

Additions to the fauna of the Boom Clay Formation of Belgium (Rupelian, Oligocene). Taxonomic adjustments on the Scyliorhinidae and Rajoidei, discovery of a dasyatid species (Pisces, Chondrichthyes) and of a curculionid species (Insecta, Coleoptera).

by

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Abstract: Large samples of the levels 35, 39 and 41 of the Boom Clay Formation (Rupelian, Oligocene, Belgium) were examined. Preliminary prospections (STEURBAUT & HERMAN, 1979) allowed to consider these levels as the richest ones for both teleost and chondrichthyan remains.

Despite the bulk of sediment residues sorted, faunistical enrichment is uncredibly poor.

The examination of the odontology of recent relative taxa (HERMAN, HOVESTADT-EULER & HOVESTADT, 1990) allows to consider the subgenus *Bythaelurus* as a genus of the subfamily Pentanchinae. *Scyliorhinus* aff. *coupatezi* is attributed to the genus *Bythaelurus*, as *Bythaelurus steurbauti* nov. sp.

Oral and rostral teeth of *Pristiophorus rupeliensis* are redescribed and reillustrated.

The taxa of the Rajoidei formerly described (1979) were reexamined: *Raja terhaegiensis* and *Raja heinzelini* are synonymized with *Raja ceciliae*. The presence of a Dasyatididae is signalled.

The extraordinary frequency (circa 70% of the fauna) of *Squalus alsaticus* is confirmed and the discovery of a little curculionid insect is mentioned.

Keywords: Oligocene - Rupelian - Chondrichthyes - Scyliorhinidae - Pristiophoridae - Rajoidei - Dasyatididae - Insecta - Curculionidae.

Résumé: D'importants prélèvements des niveaux 35, 39 et 41 de la Formation de l'Argile de Boom (Rupélien, Oligocène, Belgique) ont été effectués. Des prospections préliminaires (STEURBAUT & HERMAN, 1979) avaient désignés ces niveaux comme les plus riches en restes de téléostéens et de chondrichthyens.

Malgré la masse de sédiments traités, les apports faunistiques nouveaux sont très faibles.

L'examen de la dentition des taxons récents (HERMAN, HOVESTADT-EULER & HOVESTADT, 1990) permet d'élever le sous-genre *Bythaelurus* au niveau générique au sein de la sous-famille Pentanchinae. *Scyliorhinus* aff. *coupatezi* est attribuée au genre *Bythaelurus*, et rebaptisée *Bythaelurus steurbauti* nov.sp.

Dents orales et rostrales de *Pristiophorus rupeliensis* sont redécrites et refigurées.

Les taxons de Rajoidei précédemment décrits (1979) sont reconsidérés: *Raja terhaegiensis* et *Raja heinzelini* s'avèrent synonymes de *Raja ceciliae*. La présence d'un Dasyatididae est signalée.

L'extraordinaire abondance (circa 70% de la faune) de *Squalus alsaticus* est confirmée et la découverte d'un petit insecte curculionide est mentionnée.

Mots-clés: Oligocène - Rupélien - Chondrichthyes - Scyliorhinidae - Pristiophoridae - Rajoidei - Scyliorhinidae - Insecta - Curculionidae.

Kurzfassung: Umfangreiche Muster von den Schichten 35, 39 und 41 der Formation von Boom (Rupelium) wurden ausgegraben und ihre Chondrichthierfauna an Hand isolierten Zähne untersucht. Die Ergebnisse werden hier präsentiert und diskutiert. Der Fund einer curculioniden Spezies (Insecta, Coleoptera) wird gemeldet und illustriert. Die Rajiden Taxa der Boom Formation wurden neu beschrieben und illustriert. Vergleich mit der Odontologie und die komplexe Heterodontie rezenter rajiden Taxa führte zur synonymisierung von *Raja terhaegiensis* und *Raja heinzelini* mit *Raja ceciliae*. *Scyliorhinus* aff. *coupatezi* ist neu beschrieben als *Paleobythaelurus steurbauti*. Eine bis her unbekantem dasyatiden Art wird beschrieben.

Ein Oral-Zahn und einen Rostralstachel von *Pristiophorus rupeliensis* werden beschrieben und illustriert.

Schlüsselwörter: Oligozän - Rupelium - Chondrichthyes - Scyliorhinidae - Pristiophoridae - Rajoidei - Dasyatididae - Insecta - Curculionidae.

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Introduction

In order to elucidate the variety of the chondrichthyan fauna of the Boom Clay Formation of Belgium large samples were excavated from three clay pits about 10 to 15 km. west of Antwerp at the localities Steendorp, Kruibeke and Schelle.

According to STEURBAUT & HERMAN (1978) the levels 35, 39 and 41 of the Boom Clay Formation were expected to yield the richest chondrichthyan faunas. These levels were selected, respectively, for collecting the samples.

Over 2800 litres of clay was processed, and gave an impression of the faunas of the Boom Clay Formation by counts of the teeth.

Although the aim of this study was restricted to chondrichthyan remains only, the discovery of the remains of an insect, a specimen of the family Curculionidae (Insecta, Coleoptera) is reported and illustrated. (Determination by K. Desender, Institut Royal des Sciences Naturelles de Belgique, dept. Entomology). Further description of the specimen should be left for specialized authors only.

The chondrichthyan macro-teeth of the Boom Clay Formation were catalogued by LERICHE (1910). STEURBAUT & HERMAN (1978) added the chondrichthyan micro-teeth of *Squalus alsaticus*, *Scyliorhinus aff. coupatezi*, four new rajids: *Raja casieri*, *Raja cecilae*, *Raja heinzelini*, *Raja terhageniensis*, and one pristiophorid species *Pristiophorus rupeliensis*. More recently a new mobulid species, *Plinthicus kruibekensis* was recorded (BOR, 1990).

Comparison with the tooth morphology of living taxa of the order Rajoidei revealed, that several taxa include the morphotypes of teeth of *Raja cecilae*, *Raja heinzelini* and *Raja terhageniensis* in their sexual heterodonty and disjunct monognathic heterodonty. For example, the heterodonty of *Sympterygia bonapartei* MÜLLER & HENLE, 1847 and *Raja (Rajella) fyllea* LÜTKEN, 1888 includes the three morphotypes of *Raja cecilae*, *Raja heinzelini* and *Raja terhageniensis*, and have a closely related tooth morphology. With the additional new details, the tooth morphology of *Raja cecilae* is redescribed and illustrated with SEM-photographs. A differential diagnosis of their morphotypes with the tooth morphology of *Sympterygia bonapartei* MÜLLER & HENLE, 1847 (Plate 3: figs. 2a, 2b, 2c; plate 4: figs. 2a, 2b, 2c; plate 5: figs. 2a, 2b, 2c; plate 6: figs. 2a, 2b, 2c; plate 7: figs. 2a, 2b, 2c; plate 8: figs. 2a, 2b, 2c) and *Raja (Rajella) fyllea* (LÜTKEN, 1888) (Plate 3: figs. 3a, 3b, 3c; plate 4: figs. 3a, 3b, 3c; plate 5: figs. 3a, 3b, 3c; plate 6: figs. 3a, 3b; plate 7: figs. 3a, 3b; plate 8: figs. 3a, 3b) resulted in synonymizing *Raja heinzelini* and *Raja terhageniensis* with *Raja cecilae*.

More details were discovered about the tooth morphology of *Raja casieri* and *Pristiophorus rupeliensis*, which are included in a redescription, and illustrated with SEM-photographs.

Scyliorhinus aff. coupatezi was considered to be conspecific with the pliocene *Scyliorhinus coupatezi* HERMAN, 1975 (STEURBAUT & HERMAN, 1978). Comparison with the odontology of the living scyliorhinid taxa (HERMAN, HOVESTADT-EULER & HOVESTADT, 1990 and 1991) revealed, that the tooth morphology of *Scyliorhinus coupatezi* has strong relationships with species of the living genus *Scyliorhinus*, whereas the oligocene *Scyliorhinus aff. coupatezi* is strongly related with the former living subgenus *Halaelurus* (*Bythaelurus*), which its taxonomic rank has been elevated here to a new genus of the subfamily Pentanchinae. Presently, the fossil taxa of the Scyliorhinidae of tertiary and quarternary deposits all are included into one genus, with the exception of the eocene genus *Megascyliorhinus*, distinguished from the genus *Scyliorhinus* by CAPPETTA & WARD, (1977).

However, considering the large number of living genera of the Scyliorhinidae, the low number of genera of fossil ancestors, particularly from tertiary and quarternary deposits, is rather contrastive. A full systematic revision is needed, but is beyond the scope of this issue. Therefore, we will only deal with *Scyliorhinus aff. coupatezi* of the Boom Clay Formation.

A species of the family Dasyatididae could be added to the chondrichthyan fauna of the Boom Clay Formation, which will be described and illustrated.

Method and material

The Boom Clay Formation mostly consists of heavy clay, which is used to manufacture bricks. Besides some silt holding lenses, processing the clay for collecting fossil remains is time consuming and labour-intensive. The following method for processing the clay appeared to be the most effective one:

The clay samples were broken into nodules of approximately 3cm., deeply dried, and, after being soaked in water for over an hour, passed through a sieve (0,42mm. mesh). The residues were picked from an endless belt (Hovestadt & Hovestadt, 1981), using a binocular microscope. After processing about 10% remained as residue.

Level 35 of the Boom Clay Formation was sampled in a clay pit at the locality Steendorp (42E29). About 1000 litres of the clay were sampled. The following 377 chondrichthyan remains of 14 species were found:

<i>Cetorhinus parvus</i> (oral tooth)	1	<i>Pristiophorus rupeliensis</i> (rostral spine)	2
<i>Cetorhinus parvus</i> (gillraker elements)	31	<i>Raja casieri</i>	3
<i>Chimaera gosseleti</i> (tooth plate)	1	<i>Raja cecilae</i>	8
<i>Isurolamna vandenbroeckii</i>	2	<i>Raja heinzelini</i>	41
<i>Odontaspis</i> sp.	5	<i>Raja terhageniensis</i>	20
<i>Physogaleus latus</i>	6	<i>Scyliorhinus aff. coupatezi</i>	14
<i>Pristiophorus rupeliensis</i> (oral tooth)	1	<i>Squalus alsaticus</i>	242

Level 39 of the Boom Clay Formation was sampled in a clay pit at the locality Schelle (43E255). About 450 litres were sampled. The following 190 chondrichthyan remains of 8 species were found:

<i>Cetorhinus parvus</i> (oral tooth)	1	<i>Squalus alsaticus</i>	141
<i>Cetorhinus parvus</i> (gillraker elements)	20	<i>Raja casieri</i>	5
<i>Synodontaspis acutissima</i>	5	<i>Raja heinzeli</i>	15
<i>Pristiophorus rupeliensis</i> (oral tooth)	1	<i>Raja terhageniensis</i>	2

Level 41 of the Boom Clay Formation was sampled in a clay pit at the localities Kruibeke (28W15) and Schelle (42E255). About 700 litres of the clay were sampled at Kruibeke and 650 litres at Schelle. The following 594 chondrichthyan remains of 12 species were found:

Kruibeke

<i>Alopias exigua</i>	1	<i>Pristiophorus rupeliensis</i> (rostral tooth)	1
<i>Cetorhinus parvus</i> (gillraker elements)	8	<i>Raja casieri</i>	3
<i>Isurolamna vandenbroeckii</i>	1	<i>Raja ceciliae</i>	10
<i>Lamna rupeliensis</i>	1	<i>Raja heinzeli</i>	41
<i>Synodontaspis acutissima</i>	5	<i>Raja terhageniensis</i>	18
<i>Physogaleus latus</i>	6	<i>Squalus alsaticus</i>	161

Schelle

<i>Cetorhinus parvus</i> (gillraker elements)	3	<i>Raja ceciliae</i>	7
<i>Pristiophorus rupeliensis</i> (rostral spine)	1	<i>Raja heinzeli</i>	13
<i>Physogaleus latus</i>	1	<i>Raja terhageniensis</i>	9
<i>Raja casieri</i>	5	<i>Squalus alsaticus</i>	185

Level 41 at Schelle also yielded the insect remains. (Plate 11: figs.1a, 1b, 1c)

Odontological redescrptions

Order: Pristiophoriformes

Family: Pristiophoridae

The samples yielded one complete oral tooth and four rostral spines of *Pristiophorus rupeliensis*. One complete rostral spine was found, which revealed information about the root section.

Pristiophorus rupeliensis STEURBAUT & HERMAN, 1978
(Plate 1: figs.1a, 1b, 1c, 1d and 2a, 2b, 2c, 2d)

Both, the holotype (P. 2643) and the rostral spine of the paratype (P. 2644) were incomplete. However, a sample at Steendorp on level 35 yielded a complete additional oral tooth and one complete additional rostral spine. The teeth have a crown, with a well developed principal cusp, flanked by a pair of blades, that smoothly join with the mesial and distal cutting edges of the principal cusp.

The outer crown surface is slightly convex. The outer crown base has an apron, that overhangs more or less the medio-outer depression of the root. This apron is less developed on the tooth of the holotype. On both sides of the apron small, irregularly shaped costules are present on the outer crown base. The inner crown surface is strongly convex and presents a well developed uvula, which is strongly protuberated inwards. Poorly developed costules may be present at each side of the uvula on the inner crown base.

The root is anaulacorhizid, with a large flat base. On the outer face two large foramina are present in a median depression. The inner face has a median protuberation, that supports the uvula. At both sides of this protuberation three foramina are lined up along the crown-root junction.

Rostral spine

On the rostral spine of the holotype and on most of the additional ones the root is missing. One additional rostral spine, however, found at Steendorp level 35, is complete and will be described and illustrated below (plate 1: figs. 3a, 3b).

The elongated, dagger-like crown is slightly bent to the rear and is divided into an upper and lower part by smooth front and rear cutting edges. Both identical upper and lower parts are slightly convex.

Considering the enameloid covered part as the crown, the root is high and slender, gradually widening toward the base in upper and lower face and is undulated near the base margin. The base itself is more or less oval shaped and is divided into two equal root lobes by a deep V-shaped median groove. The root lobes are long in front-rear direction but narrow in upper-lower direction. Other than in oral teeth, the median groove fits on the rostrum by its V-shape. Like dermal denticles the vascularization enters via a large aperture, situated in about the mid-section of the median groove.

Order: Myliobatiformes

Family: Dasyatididae JORDAN, 1888

General

Still very little is known about the odontology of the taxa of the Dasyatididae. After LAST & STEVENS (1994) the family comprises the seven genera: *Dasyatis*, *Himantura*, *Hypolophus*, *Pastinachus*, *Taeniura*, *Urogymnus* and *Urolophoides*. Due to the lack of information of the tooth morphology of the living genera, the fossil taxa of the Dasyatididae are mostly included into the genus *Dasyatis*, of which only the genera *Hypolophites* and *Hypolophodon* could be distinguished so far (CAPPETTA, 1987).

The species collected in the Boom Clay Formation have not any odontological relationship with the latter genera, mentioned above, and pending a revision of Dasyatididae, will be tentatively assigned to the genus *Dasyatis*.

Genus: *Dasyatis* RAFINESQUE, 1810

Dasyatis sp.

(Plate 2: figs. 2a, 2b, 2c)

Material:

The illustrated tooth (P.6357) was collected by Mr. R. Smith and a second one by Dr. J. Herman and were kindly placed at our disposal.

Depository: Institut Royal des Sciences naturelles de Belgique (I.R.Sc.n.B.).

Locality and horizon: Schelle, Flanders; Boom Clay Formation, level 41.

Terminology: after CAPPETTA (1987), with labial and lingual replaced by outer and inner, respectively.

Heterodonty:

A significant sexual heterodonty is common in the genus *Dasyatis*, and is presented by a rounded, low transversal crest in females, whereas in males the transversal crest is replaced by a true principal cusp. The tooth of *Dasyatis* sp. has a transversal crest, and therefore, belongs to a female specimen.

The crown has an inwardly bent high transversal crest, which divides the crown into an inner and outer part. The edge of the crown is arched on the outer part and more or less trapezoid on inner part, joining in a mesial and distal marginal angle. The slightly convex inner part is smooth and slopes toward the rounded inner crown rim or visor. The inner part of the transversal crest is also smooth. The centro-inner ridge is poorly developed. The outer part of the transversal crest is integrated in the slightly concave surface of the outer part of the crown, which shows a large median depression. A coarse, reticulated ornamentation, consisting of numerous small depressions, is present on the whole outer surface. The basal face shows a rather, broad, slightly convex crown rim (visor) at the

outer part, gradually narrowing to half its size at the inner part. The crown-root junction lies in a shallow depression in the centre of the basilar surface.

The massive root has a more or less oval shaped cross-section, is oblique toward the rear of the tooth, and more or less gradually widening at the root base. The root base presents a broad and deep median groove, that encloses two foramina, and has rounded margins.

Order: Rajiformes

General

The supraspecific classification within the order rajiformes is still in discussion. After several revisions in the past they presently are divided into approximately 35 genera, and subgenera (McEACHRAN & MIYAKE, 1990a). However, still little is known about their tooth morphology. Therefore, the tooth morphology of over 75 species of 15 genera and subgenera, including their complex heterodonty, was examined and compared with the Rajoidei of the Boom Clay Formation. This revealed sufficient information to elucidate their relationships. The heterodonty of the living taxa examined could be divided into two main groups: Sexual heterodonty present or absent, and if present, the males had disjunct or gradient monognathic heterodonty, whereas females always are gradient monognathic heterodont.

According to the numerous genera and subgenera of the living Rajoidei, fossil records assigned to the genus *Raja* need a general taxonomic revision. However, pending stabilization of the systematic of the living Rajoidei, the fossil Rajiformes here concerned will not be further differentiated.

The distinct tooth morphology of *Raja casieri* could not be further related to *Raja cecilae*, *Raja heinzelini* or *Raja terhageniensis*, and therefore, is possibly gradient monognathic heterodont and sexual heterodonty will be absent. Originally, *Raja terhageniensis* was compared with *Raja (Leucoraja)*, but the latter one has an extreme narrow crown base with a rectangular apron. Although further odontological details strongly differ, several taxa of the family Rajidae basically include the morphotypes of *Raja cecilae*, *Raja heinzelini* and *Raja terhageniensis* in their sexual heterodonty and disjunct monognathic heterodonty. The tooth morphology of *Sympterygia bonapartei* MÜLLER & HENLE, 1841 and *Raja (Rajella) fyllae* LÜTKEN, 1888 is strongly related to that of the latter ones and therefore was selected for comparing and will be illustrated additionally.

Raja casieri STEURBAUT & HERMAN, 1978 (Plate 2: figs. 1a, 1b, 1c, 1d)

The samples yielded 21 teeth, which could be referred to *Raja casieri*.

The holotype is registered as P. 2645 with nine paratypes.

The low principal cusp of the crown is upright and directed inward. Both mesial and distal cutting edges are concavely arched and smoothly join with the more or less rounded mesial and distal blades.

The outer crown surface is slightly convex. The outer basal crown rim is rounded and slightly overhangs the crown-root junction. An apron and basal ornamentation are absent.

The convex inner surface of the crown presents a large, but poorly developed uvula. A basal ornamentation is absent. The holaulacorhizid root is high and broad. The root gradually widens in all directions from the crown-root junction toward the smooth root base margin. A deep, well developed median groove divides the root into two root lobes and encloses one to three foramina. Just above the median groove one or two foramina may be present. The inner face of the root shows a slight protuberance which supports the uvula. On both sides of the protuberance a foramen may be present.

Raja cecilae STEURBAUT & HERMAN, 1978

(Plate 3: figs. 1a, 1b, 1c, 1d; Plate 4: figs. 1a, 1b, 1c, 1d; Plate 5: figs. 1a, 1b, 1c, 1d; Plate 6: figs. 1a, 1b, 1c; Plate 7: figs. 1a, 1b, 1c; Plate 8: figs. 1a, 1b, 1c)

Synonymy

1978 *Raja heinzelini* nov. sp. STEURBAUT & HERMAN p.306 and 307 pl.2: fig.2a, 2b and 2c.

1978 *Raja terhageniensis* nov.sp. STEURBAUT & HERMAN p.307 pl.2: fig.3a, 3b and 3c.

1980 *Raja heinzelini* STEURBAUT & HERMAN Van den Bosch tab.1.

1980 *Raja terhageniensis* STEURBAUT & HERMAN Van den Bosch tab.1.

1984 *Raja heinzelini* STEURBAUT & HERMAN Ward p.66.

- 1984 *Raja terhageniensis* STEURBAUT & HERMAN Ward p.66.
1985 *Raja heinzelini* STEURBAUT & HERMAN Bor, p.101 pl.5 fig.3
1986 *Raja heinzelini* STEURBAUT & HERMAN Von der Hocht p.505 tab.1.
1986 *Raja heinzelini* STEURBAUT & HERMAN Nolf p.36.
1986 *Raja terhageniensis* STEURBAUT & HERMAN Nolf p.36.
1987 *Raja heinzelini* STEURBAUT & HERMAN Cappetta p.144.
1987 *Raja terhageniensis* STEURBAUT & HERMAN Cappetta p.144.

Material Including the former holotypes and paratypes HERMAN & STEURBAUT (1979) reported 60 teeth added with 184 teeth from the samples mentioned above, of which 25 teeth could be referred to the *Raja cecilae*-morphotype, 110 teeth to the *Raja heinzelini*- morphotype and 49 to the *Raja terhageniensis*-morphotype.

Holotype P2648

Differential diagnosis

Males of the genus *Sympterygia bonapartei* and *Raja (Rajella) fyllea* have anterior and lateral teeth similar to the morphotype of *Raja terhageniensis* with an elongated cusp and broad holaulacorhizid root, while the posterior teeth have a flat outer surface with mesial and distal cutting edges convexly arched, corresponding with the morphotype of *Raja cecilae*. The females have a low crown with mesial and distal cutting edges more or less concavely arched and a low root, corresponding with the morphotype of *Raja heinzelini*.

Heterodonty

Males of *Raja cecilae* are disjunct monognathic heterodont by having anterior and antero-lateral teeth with a narrow, elongated principal cusp, whereas lateral and commissural teeth have a broad principal cusp with mesial and distal cutting edges convexly arched and a flat outer surface. Sexual heterodonty is presented by gradient monognathic heterodonty in females with teeth that have a low crown with mesial, distal cutting edges concavely arched and a more or less flat outer surface.

Anterior and antero-lateral teeth of males

The occlusal view of the crown base shows a circular to slightly oval shape. The elongated principal cusp of the crown arises from the crown base, which is strongly directed inward and sometimes moderately oblique distally. Both mesial and distal cutting edges are absent.

The outer basal crown rim is rounded, and in general, slightly overhangs the crown-root junction. An apron, uvula and basal ornamentation are absent.

The root is high and holaulacorhizid. The root gradually widens strongly in all directions from the crown-root junction toward the sometimes slightly undulated root base margin. A deep, well developed median groove divides the root into two root lobes, and encloses one or two foramina. At each side of the median groove an inner foramen may be observed.

Lateral and commissural teeth of males

The crown has a principal cusp, which is directed inward and moderately oblique distally. Both mesial and distal cutting edges are arched in a convex manner, joining at the apex of the principal cusp.

The outer crown surface is more or less flat. The outer basal crown rim is rounded, and slightly overhangs the crown-root junction. An apron and basal ornamentation are absent.

The convex inner surface of the crown presents a poorly developed uvula. A basal ornamentation is absent.

The root is high and holaulacorhizid. The root gradually widens in all directions from the crown-root junction toward the undulated root base margin. A deep, well developed median groove divides the root into two root lobes, and encloses one or two foramina. At each side of the median groove an inner foramen may be observed.

Females

The crown has a low principal cusp, which is directed inward and moderately oblique distally. Both mesial and distal cutting edges are slightly arched in a concave manner, joining at the apex of the principal cusp.

The outer crown surface is more or less flat. The outer basal crown rim is rounded, and slightly overhangs the crown-root junction. An apron and basal ornamentation are absent.

The convex inner surface of the crown presents a small uvula. A basal ornamentation is absent.

The root is low, broad and holaulacorhizid. The root gradually widens in all directions from the crown-root junction toward the slightly undulated root base margin. A deep, well developed median groove divides the root into two root lobes, and encloses one or two foramina.

At each side of the median groove an inner foramen may be observed.
At the outer face a foramen may be present just above the median groove.

Order: Carcharhiniformes

Family: Scyliorhinidae

General

The living Scyliorhinidae are divided (after COMPAGNO, 1988) into four subfamilies: Atelomycterinae with the genera *Atelomycterus* and *Aulohalaelurus*; Schroederichthyinae with the genus *Schroederichthys*; Scyliorhininae with the genera *Cephaloscyllium*, *Poroderma* and *Scyliorhinus* and Pentanchinae with two tribes: Galeini comprising *Asymbolus*, *Cephalurus*, *Galeus*, *Halaelurus*, *Haploblepharus*, *Holohalaelurus* and *Parmaturus* and Pentanchini comprising *Apristurus* and *Pentanchus*.

A comprehensive odontological study of the Carcharhinidae by HERMAN, HOVESTADT & HOVESTADT-EULER (1990 and 1991) supports more or less this classification, but also gave evidence to include the proscyllid genera *Proscyllium*, *Eridacnis*, *Gollum* and *Ctenacis* and the pseudotriakid genus *Pseudotriakis* into the Scyliorhinidae. The odontological results of this study allowed subdividing of the Scyliorhinidae into 6 groups. These groups are considered as the living results of independent evolutionary lineages and will be treated so below. Despite some differences the four subfamilies introduced by COMPAGNO (1988) comprise fairly the same taxa as four of these groups, and therefor, these subfamilies are adopted below for the concerned groups. According the results of comparing the odontological characters, the living Scyliorhinidae are subdivided into the following subfamilies: Atelomycterinae comprising the genera *Atelomycterus* and *Aulohalaelurus*.

Scyliorhininae comprising the genera *Cephaloscyllium*, *Poroderma* and *Scyliorhinus*.

Pentanchinae comprising the genera *Apristurus*, *Galeus*, *Holohalaelurus*, *Haploblepharus*, *Parmaturus*, *Asymbolus*, *Gollum*, *Ctenacis*, *Eridacnis* and *Bythaelurus*.

Schroederichthyinae comprising the genera *Halaelurus*, *Proscyllium* and *Schroederichthys*.

The genera *Cephalurus* and *Pseudotriakis* should be placed in separate subfamilies.

The genus *Halaelurus* has been subdivided by COMPAGNO into the subgenera *Halaelurus* (*Halaelurus*) and *Halaelurus* (*Bythaelurus*). However, the odontological study mentioned above has demonstrated by odontological characters, that the genus *Halaelurus* should belong to the subfamily Schroederichthyinae, *Bythaelurus* should be ranked as a genus of the subfamily Pentanchinae and the tribes Galeini and Pentanchini of the subfamily Pentanchinae were not confirmed.

The tooth morphology of the oligocene representative "*Scyliorhinus*" *aff. coupatezi* from the Boom Clay Formation of Belgium is strongly related to the living genus *Bythaelurus* of the subfamily Pentanchinae.

However, "*Scyliorhinus*" *aff. coupatezi* has no odontological affinities with the genus *Halaelurus*. This, along with the results of the odontological study mentioned above, makes it inevitable to separate *Bythaelurus* from *Halaelurus* and ranked as a new genus of the subfamily Pentanchinae as described above.

Systematics

Class: Chondrichthyes

Subclass: Elasmobranchii BONAPARTE, 1838

Cohort: Euselachii HAY, 1902

Superorder: Galeomorphii COMPAGNO, 1973

Order: Carcharhiniformes sensu COMPAGNO, 1988

Family: Scyliorhinidae GILL, 1862A

Subfamily: Pentanchinae SMITH & RADCLIFFE, 1912

Genus: *Bythaelurus* gen.nov.

Type species: *Bythaelurus canescens* (GÜNTHER, 1878)

Generic diagnosis and description

For a generic diagnosis, description and illustrations of the tooth morphology of the living *Bythaelurus* we refer to HERMAN, HOVESTADT-EULER & HOVESTADT (1990).

Bythaelurus steurbauti gen.nov, spec.nov.
(Plate 9: figs.1a, 1b, 2a, 2b)

Synonymy:

1978 *Scyliorhinus* aff. *coupatezi* HERMAN, 1975 Steurbaut & Herman p.304 pl.1: fig.5
1980 *Scyliorhinus* aff. *coupatezi* HERMAN, 1975 Van den Bosch tab.1.
1993 *Scyliorhinus* aff. *coupatezi* HERMAN, 1975 Génault p.18

Material:

STEURBAUT & HERMAN (1978) reported 3 teeth, added with 14 teeth from the samples mentioned above.

Derivatio nominis: In honour of Dr. E. Steurbaut, who discovered the first teeth of the species.

Specific diagnosis

The taxa of the subfamily Pentanchinae all share more or less characteristics of the tooth morphology of *Bythaelurus steurbauti*, but *Bythaelurus canescens* is most closely related to *Bythaelurus steurbauti*. Both possess a rather short principal cusp with one or two cusplets at each side and irregularly shaped, well developed outer costule-like striae. Finer, more irregularly shaped, inner striae are more developed on teeth of *Bythaelurus steurbauti*. They have similar shaped, slender root lobes, and have a holaulacorhizid to secondary hemiaulacorhizid vascularization type (see Hovestadt & Hovestadt-Euler 1993). The most significant feature on teeth of *Bythaelurus canescens* is the slight, but well perceptible, broad, outer basal depression of the crown, which is particularly presented on upper teeth, whereas on lower teeth the crown base more or less overhangs the crown-root junction. This kind of heterodonty is also presented by the teeth of *Bythaelurus steurbauti*.

Scyliorhinus coupatezi has the tooth morphological characters of the genera of the subfamily Scyliorhininae (Plate 10, fig.1a 1b, 2a, 2b, 3a, 3b, 4a and 4b). Teeth of *Bythaelurus steurbauti* can be separated from *Scyliorhinus coupatezi* HERMAN, 1975 by the absence of outer basal costules or striae on the crown of anterior teeth and short basal costules present on lateral teeth of *Scyliorhinus coupatezi* with an arched outer crown base, and arched root lobes.

The principal cusp is broad and more or less triangularly shaped, which is narrow and slender in *Bythaelurus*.

The stratigraphical range of "*Scyliorhinus*" *dachiardi* (LAWLEY, 1876) has recently been extended to the Oligocene of France by GENAULT (1993). Its tooth morphology, however, resembles that of the genera of the subfamily Scyliorhininae, and widely differs from *Bythaelurus*. The bilobated root of "*Scyliorhinus*" *dachiardi* has shorter, more compact root lobes, which are divided by a deep, well developed median groove. The outer and inner faces are strongly convex. Inner striae are commonly absent and outer striae may vary between hardly perceptible to absent. The principal cusp of "*Scyliorhinus*" *dachiardi* is broader and gives a more massive impression.

The teeth of *Bythaelurus* are closely related to those of "*Scyliorhinus*" *woodwardi* CAPPETTA, 1976 from the English Ypresian (early Eocene), and they could well be congeneric. They can be separated by the following characters: Teeth of the latter species have more pronounced inner striae at the principal cusp, which reach higher than on the oligocene species, whereas the oligocene species have a slightly more slender principal cusp.

A miocene representative of *Bythaelurus* has not yet been reported.

Holotype: P.2642 (Plate 9: figs.1a, 1b)

Paratype: two paratypes

Depository: Institut Royal des Sciences naturelles de Belgique (I.R.Sc.n.B.).

Type locality and horizon: Steendorp, Flanders; Boom Clay Formation, level 35.

Terminology: after HERMAN, HOVESTADT-EULER, HOVESTADT, 1992.

Heterodonty: *Bythaelurus steurbauti* is generally gradient monognathic heterodont. However, the crown of upper teeth have a weak outer basal depression near the crown-root junction, whereas in lower teeth the crown more or less overhangs the outer crown-root junction. Sexual heterodonty is not to be expected, because this was never observed in Scyliorhinidae.

Ontogenetic heterodonty is presented by more developed inner and outer striae on the crown surfaces in juveniles.

Description

The teeth of this species have a relatively short, slender principal cusp. The principal cusp is orientated vertically in anterior teeth and little oblique, in teeth toward the commissure, having two, also short mesial and distal cusplets.

The root is secondary hemiaulacorhizid, showing two relatively long and slender lobes, forming an obtuse angle at the central root base. The dimensions of the teeth are plurimillimetrical in range.

The outer face of the principal cusp and cusplets is weakly convex, presenting well developed, irregularly shaped striae at the crown base, that may run to about half the crown height on cusp and cusplets of upper teeth. A broad, basal depression is present on upper teeth, whereas the crown of lower teeth overhangs the crown-root junction. The inner face of the principal cusp and cusplets is strongly convex, presenting basal costules and poorly developed striae.

The outer face of the root is rather high, presenting a series of about three small, well developed foramina on each root lobe and one central aperture.

The inner face shows a protuberated ridge, that has about the same shape as the angle of the root lobes. It divides the inner face of the root into an upper and a lower section and its central part is strongly protuberant. A foramen is present in the centre of the ridge and some foramina may be present along the crown-root junction on each root lobe. The lower section of the inner root part (root base) may present a poorly developed, shallow median groove.

Phylogeny

Scyliorhinus dachiardi and *Scyliorhinus gilberti* have a very close related tooth morphology and could well be part of one evolutionary lineage. Their odontological morphotypes are similar to genera of the subfamily Scyliorhininae as described by HERMAN, HOVESTADT-EULER & HOVESTADT (1991). *Bythaelurus steurbauti* and "*Scyliorhinus*" *woodwardi* are closely related also. Their odontological morphotypes are similar and both are part of another evolutionary lineage via the subfamily Pentanchinae.

Remarks

The chondrichthyan remains of the Boom Clay Formation as described by STEURBAUT & HERMAN, 1979 showed a rather odd quantity ratio: *Squalus alsaticus* is abundant and the number of rajoid species is low. All other species are very rare, including large ones like *Isurolamna vandenbroecki*, *Cetorhinus parvus*, *Physogaleus latus* etc.

The count of chondrichthyan species yielded by the bulk sampling residues for this study did confirm these extraordinary quantities: About 70% of the fauna was *Squalus alsaticus*, 14% were "*Raja*" *ceciliae*, 5% were gillraker elements of *Cetorhinus parvus* and all other species were presented by a few teeth. Considering that generally *Squalus acanthias* has a lower number of tooth rows than rajoid species, it must have been even more abundant. Living *Squalus*, in general, are known to form large schools. The relatively large concentration of teeth of *Squalus alsaticus* suggests, that *Squalus alsaticus* also must have lived in large schools.

Acknowledgements

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The SEM-photographs were taken by J. CILLIS, Institut Royal des Sciences naturelles de Belgique, Brussels, and the photographs were printed by Mr. G. BROGNET, Mr. J. DEGREEF and Mr. M. VALLE, Brussels.

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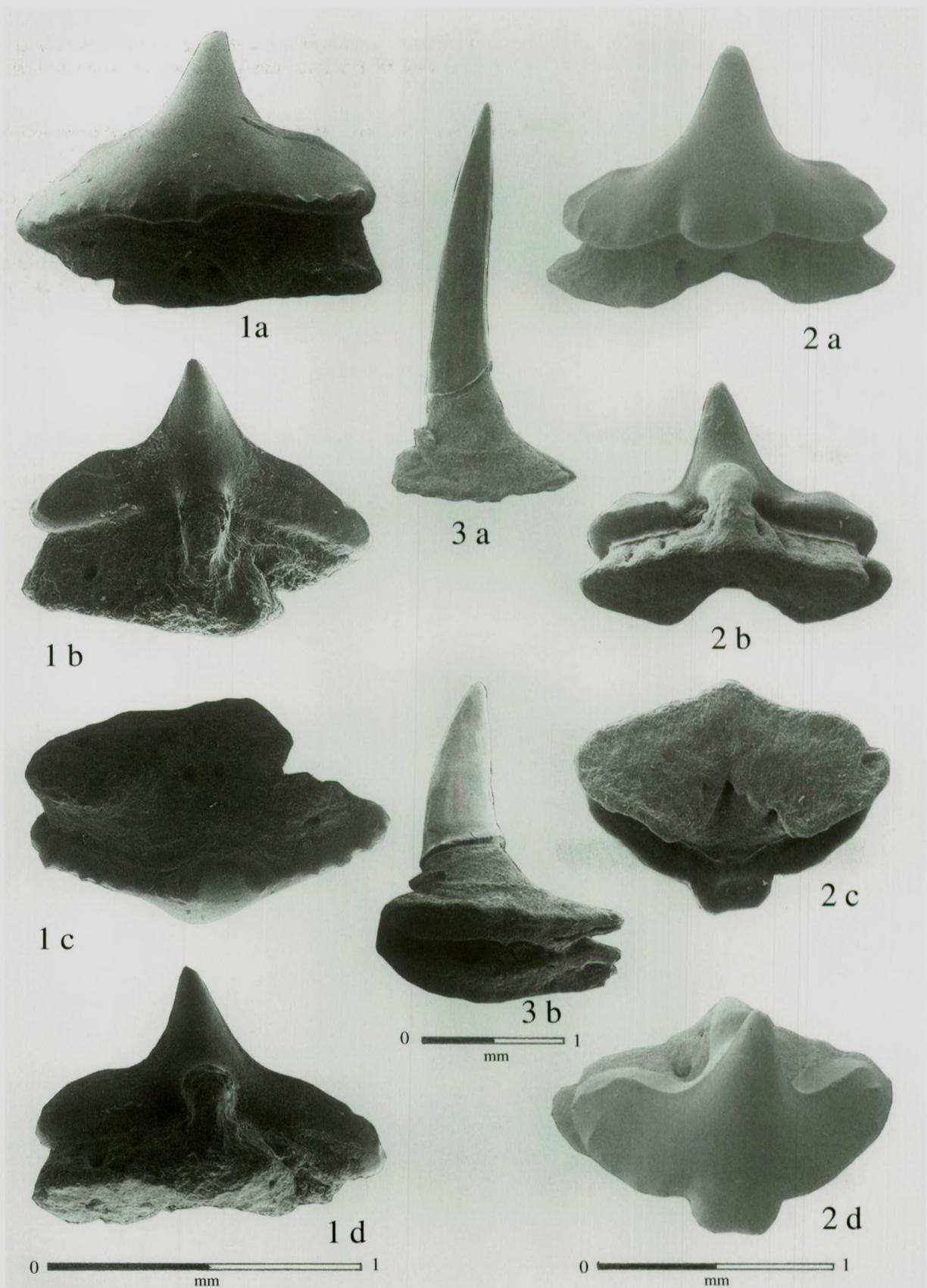


Plate 1. *Pristiophorus rupeliensis*. Oral teeth; Holotype, **a**: outer, **b**: outer-basal, **c**: inner and **d**: inner-basal views; 2. **a**: outer, **b**: occlusal, **c**: inner and **d**: basal views; 3. rostral spine, **a**: upper, **b**: basal views.

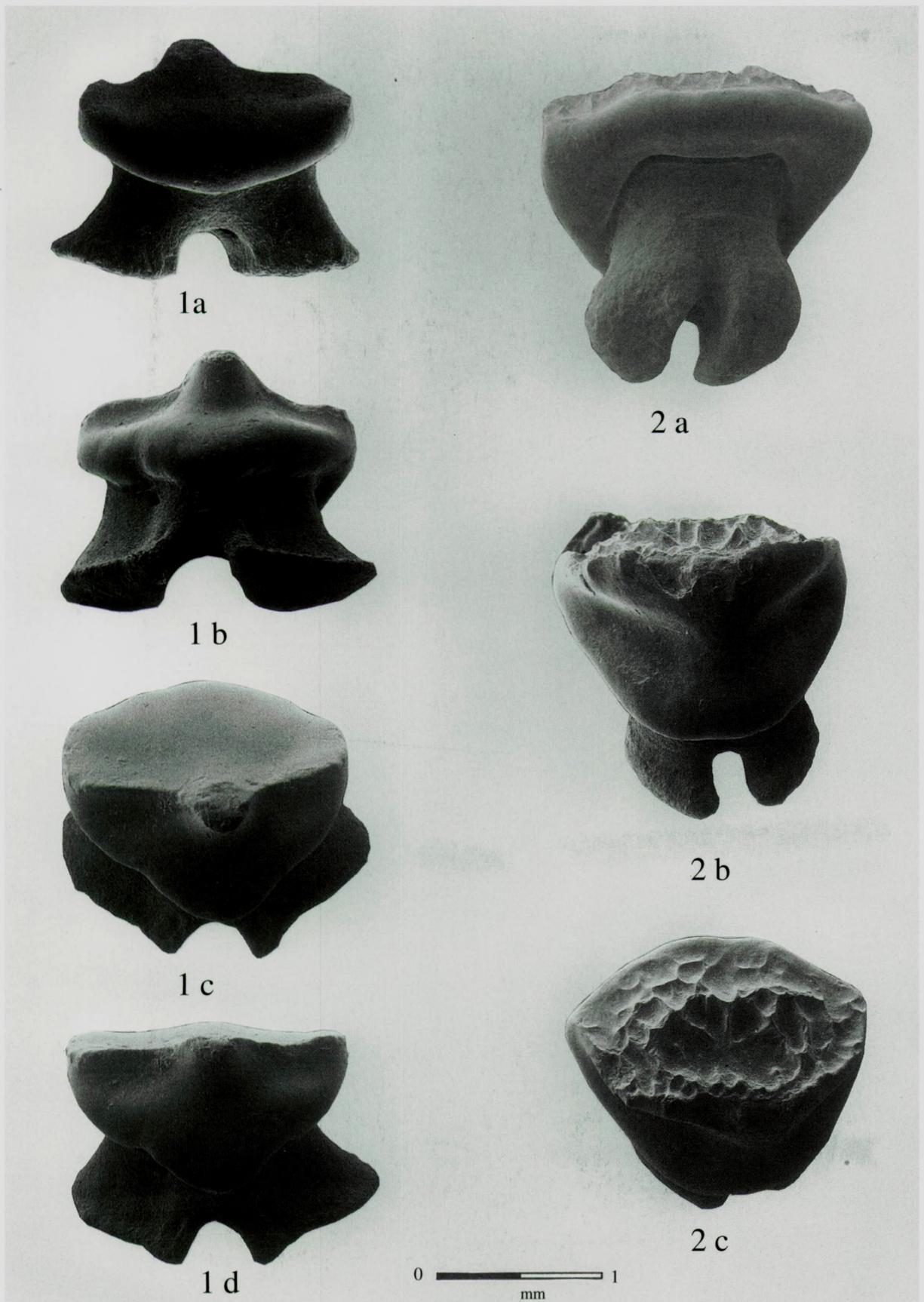


Plate 2. 1: *Raja casieri*, a: outer, b: inner, c: occlusal and d: inner-occlusal views; 2: *Dasyatis* sp., a: outer, b: inner and c: occlusal views.

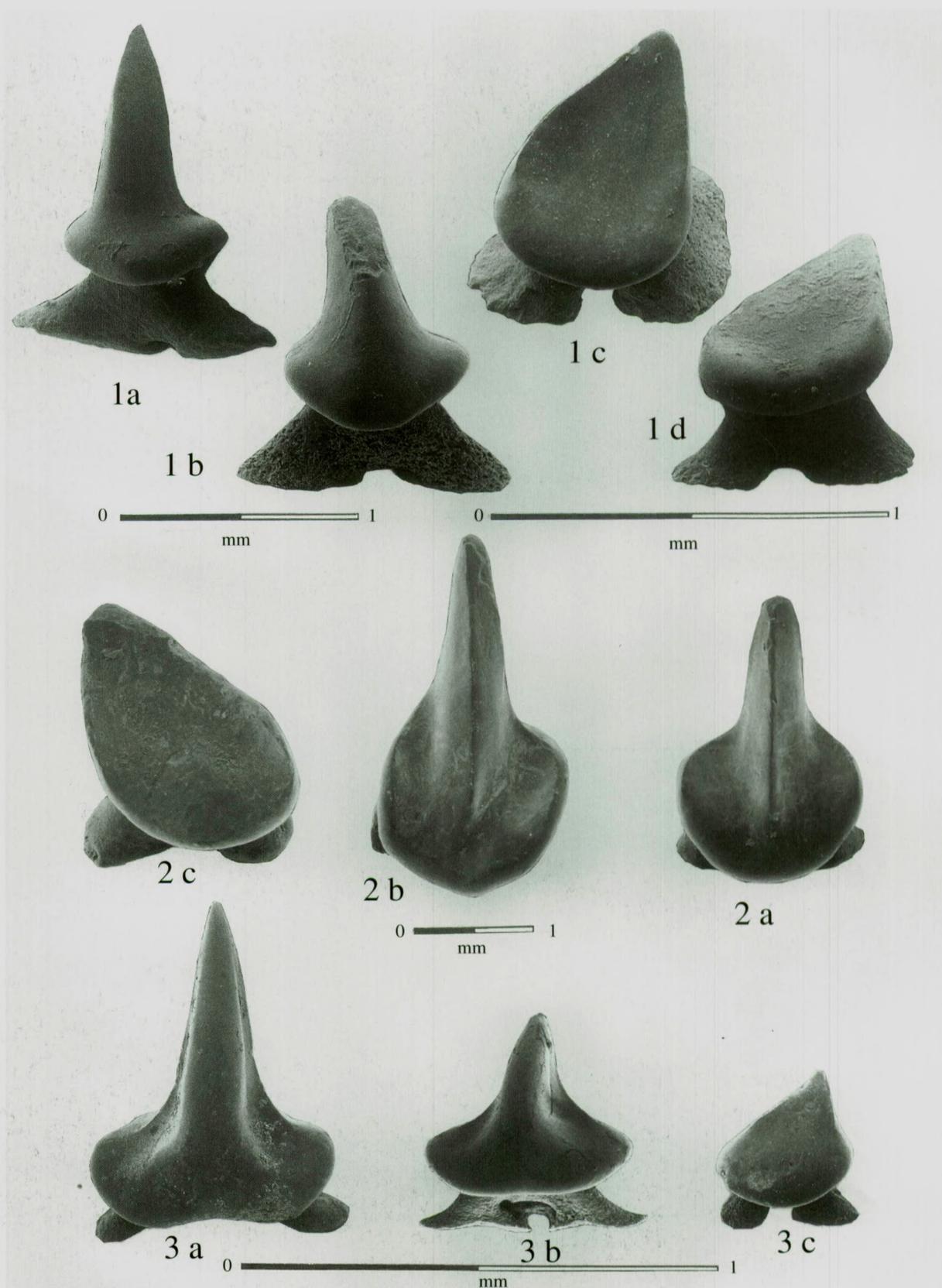


Plate 3. Outer views of teeth of 1: *Raja ceciliae* male, **a**: anterior (Holotype of former *R. terhageniensis*), **b**: anterior (former *R. terhageniensis*), **c**: lateral, **d**: posterior (Holotype); 2: *Sympterygia bonapartei* adult male, **a**: anterior, **b**: lateral, **c**: posterior; 3: *Raja (Rajella) fyllae* adult male, **a**: anterior, **b**: lateral, **c**: posterior.

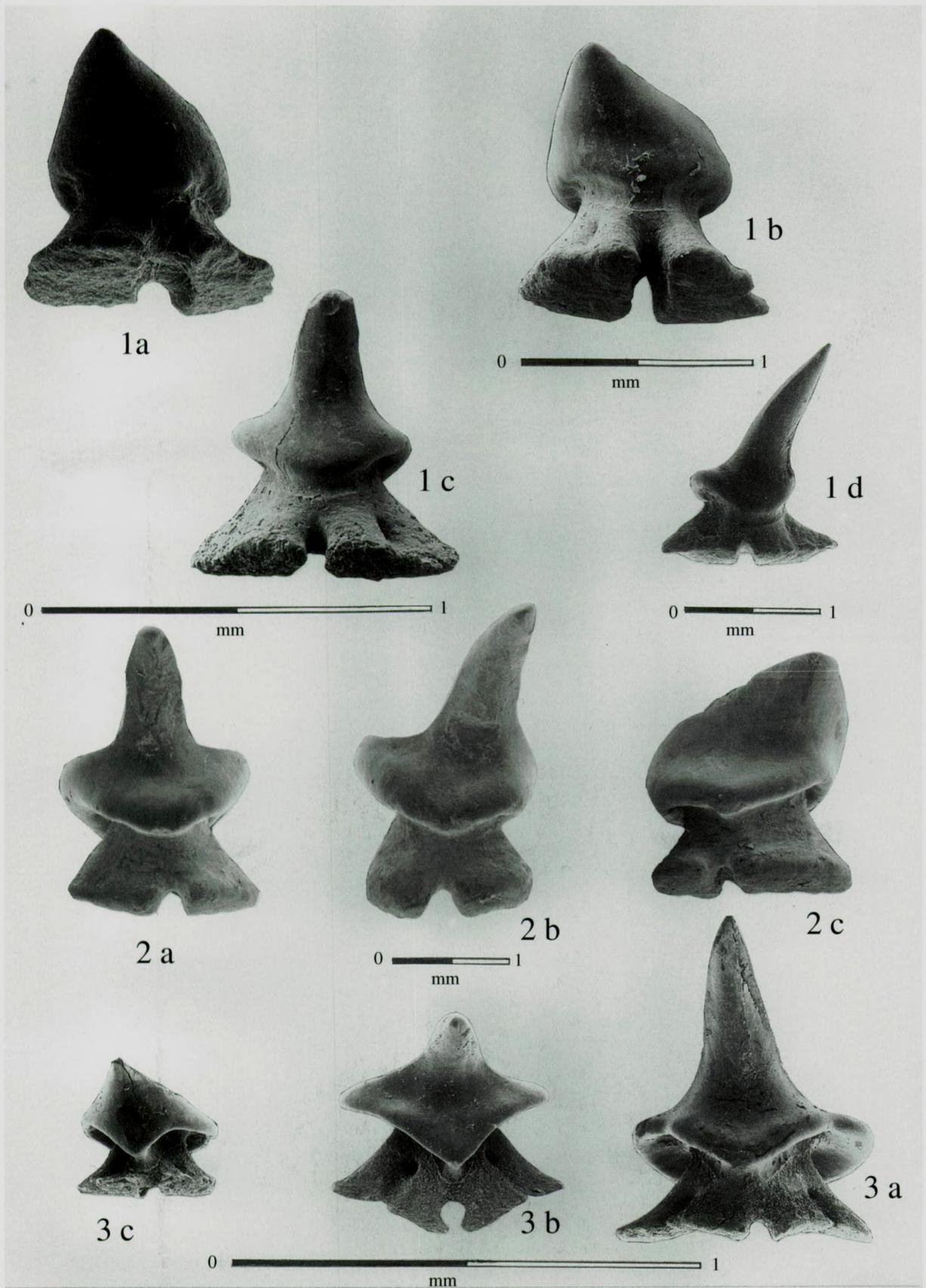


Plate 4. Inner views of teeth of 1: *Raja ceciliae* male, a: posterior (Holotype), b: lateral, c: antero-lateral and d: anterior (former, and former holotype of *R. terhageniensis*); 2: *Sympterygia bonapartei* adult male, a: posterior, b: lateral, c: anterior; 3: *Raja (Rajella) fyllae* adult male, a: posterior, b: lateral, c: anterior.

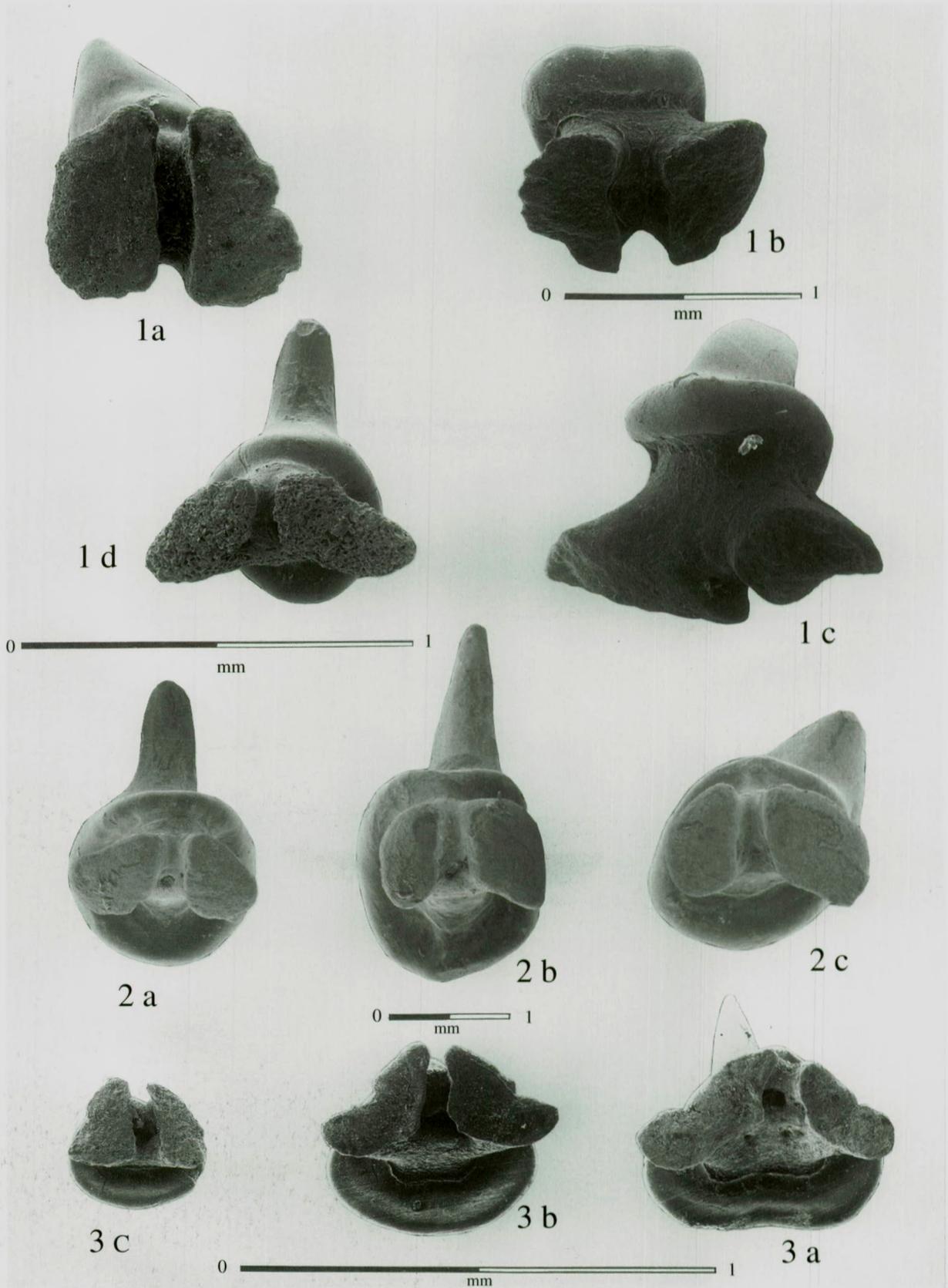


Plate 5. Basal views of teeth of **1:** *Raja ceciliae* male, **a:** posterior (Holotype), **b:** lateral, **c:** antero-lateral and **d:** anterior (former, and former holotype of *R. terhageniensis*); **2:** *Sympterygia bonapartei* adult male, **a:** posterior, **b:** lateral, **c:** anterior; **3:** *Raja (Rajella) fyllae* adult male, **a:** posterior, **b:** lateral, **c:** anterior.

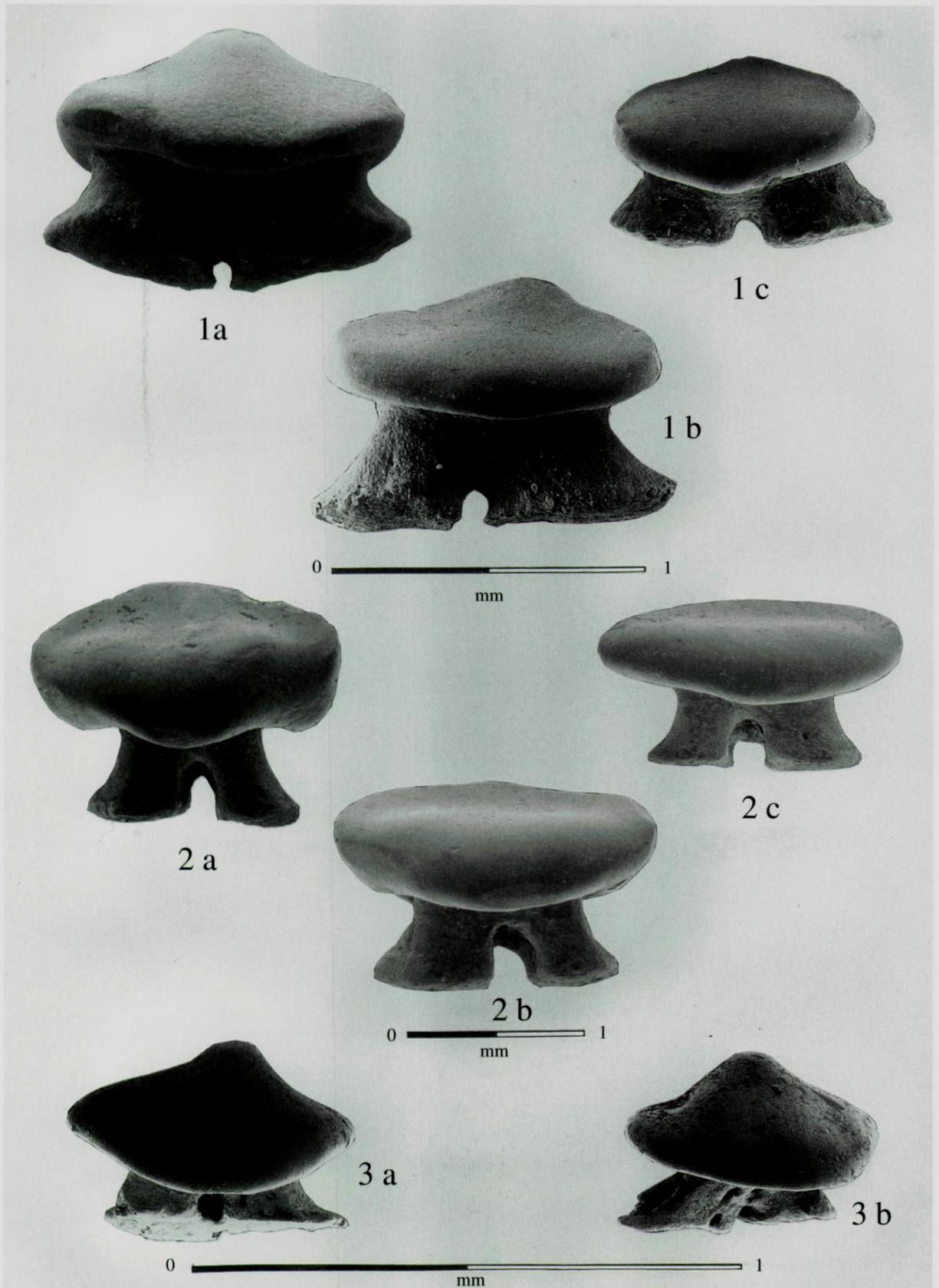


Plate 6. Outer views of teeth of 1: *Raja ceciliae* female; a: anterior (Holotype of former *R. heinzellini*); b: lateral and c: posterior (both former *R. heinzellini*); 2: *Sympterygia bonapartei* adult female, a: anterior, b: lateral, c: posterior; 3: *Raja (Rajella) fyllae* adult female, a: anterior, b: posterior.

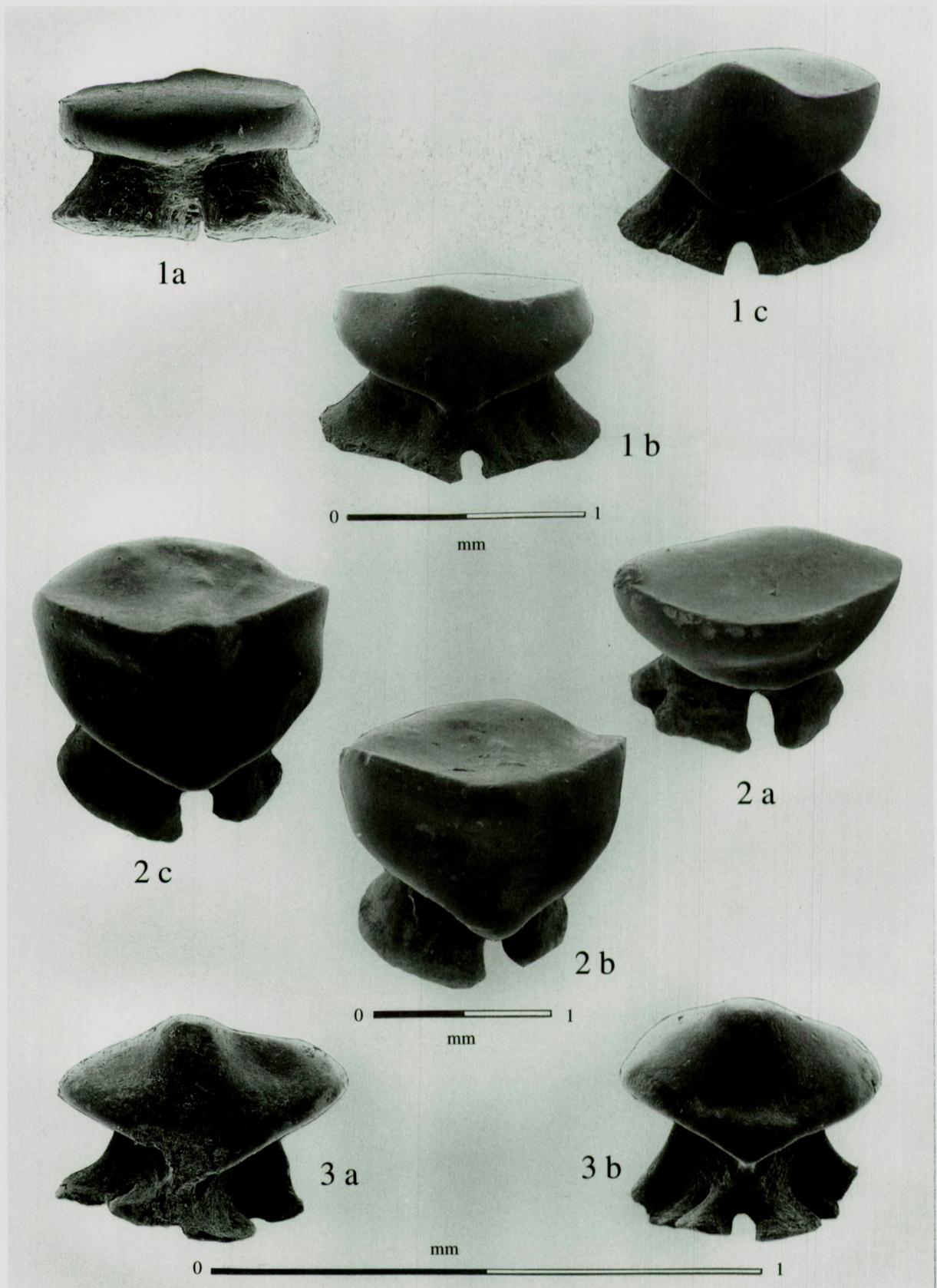


Plate 7. Inner views of teeth of 1: *Raja ceciliae* female; a: posterior (former *R. heinzellini*), b: lateral (former *R. heinzellini*), c: anterior (Holotype of former *R. heinzellini*); 2: *Sympterygia bonapartei* adult female; a: posterior, b: lateral, c: anterior; 3: *Raja (Rajella) fyllae* adult female, a: posterior, b: anterior.

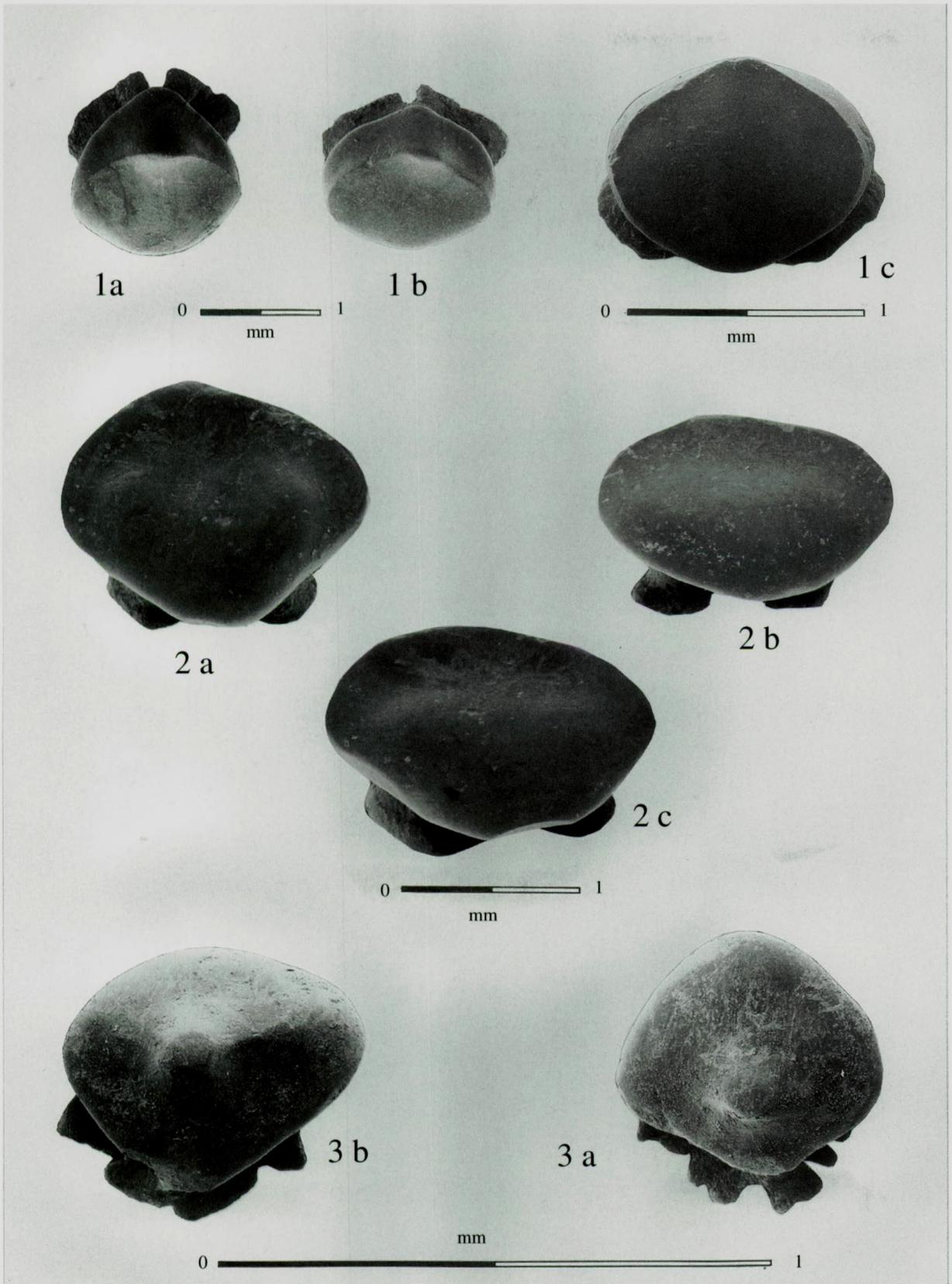


Plate 8. Occlusal views of teeth of 1: *Raja ceciliae* female; a: anterior (Holotype of former *R. heinzellini*), b: lateral (former *R. heinzellini*), c: posterior (former *R. heinzellini*); 2: *Sympterygia bonapartei* adult female; a: anterior, b: lateral, c: posterior; 3: *Raja (Rajella) fyllae* adult female; a: anterior, b: posterior.

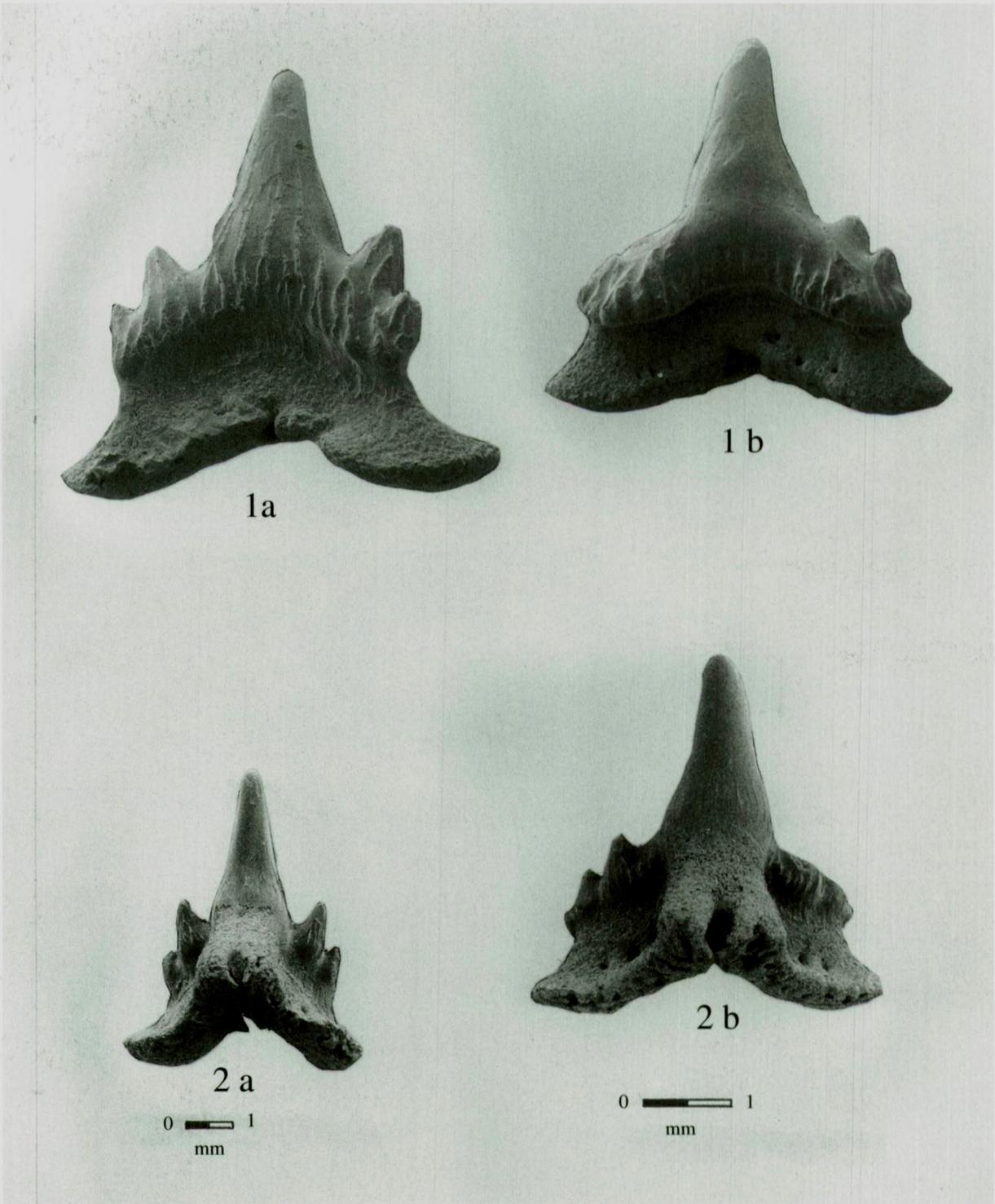


Plate 9. *Bythaelurus sturbauti* 1 (Holotype): outer (1a) and inner (1b) views ; 2 (Paratype): outer (2a) and inner (2b) views.

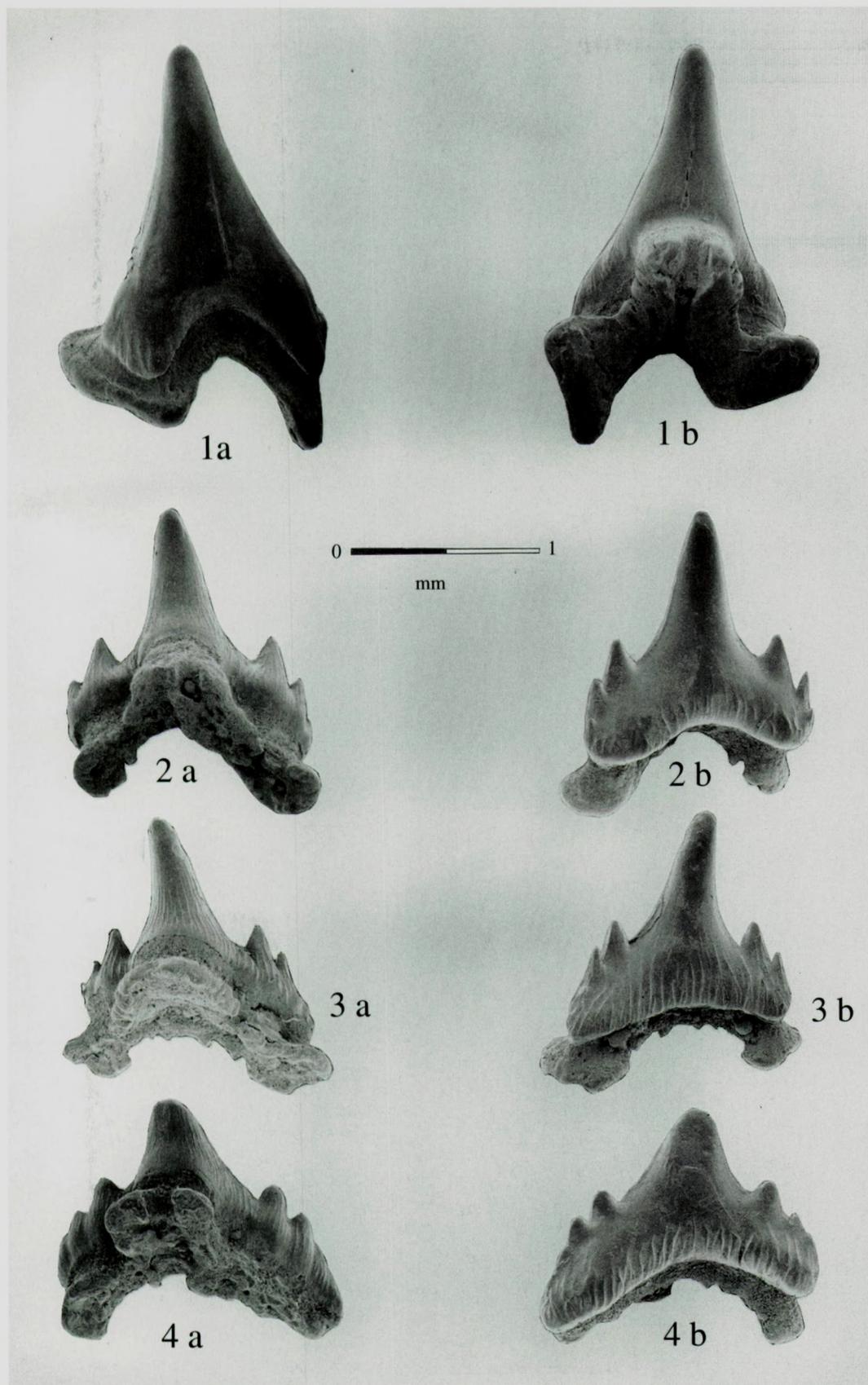


Plate 10. *Scyliorhinus coupatezi* 1 (Holotype): outer (1a) and inner views (1b); 2 (Paratype 1), 3 (Paratype 2) and 4 (Paratype 3): inner (a) and outer views (b).



a



b



c

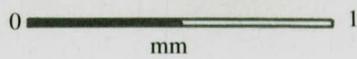


Plate 11. Insecta, Coleoptera, undetermined Curculionid; a: dorsal view; b: side view; c: ventral view.