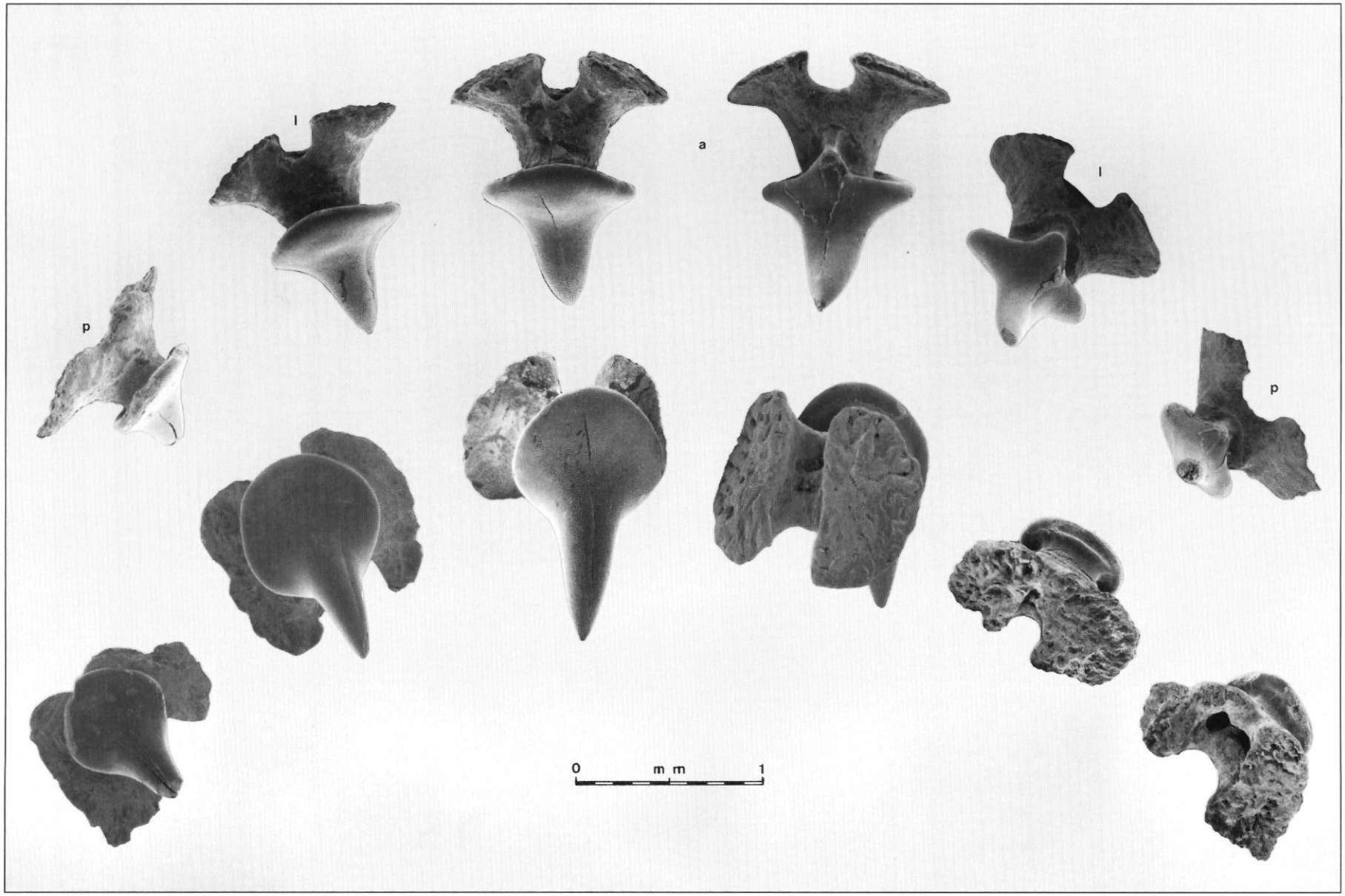

Plate 5. – Bathyraja richardsoni *(GARRICK, 1961). Male juvenile 38 cm (t.l.) BMNH uncat., NE Atlantic. Upper teeth.*

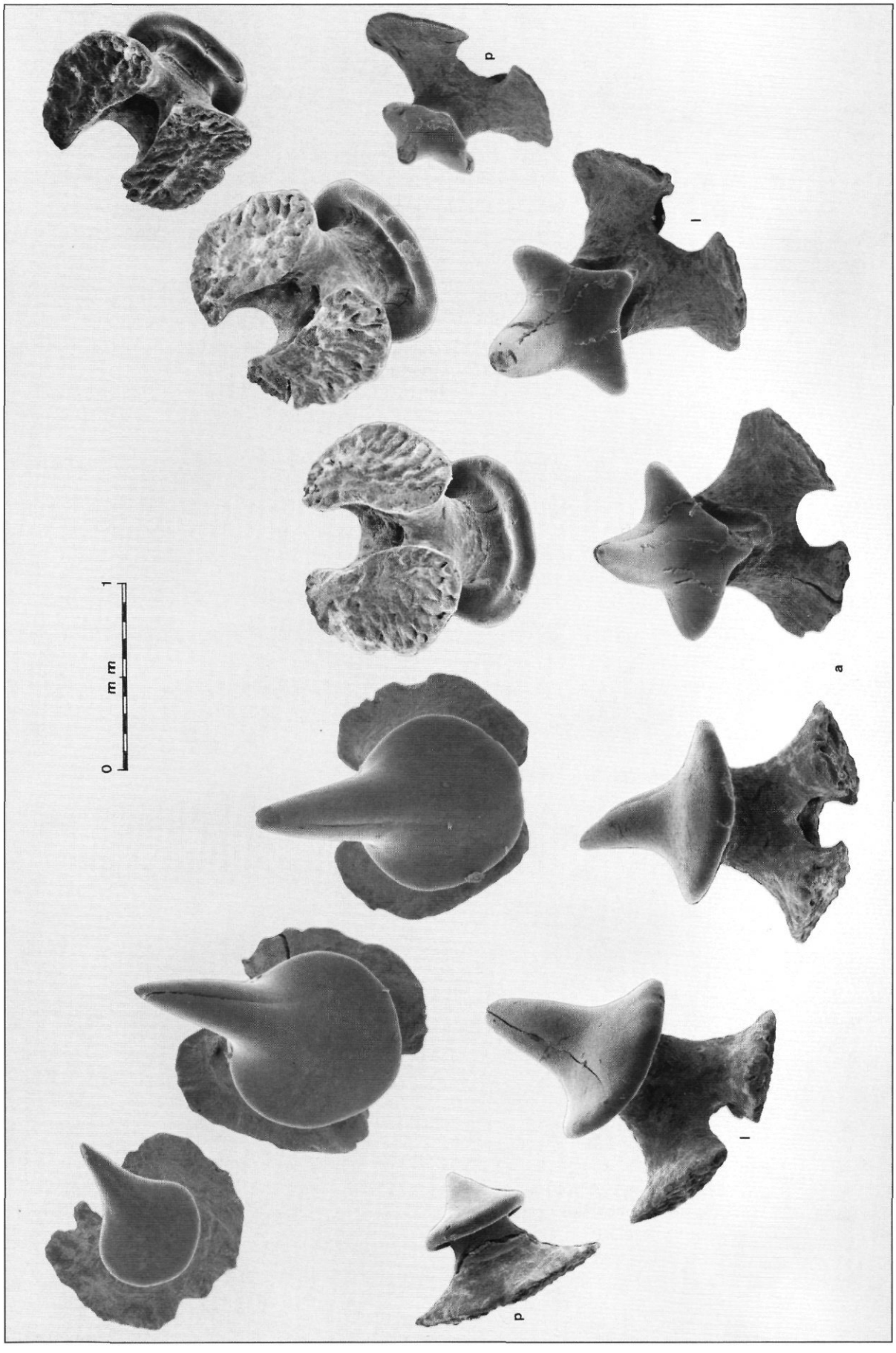

Plate 6. – Bathyraja richardsoni *(Garrick, 1961). Male juvenile 38 cm (t.l.) BMNH uncat., NE Atlantic. Lower teeth.*

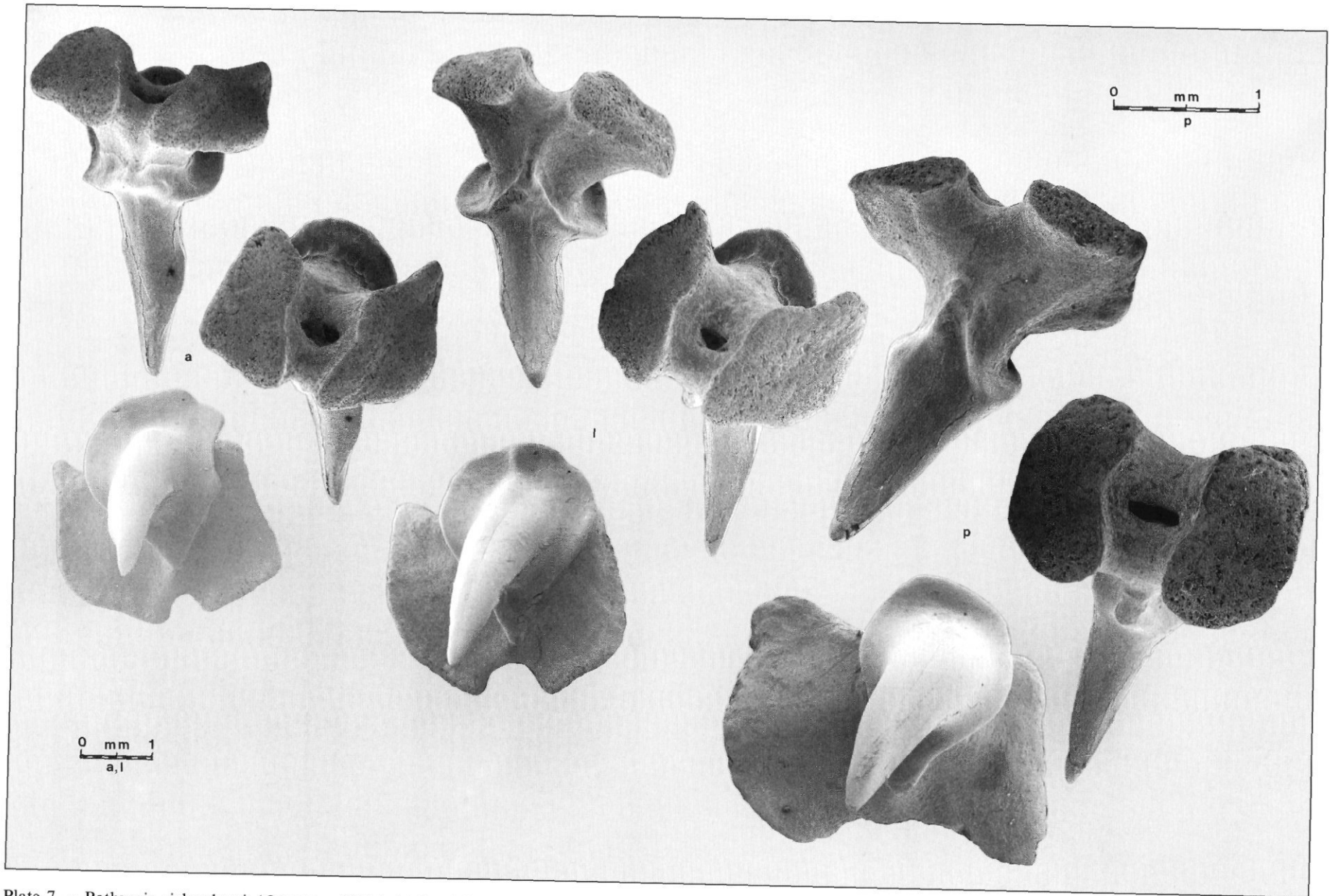

Plate 7. – Bathyraja richardsoni *(GARRICK, 1961). Male adult 180 cm (t.l.) BMNH uncat., NE Atlantic. Upper teeth.*

Plate 8. – Bathyraja richardsoni *(GARRICK, 1961). Male adult 180 cm (t.l.) BMNH uncat., NE Atlantic. Lower teeth.*

Plate 9. – Cruriraja parcomaculata *(Von Bonde & Swart, 1923). Female juvenile 38 cm (t.l.) AFRICANA 4329 0460324131. West Cape, off South Africa. Upper teeth.*

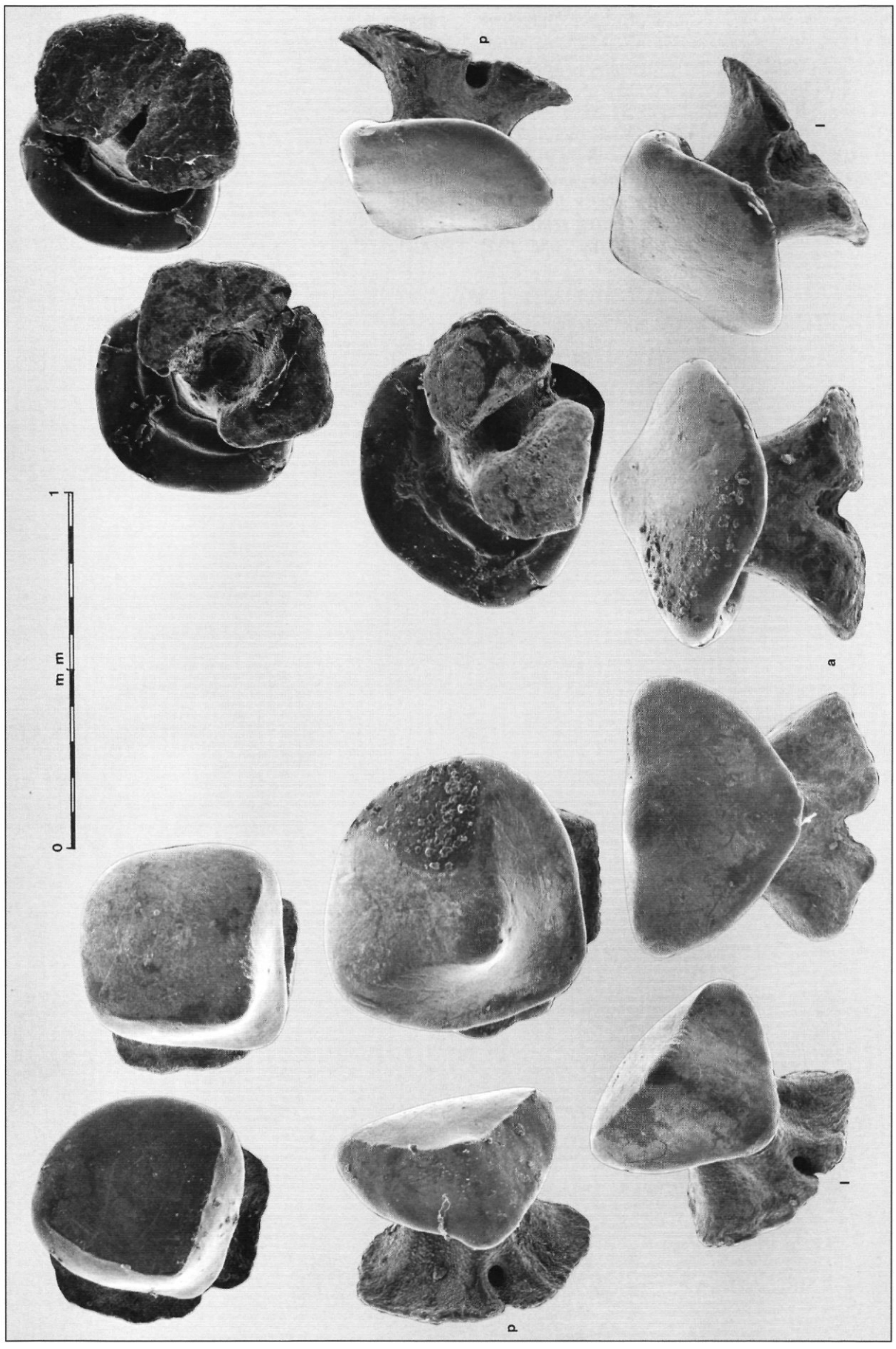

Plate 10. – Cruriraja parcomaculata *(Von Bonde & Swart, 1923). Female juvenile 38 cm (t.l.) AFRICANA 4329 0460324131. West Cape, off South Africa. Lower teeth.*

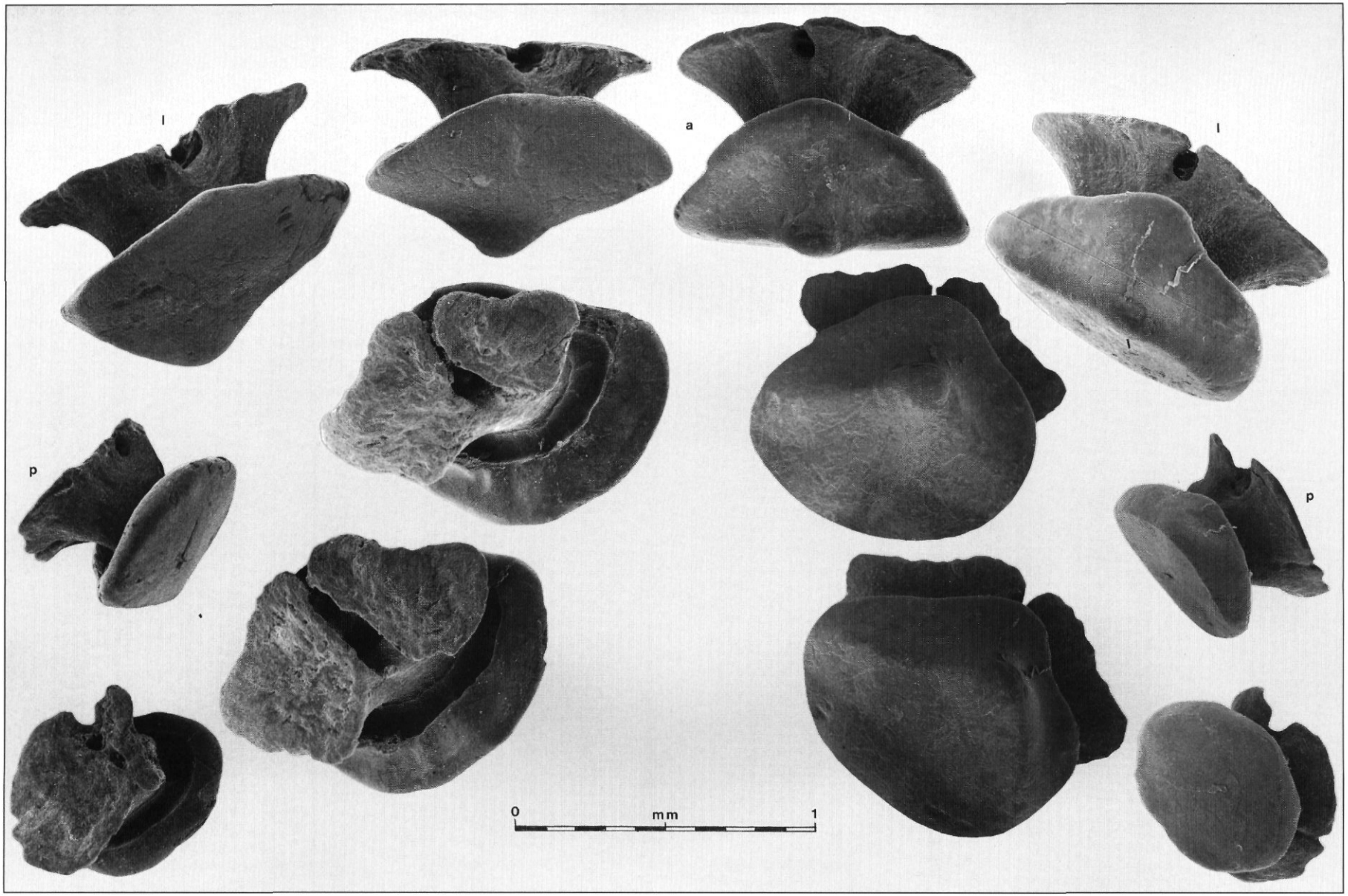

Plate 11. – Cruriraja parcomaculata *(Von Bonde & Swart, 1923). Female adult 50 cm (t.l.) ISH 44 1967, off Western South Africa. Upper teeth.*

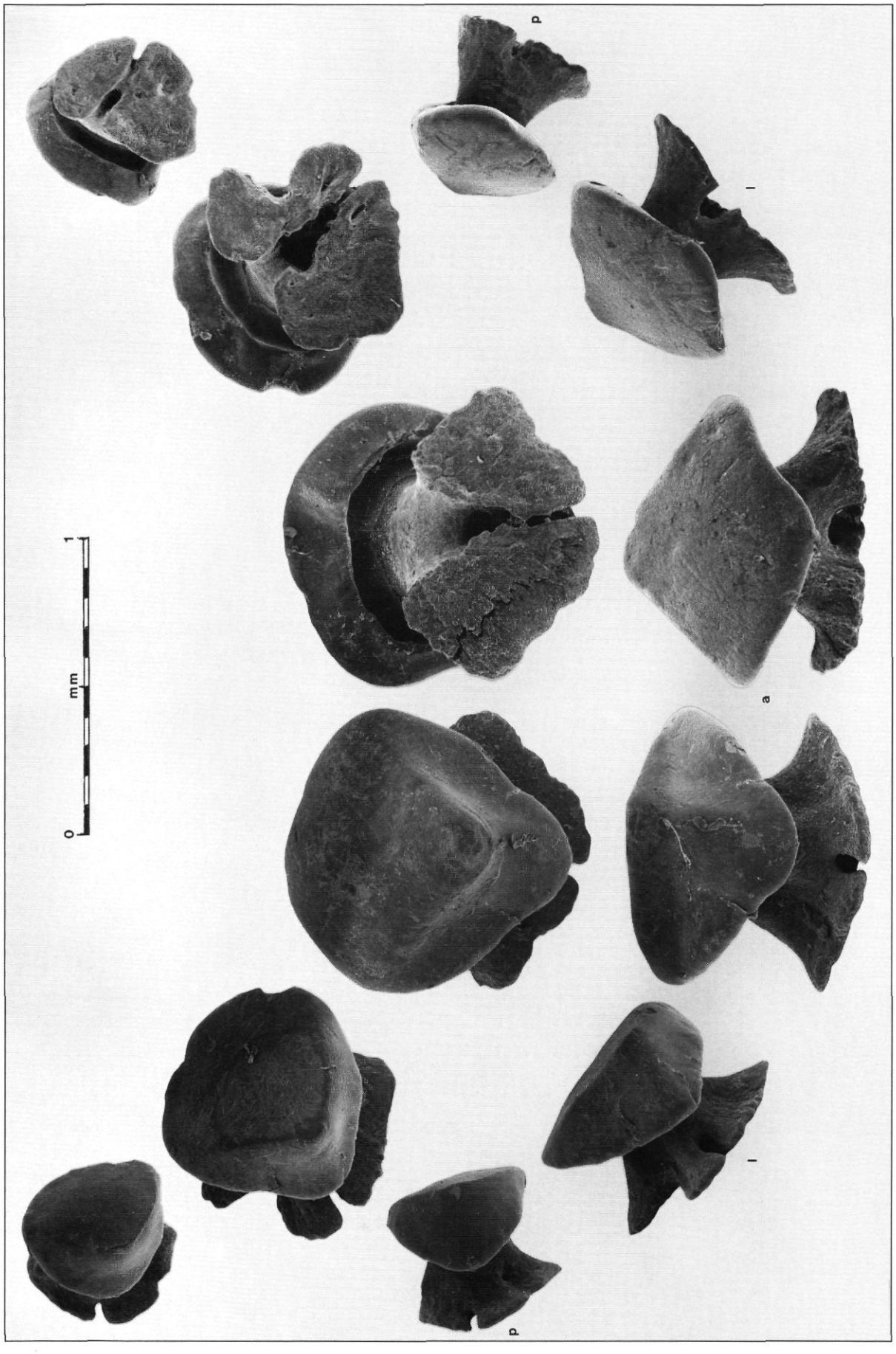

Plate 12. – Cruriraja parcomaculata *(Von Bonde & Swart, 1923). Female adult 50 cm (t.l.) ISH 44 1967, off Western South Africa. Lower teeth.*

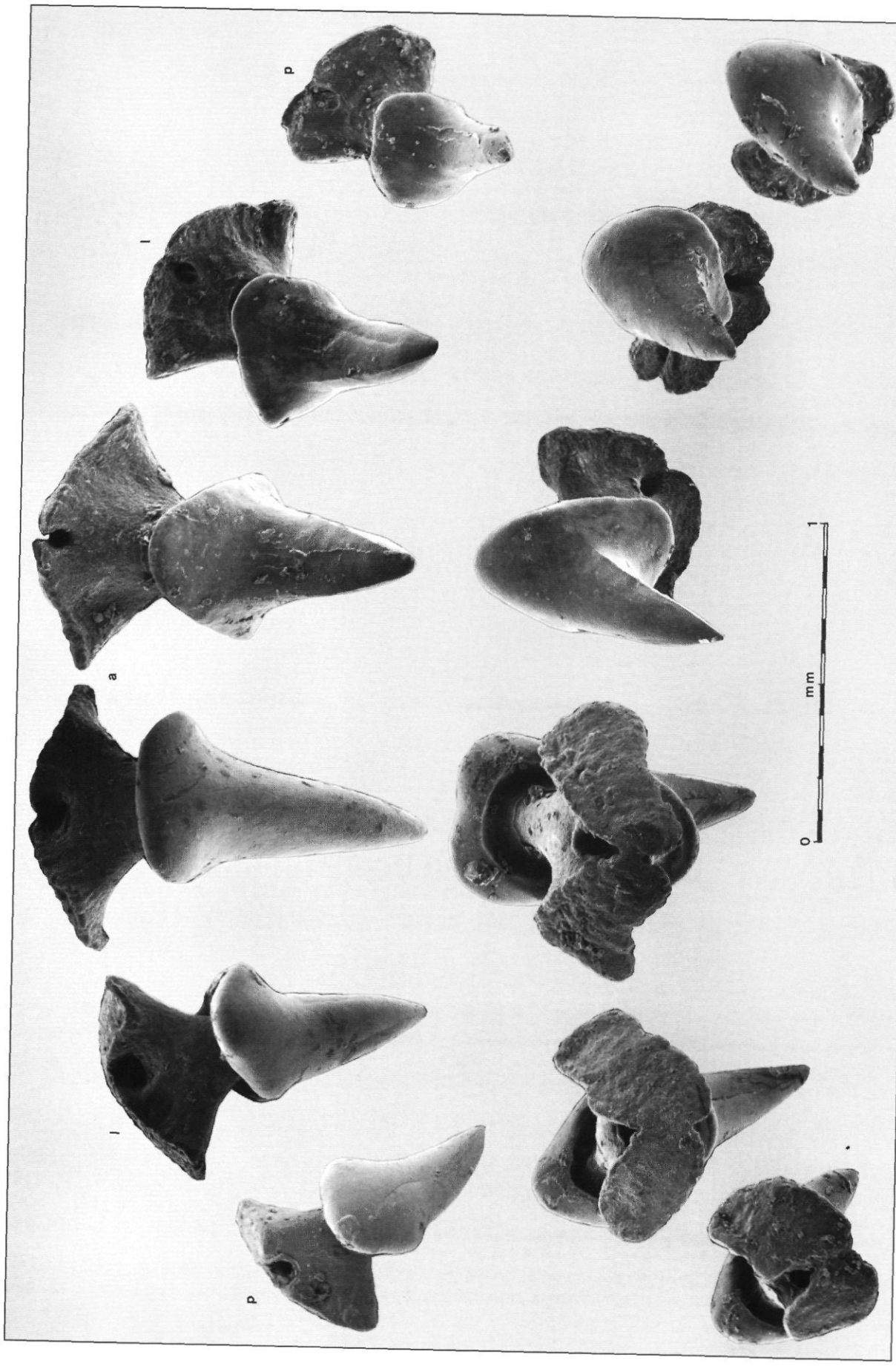

Plate 13. – Cruriraja parcomaculata *(Von Bonde & Swart, 1923). Male adult 46.5 cm (t.l.) AFRICANA 4384 0460804081. West Cape, off South Africa. Upper teeth.*

Plate 14. – Cruriraja parcomaculata *(Von Bonde & Swart, 1923). Male adult 46.5 cm (t.l.) AFRICANA 4384 0460804081. West Cape, off South Africa. Lower teeth.*

Plate 15. – Irolita waitii *(McCulloch, 1911). Female 25 cm (t.l.) CSIRO H 124 1. NW Geralton, off Australia. Upper teeth.*

Plate 16. – Irolita waitii *(McCulloch, 1911). Female 25 cm (t.l.) CSIRO H 124 1. NW Geralton, off Australia. Lower teeth.*

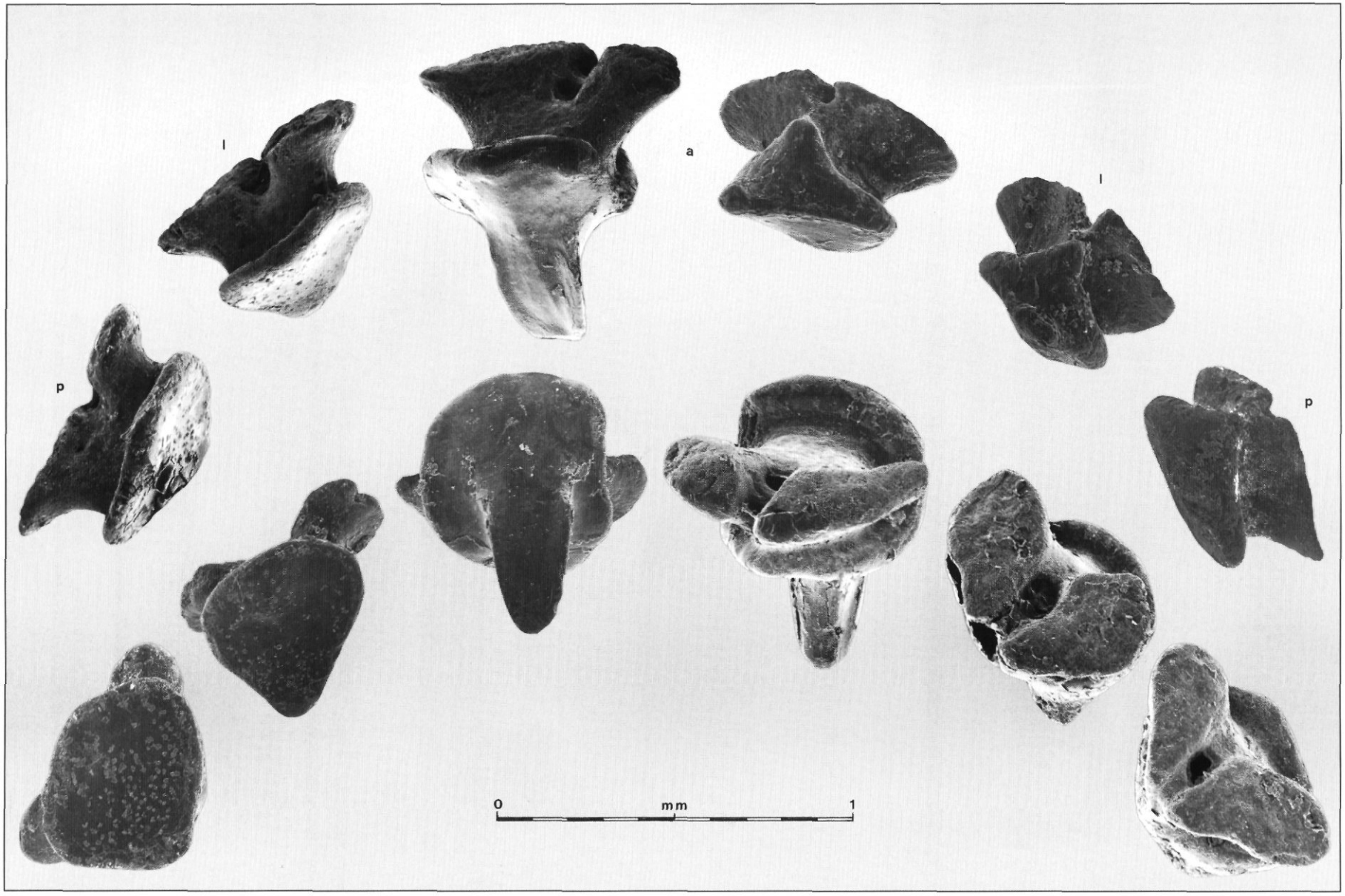

Plate 17. – Irolita waitii *(McCulloch, 1911). Male 22 cm (t.l.) CSIRO H 123 1. NW Geralton, off Australia. Upper teeth.*

Plate 18. – Irolita waitii *(McCulloch, 1911). Male 22 cm (t.l.) CSIRO H 123 1. NW Geralton, off Australia. Lower teeth.*

Plate 19. – Notoraja tobitukai *(HIYAMA, 1940). Male juvenile 36.5 cm (t.l.) ISH 30 1984, off Japan. Upper teeth.*

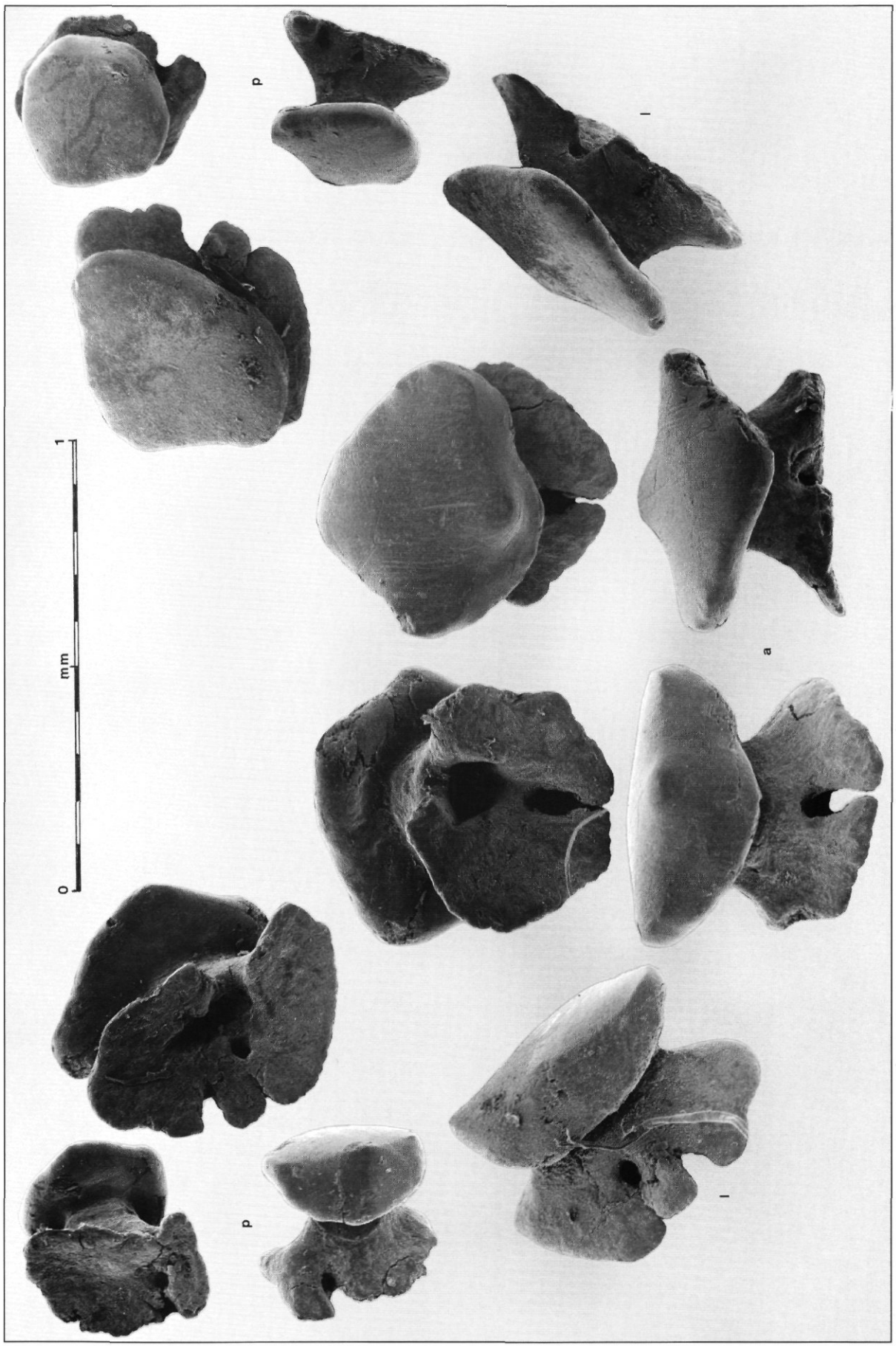

Plate 20. – Notoraja tobitukai *(Hiyama, 1940). Male juvenile 36.5 cm (t.l.) ISH 30 1984, off Japan. Lower Teeth.*

Plate 21. – Pavoraja (Insentiraja) laxipella *YEARSLEY & LAST, 1992. Female 43.5 cm (t.l.) CSIRO H 716 1, off Australia. Upper teeth.*

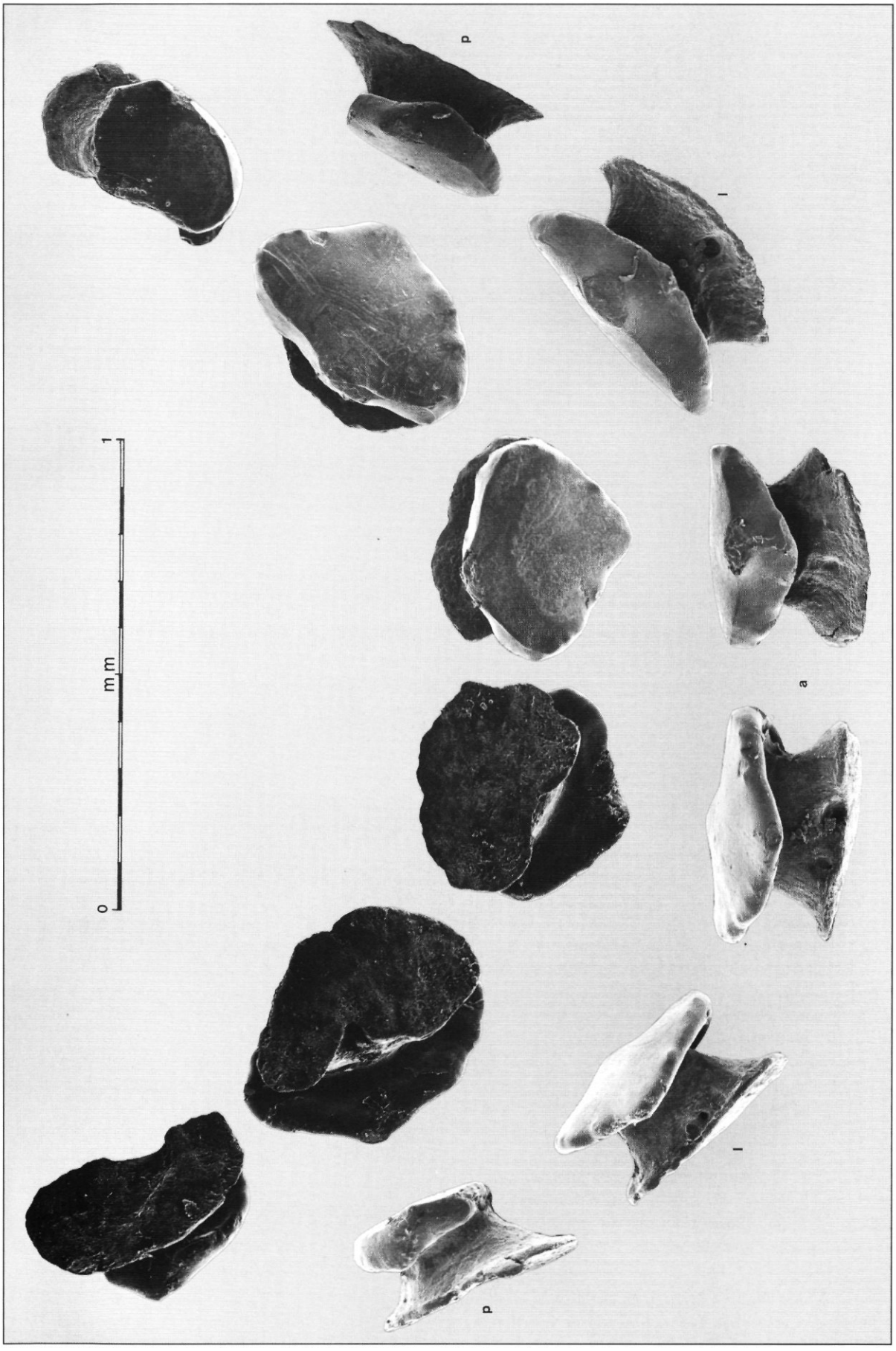

Plate 22. – Pavoraja (Insentiraja) laxipella *Yearsley & Last, 1992. Female 43.5 cm (t.l.) CSIRO H 716 1, off Australia. Lower teeth.*

Plate 23. – Pavoraja (Pavoraja) nitida *(GÜNTHER, 1870). Female 37 cm (t.l.) CSIRO H 3524 03. South Cape Everard, off Australia. Upper teeth.*

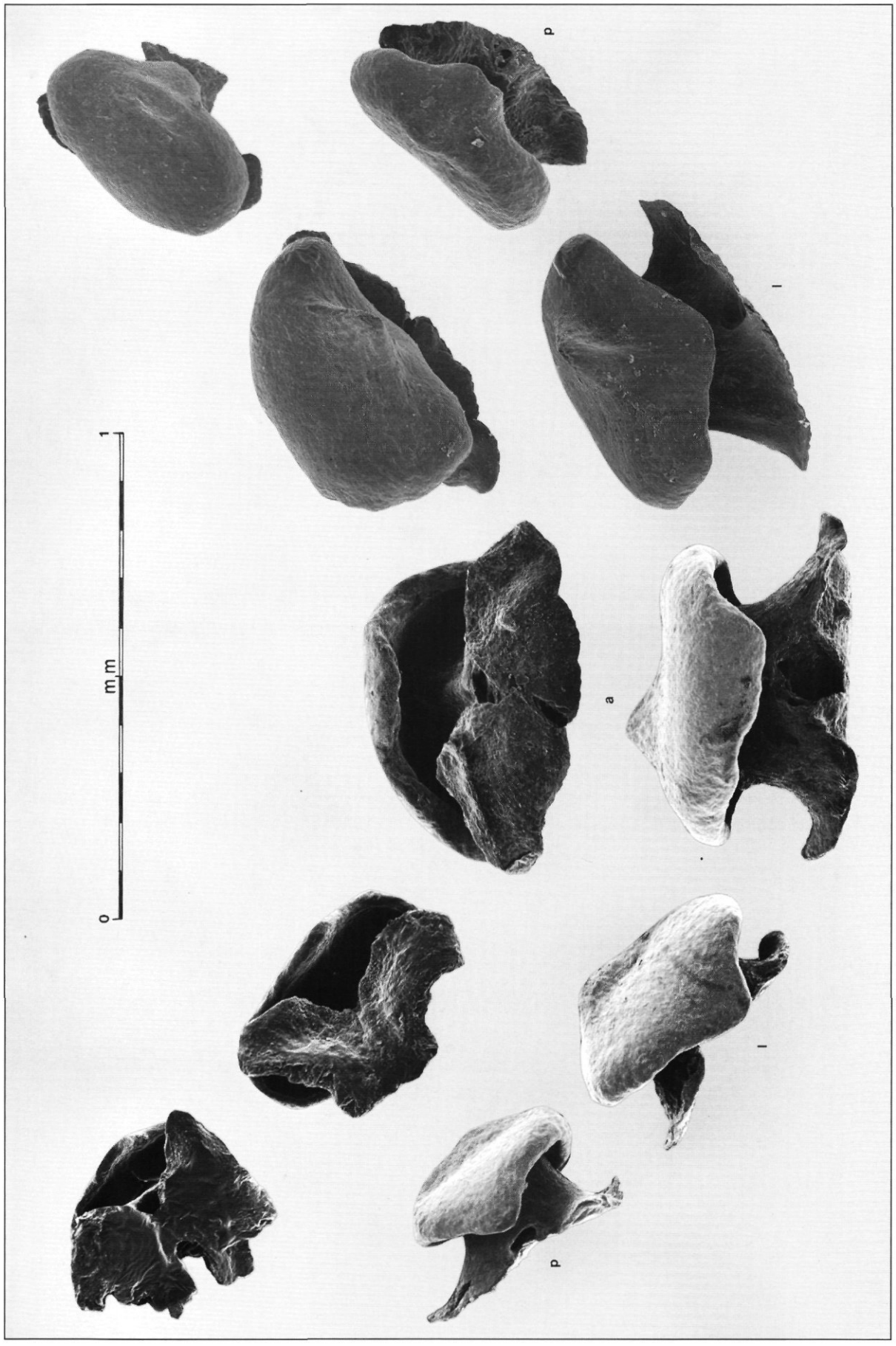

Plate 24. – Pavoraja (Pavoraja) nitida *(GÜNTHER, 1870). Female 37 cm (t.l.) CSIRO H 3524 03. South Cape Everard, off Australia. Lower teeth.*

Plate 25. – Pavoraja (Pavoraja) nitida *(GÜNTHER, 1870). Male 35 cm (t.l.) CSIRO H 3507 05. SSE Lake Entrance, off Australia. Upper teeth.*

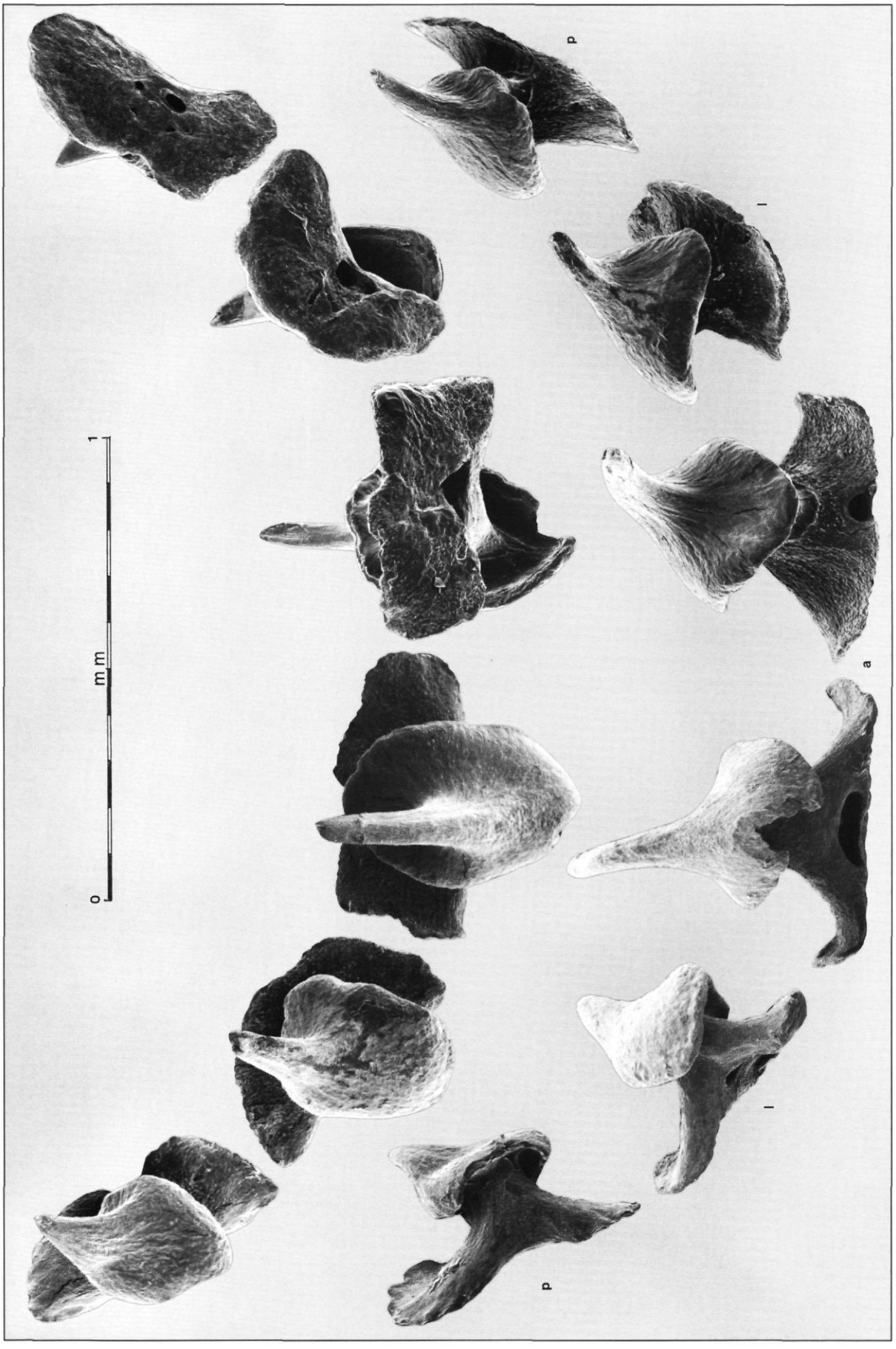

Plate 26. – Pavoraja (Pavoraja) nitida *(GÜNTHER, 1870). Male 35 cm (t.l.) CSIRO H 3507 05. SSE Lake Entrance, off Australia. Lower teeth.*

Plate 27. – Pseudoraja fischeri *Bigelow & Schroeder, 1954. Female 36.5 cm (t.l.) MCZ 41851. Gulf of Mexico. Upper teeth.*

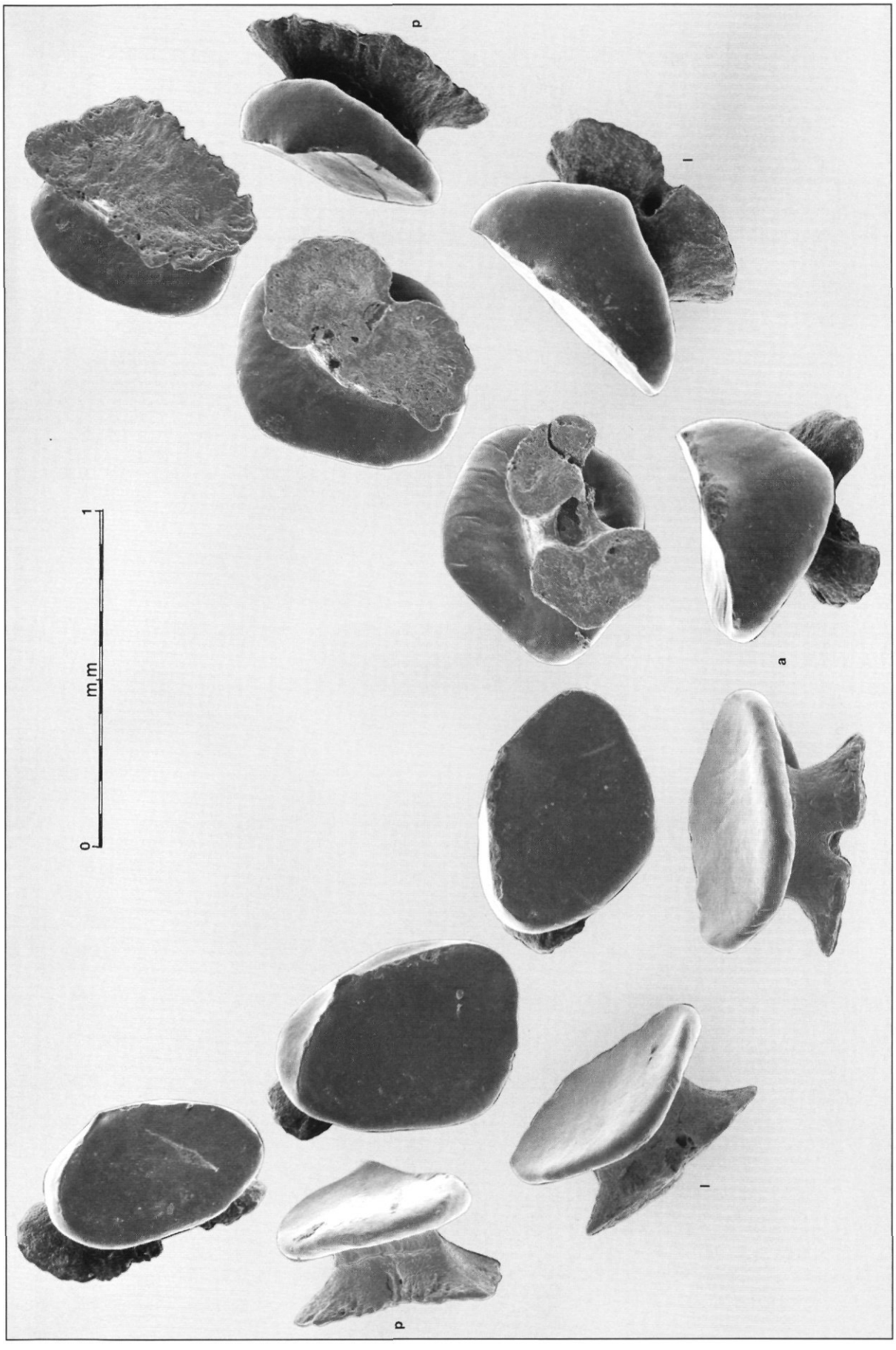

Plate 28. – Pseudoraja fischeri *Bigelow & Schroeder, 1954. Female 36.5 cm (t.l.) MCZ 41851. Gulf of Mexico. Lower teeth.*

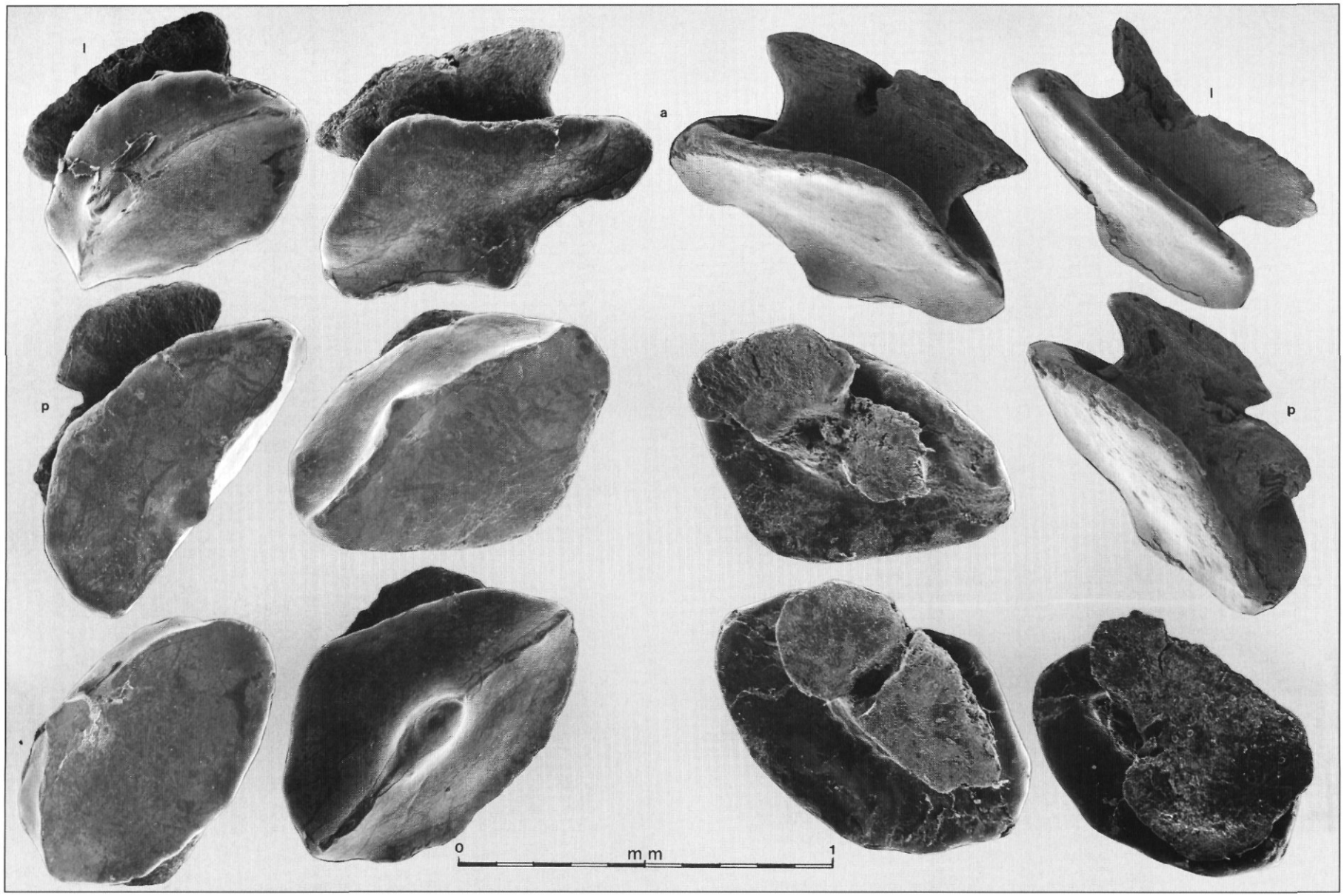

Plate 29. – Pseudoraja fischeri *BIGELOW & SCHROEDER, 1954. Male juvenile 24 cm (t.l.) MCZ 52241. Gulf of Mexico. Upper teeth.*

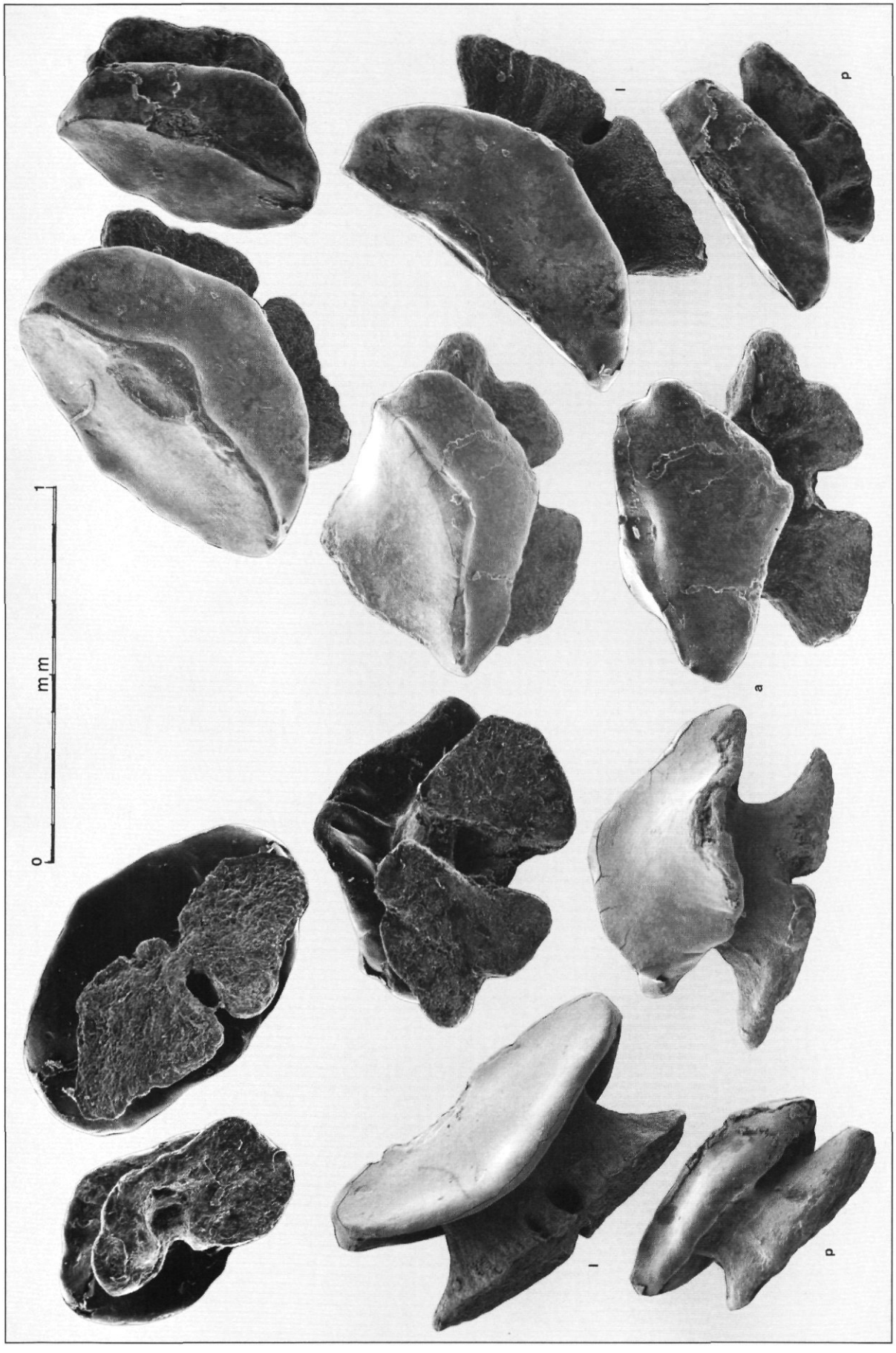

Plate 30. – Pseudoraja fischeri *BIGELOW & SCHROEDER, 1954. Male juvenile 24 cm (t.l.) MCZ 52241. Gulf of Mexico. Lower teeth.*

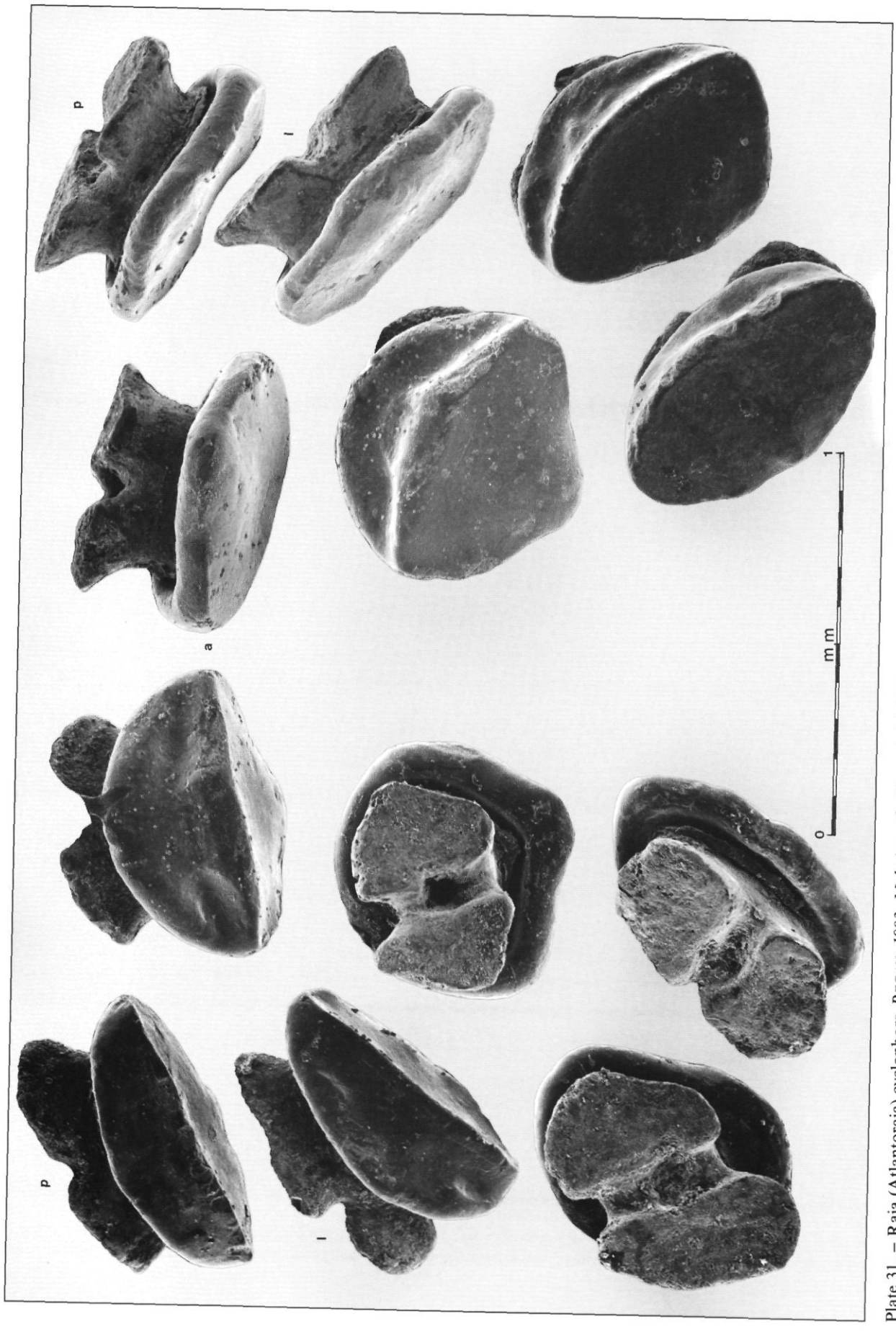

Plate 31. – Raja (Atlantoraja) cyclophora *Regan, 1903. Male juvenile 33 cm (t.l.) ISH 1082 1966, Rio de la Plata, Argentina. Upper teeth.*

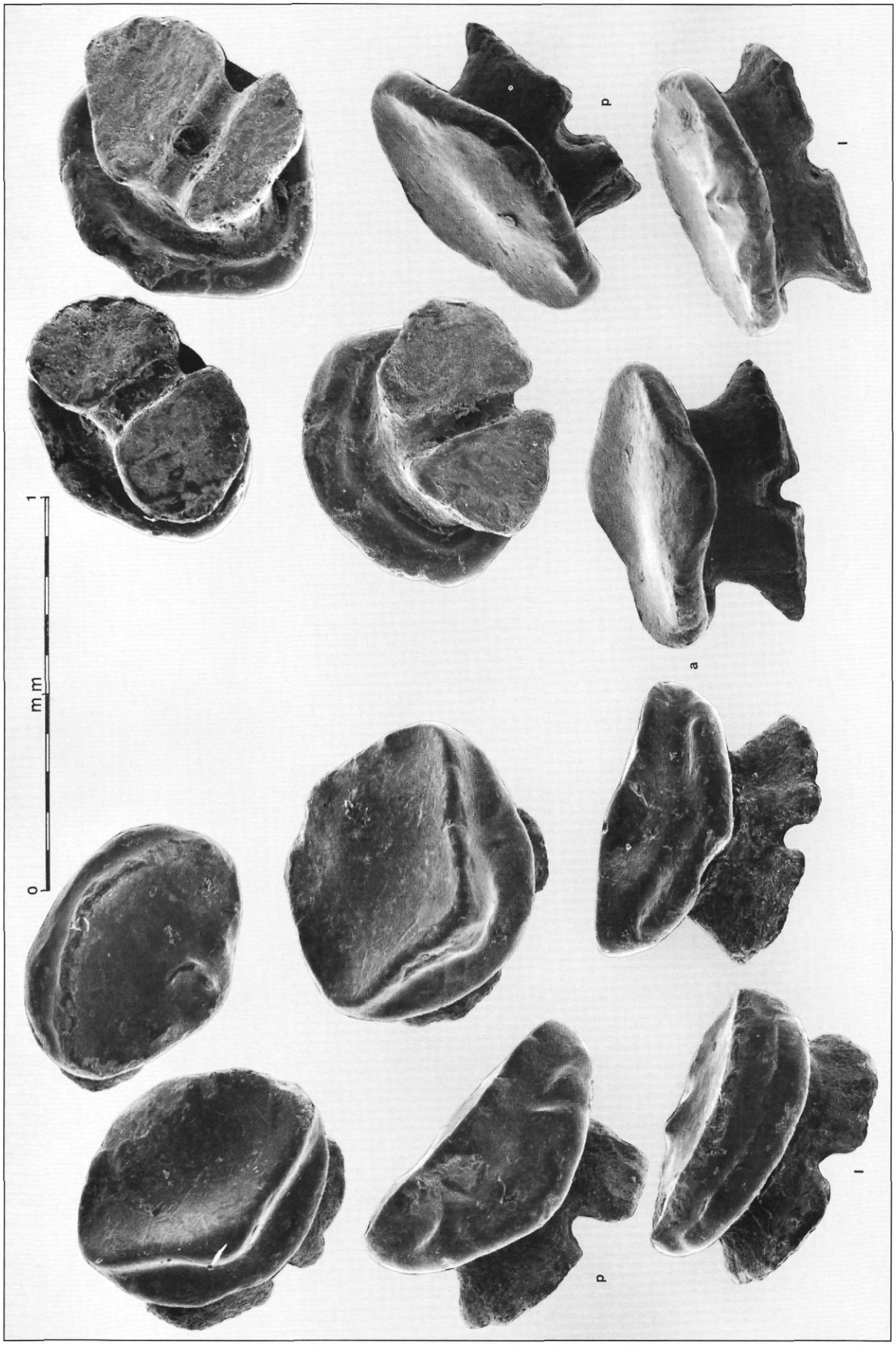

Plate 32. – Raja (Atlantoraja) cyclophora *Regan, 1903. Male juvenile 33 cm (t.l.) ISH 1082 1966, Rio de la Plata, Argentina. Lower teeth.*

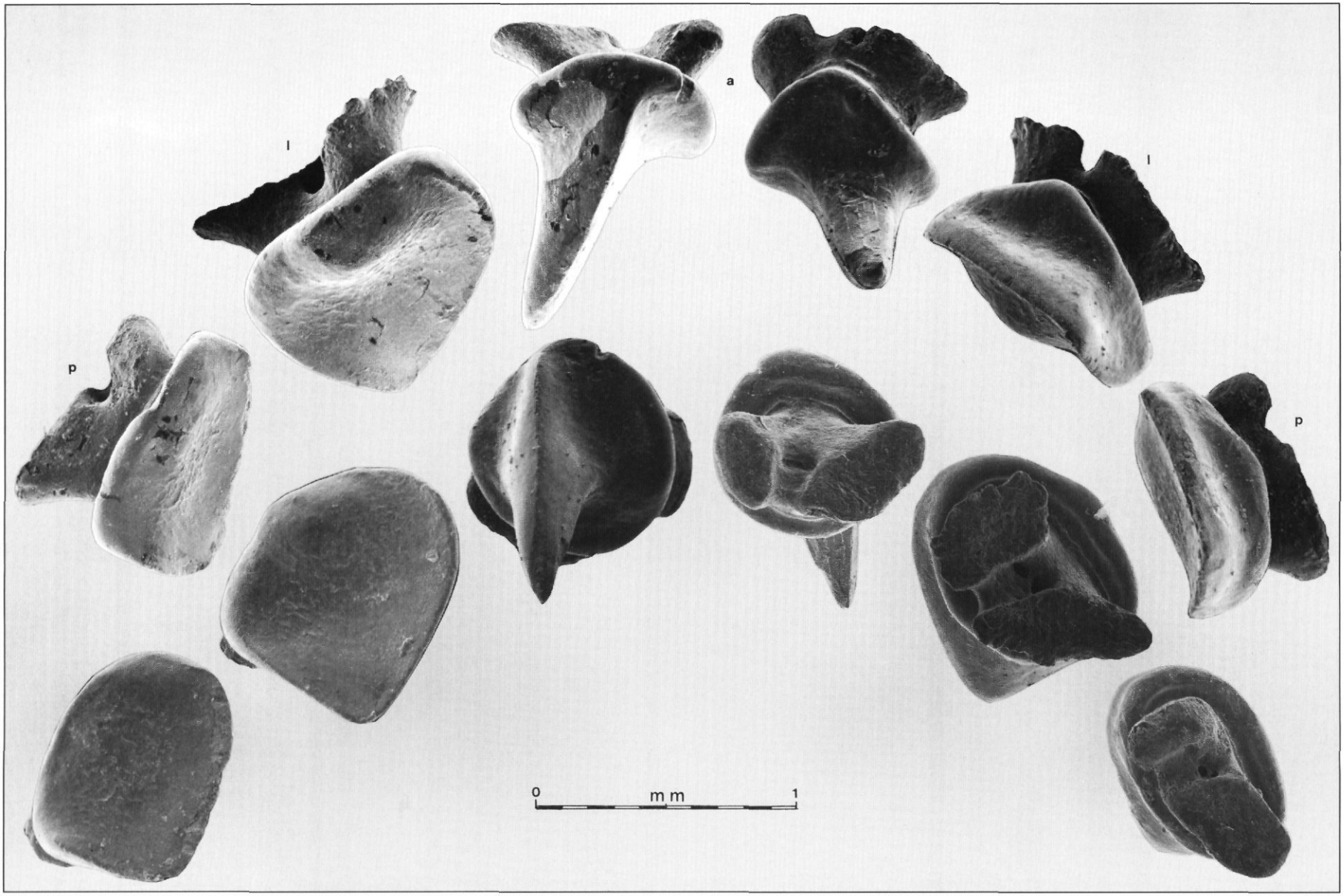

Plate 33. – Raja (Atlantoraja) cyclophora *REGAN, 1903. Male adult 58 cm (t.l.) ISH 1562 1966, off Uruguay. Upper teeth.*

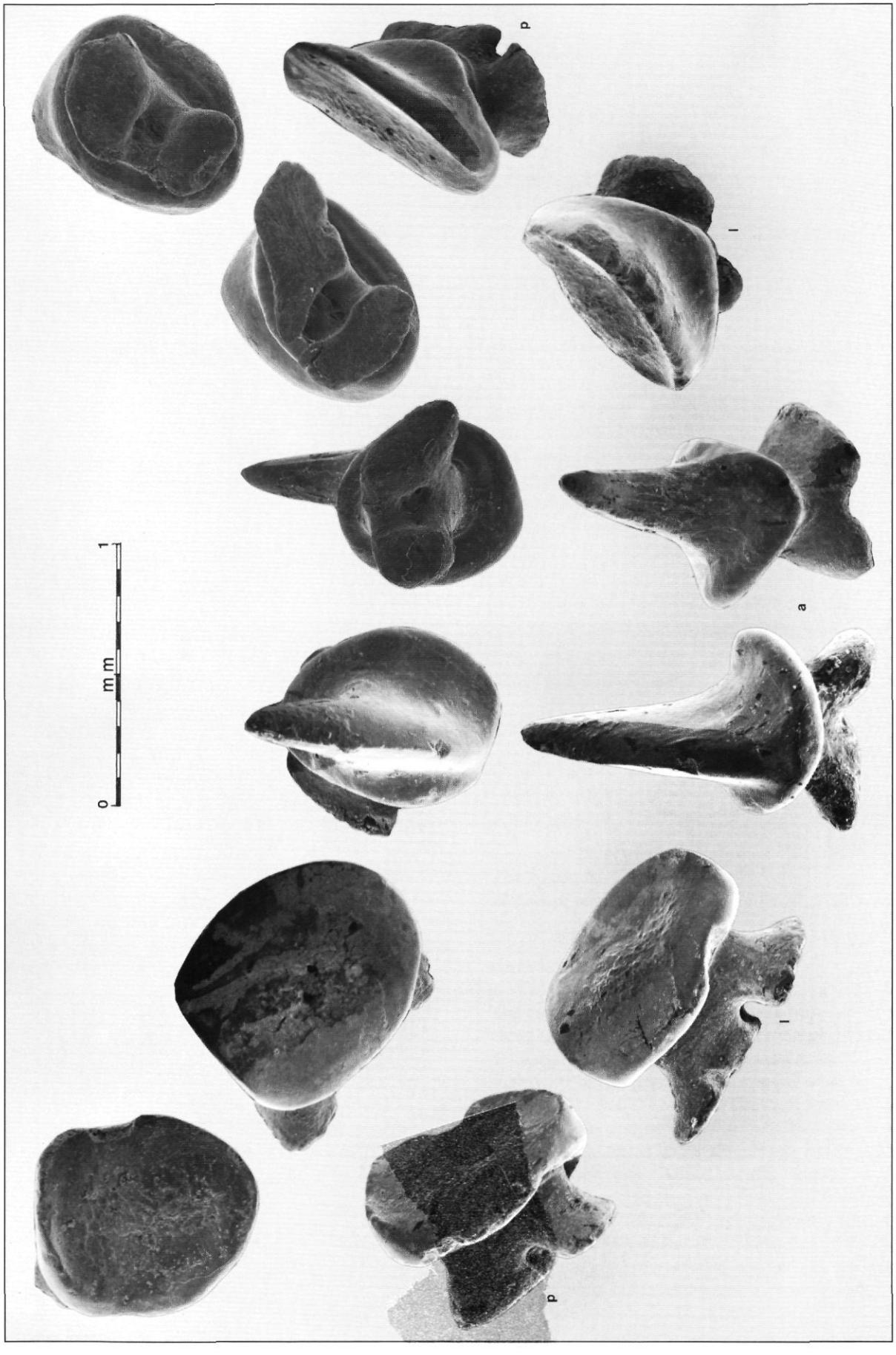

Plate 34. – Raja (Atlantoraja) cyclophora *Regan, 1903. Male adult 58 cm (t.l.) ISH 1562 1966, off Uruguay. Lower teeth.*

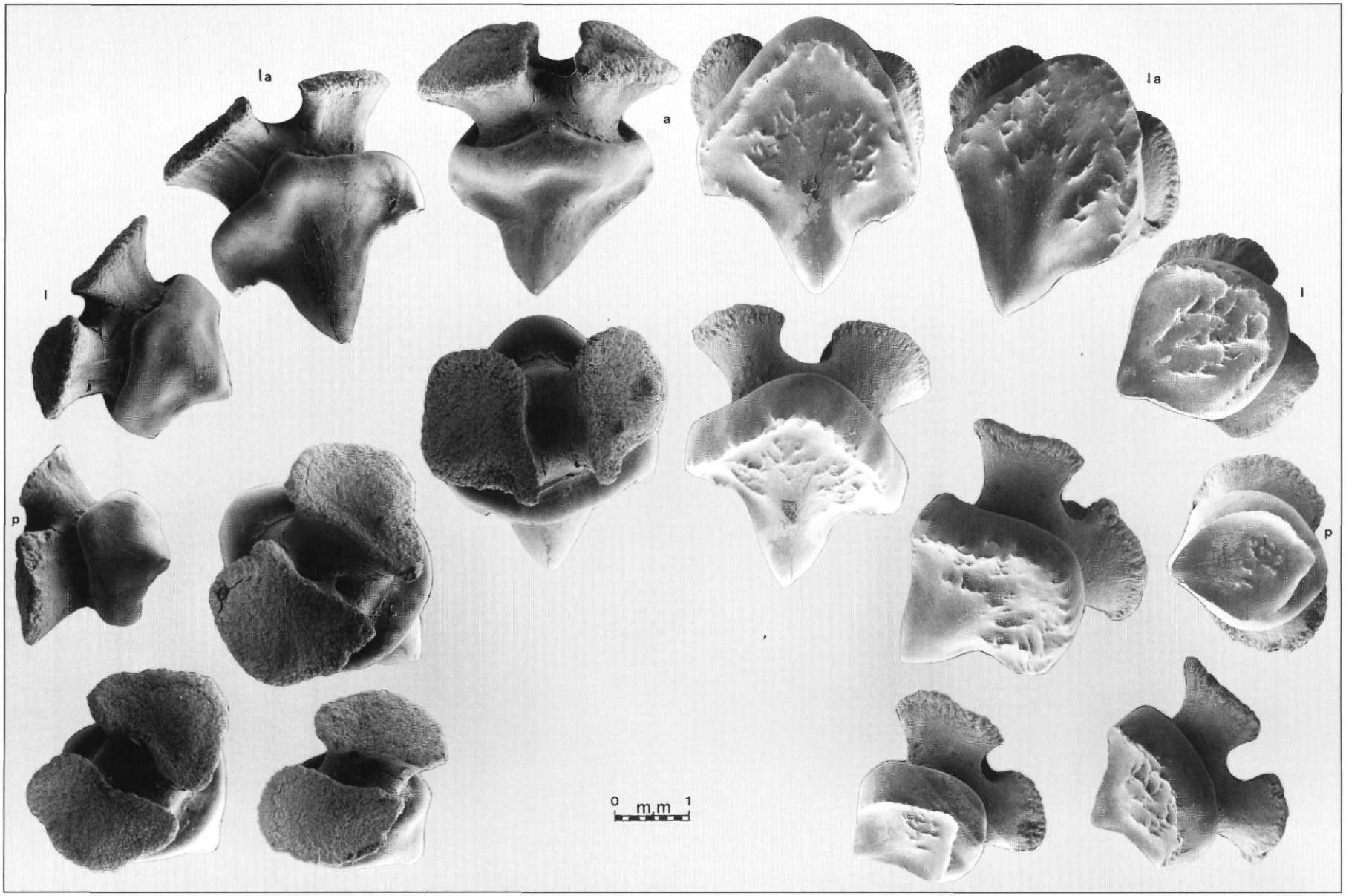

Plate 35. – Raja (Dipturus) nidarosiensis *STORM, 1881. Female 180 cm (t.l.). Porcupine, NE Atlantic. Upper teeth.*

Plate 36. – Raja (Dipturus) nidarosiensis *Storm, 1881. Male 178 cm (t.l.). Porcupine, NE Atlantic. Upper teeth.*

Plate 37. – Raja (Okameji) kenojei *MÜLLER & HENLE, 1841. Male juvenile 30 cm (t.l.), RMNH 7434, off Japan. Upper teeth.*

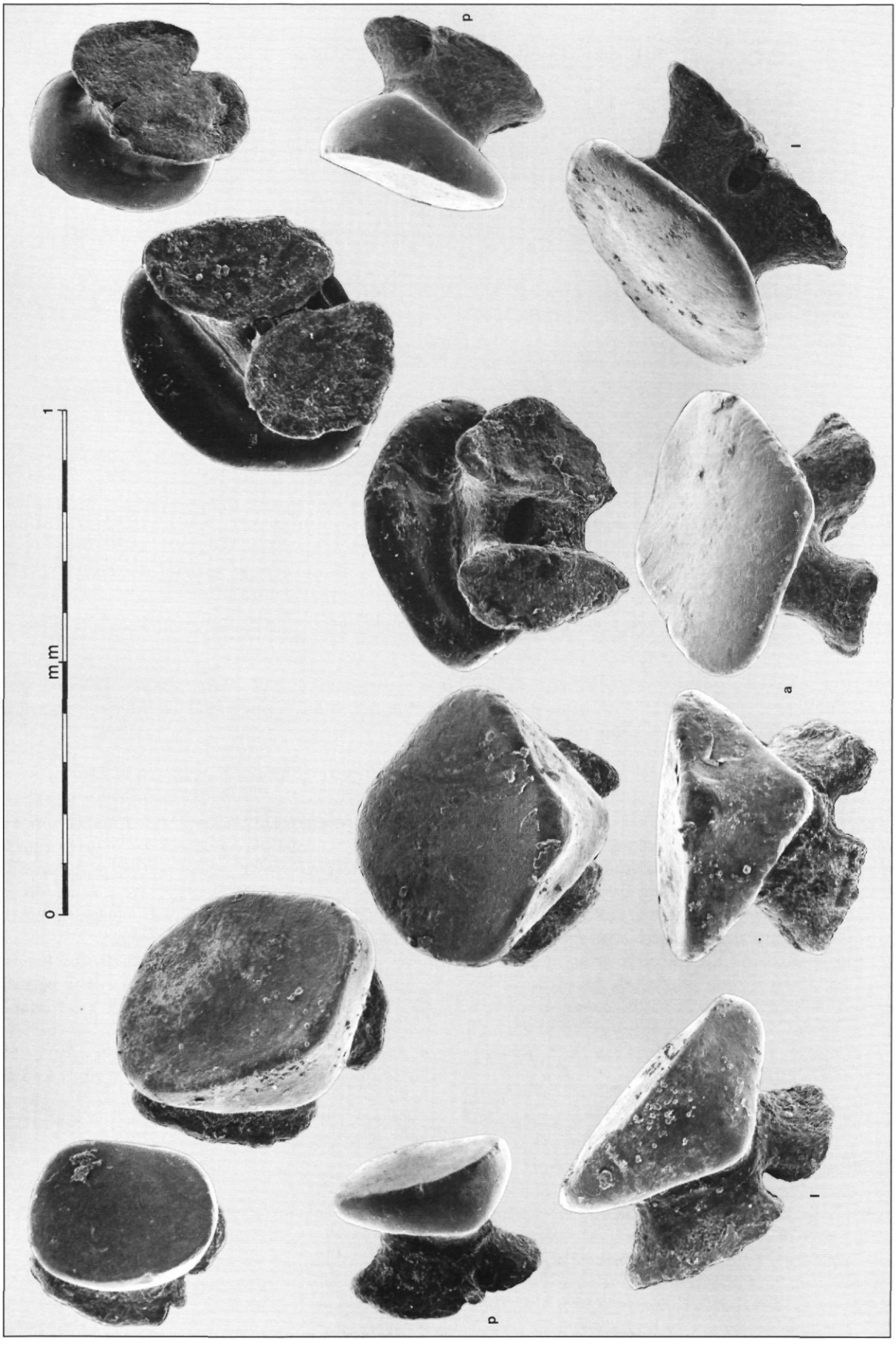

Plate 38. – Raja (Okamejі) kenojei *MÜLLER & HENLE, 1841. Male juvenile 30 cm (t.l.), RMNH 7434, off Japan. Lower teeth.*

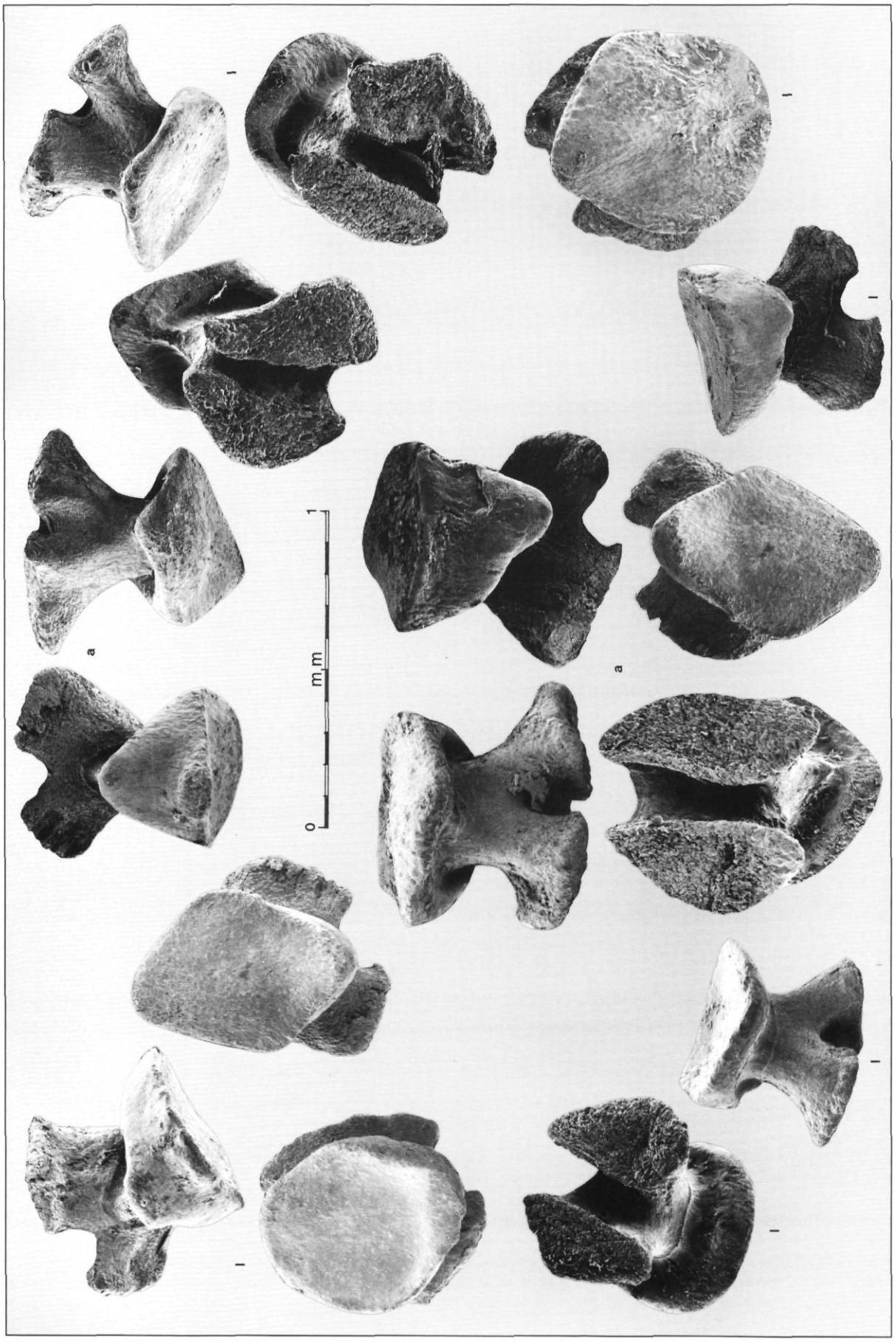

Plate 39. – Raja (Okamejei) kenojei *MÜLLER & HENLE, 1841. Female adult 46.5 cm (t.l.) ZMH 8406, off Japan. Upper and lower teeth.*

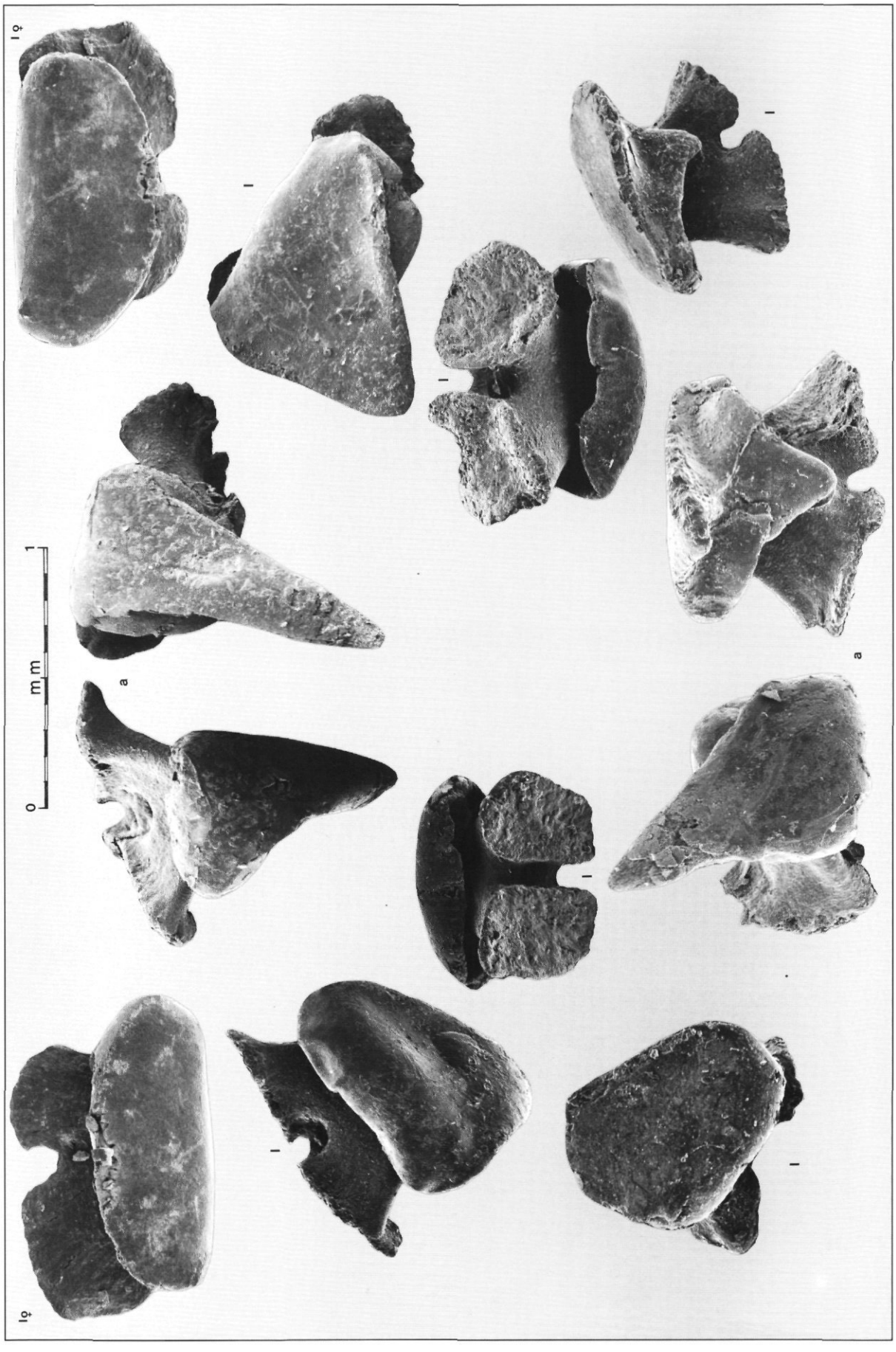

Plate 40. – Rhinoraja longicauda *Ishiyama, 1952. Male 43 cm (t.l.) ISH 11 1984 (two upper and two lower teeth), off Japan Female 58 cm (t.l.) MUHZ 34923 (one upper lateral tooth), off Japan.*

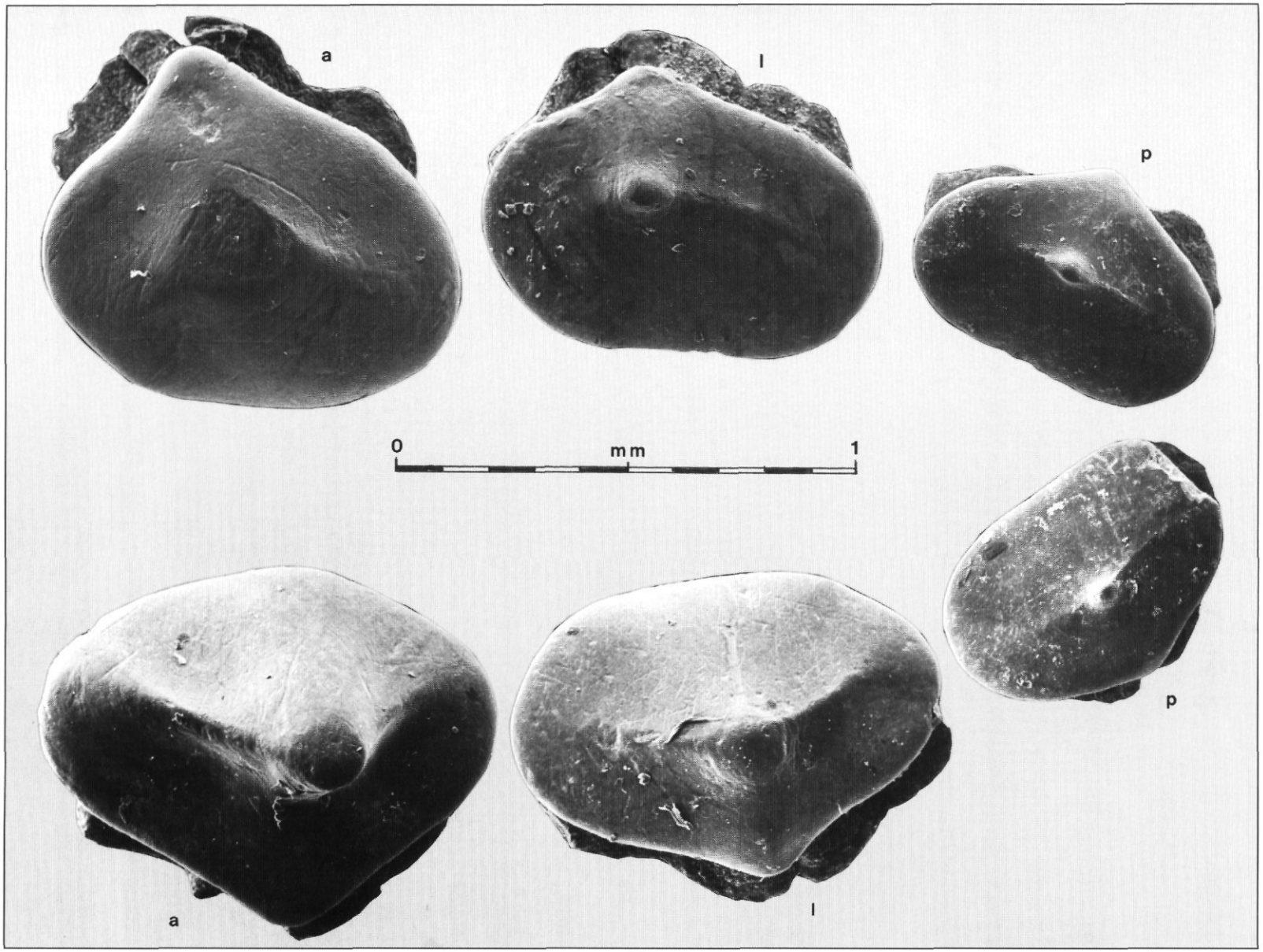

Plate 41. – Raja (Rajella) fyllae *LÜTKEN, 1888. Female 27 cm (disk width), Hatton Bank, NE Atlantic. Occlusal views of upper and lower teeth.*