

### Additions to the Fish Fauna of N.W. Europe.

### 3. Three new species of the genus *Scyliorhinus* from the Late Cretaceous (Campanian and Maastrichtian) of the Limburg area (Belgium and The Netherlands) with a reassignment of four additional fossil species to the genus *Scyliorhinus sensu stricto*.

by

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**Abstract:** Teeth of *Scyliorhinus biddlei* sp. nov., *Scyliorhinus luypaertsii* sp. nov. from the Late Cretaceous (Late Maastrichtian, Maastricht Formation) and *Scyliorhinus reyniersi* sp. nov. from the Late Cretaceous (Late Campanian, Gulpen Formation) of Belgium and The Netherlands are described and illustrated. The new species, together with *Scyliorhinus antiquus* (AGASSIZ, 1843), *Scyliorhinus elongatus* (DAVIS, 1887), *Scyliorhinus fossilis* (LERICHE, 1927 non PROBST, 1879) and *Scyliorhinus coupatezi* HERMAN (1974), are separated from all other fossil species previously described as ?*Scyliorhinus* and reassigned to the genus *Scyliorhinus sensu stricto*.

**Key words:** Chondrichthyes, *Scyliorhinus*, Late Cretaceous, Belgium, The Netherlands.

**Résumé:** Les dents de trois nouvelles espèces: *Scyliorhinus biddlei* sp. nov., *Scyliorhinus luypaertsii* sp. nov. du Crétacé supérieur (Maastrichtien supérieur, Formation de Maastricht) et *Scyliorhinus reyniersi* sp. nov. du Crétacé supérieur (Campanien supérieur, Formation de Gulpen) de Belgique et des Pays-Bas sont décrites et figurées. Ces nouvelles espèces, ainsi que *Scyliorhinus antiquus* (AGASSIZ, 1843), *Scyliorhinus elongatus* (DAVIS, 1887), *Scyliorhinus fossilis* (LERICHE, 1927 non PROBST, 1879) et *Scyliorhinus coupatezi* HERMAN (1974), sont séparées des autres espèces fossiles attribuées précédemment au genre ?*Scyliorhinus* et présentement réassignées au genre *Scyliorhinus sensu stricto*.

**Mots-clefs:** Chondrichthyes, *Scyliorhinus*, Crétacé supérieur, Belgique, Pays-Bas.

**Kurzfassung:** Zähne von *Scyliorhinus biddlei* sp. nov., *Scyliorhinus luypaertsii* sp. nov. aus dem Oberen Maastrichtium (Formation von Maastricht) und *Scyliorhinus reyniersi* sp. nov. aus dem Oberen Campanium (Formation von Gulpen) der Oberkreide von Belgien und den Niederlanden werden beschrieben und abgebildet. Die neu beschriebenen Arten werden zusammen mit *Scyliorhinus antiquus* (AGASSIZ, 1843), *Scyliorhinus elongatus* (DAVIS, 1887), *Scyliorhinus fossilis* (LERICHE, 1927 non PROBST, 1879) und *Scyliorhinus coupatezi* HERMAN (1974) als Vertreter der Gattung *Scyliorhinus sensu stricto* von der großen Zahl fossiler, bislang als ?*Scyliorhinus* beschriebenen Arten abgetrennt.

**Schlüsselwörter:** Chondrichthyes, *Scyliorhinus*, Oberkreide, Belgien, Niederlande.

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## INTRODUCTION

The majority of fossil species of the family Scyliorhinidae has been assigned to the genus *Scyliorhinus*, although many of the species obviously belong to various genera. A more detailed has not been possible because comparative tooth material from living genera and species of this family has never or only insufficiently been figured. With the work on the odontology of living Scyliorhinidae by HERMAN, HOVESTADT-EULER & HOVESTADT (1990) it is now possible to reassign some of the fossil species of this family. Although a complete revision of all these species is beyond the scope of this paper, five fossil species, along with the newly described ones, are separated and reassigned to the genus *Scyliorhinus sensu stricto*.

*Scyliorhinus biddlei* sp. nov. and *Scyliorhinus luypaertsii* sp. nov. are the first representatives of the genus *Scyliorhinus sensu stricto* described from the Maastrichtian.

All specimens illustrated in this paper are housed in the collections of the Institut Royal des Sciences Naturelles (I.R.S.N.B.), Brussels, Belgium.

## LOCALITY AND STRATIGRAPHY

### Locality 1 : Quarry C.B.R. Romontbos, Eben-Emael, Belgium

Grid reference : 107E 258 (Geological Survey of Belgium)

Age : Late Cretaceous (Late Maastrichtian)

Horizon 1 : Crinoid-dominated fossil grit layer between flint stone layers 20 and 21 of the Lanaye Chalk Member (IIIg), Gulpen Formation (Textfigure 3).

Horizon 2 : Bryozoan-dominated fossil grit layer at the base of the Emael Chalk Member (IVd), Romontbos Horizon, Maastricht Formation (Textfigure 3).

### Locality 2 : Quarry E.N.C.I., Maastricht

Grid reference : 61F-19 (Geological Survey of The Netherlands)

Age : Late Cretaceous (Late Maastrichtian)

Horizon : Crinoid-dominated fossil grit layer at the base of the Valkenburg Chalk Member (IVa), Lichtenberg Horizon, Maastricht Formation (Textfigure 4).

### Locality 3 : Quarry Nekami, t' Rooth, The Netherlands

Grid reference : 62A-7 (Geological Survey of The Netherlands)

Age : Late Cretaceous (Late Maastrichtian)

Horizon 1 : Bryozoan-dominated fossil grit layer at the base of the Schiepersberg Chalk Member (IVc), Schiepersberg Horizon, Maastricht Formation (Textfigure 5).

Horizon 2 : Bryozoan-dominated fossil grit layer at the base of the Emael Chalk Member (IVd), Romontbos Horizon, Maastricht Formation (Textfigure 5).

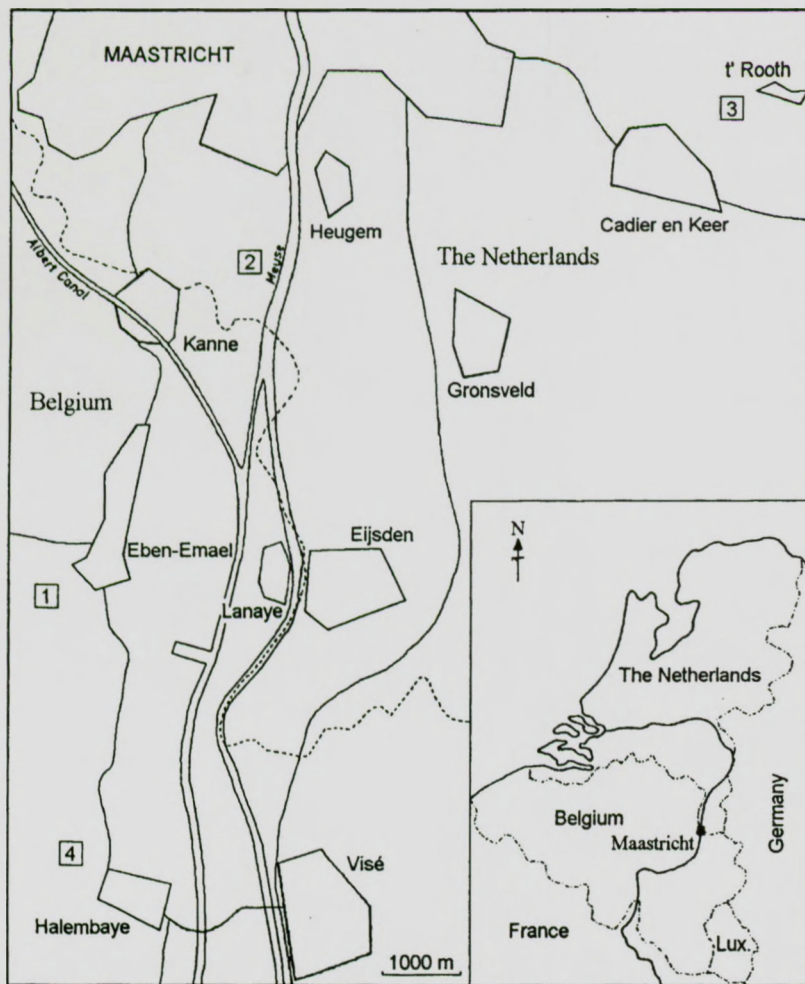
### Locality 4 : Quarry C.P.L., Halembaye, Belgium

Grid reference : 107E 215 (Geological Survey of Belgium)

Age : Late Cretaceous (Late Campanian)

Level 1 : Fossil grit lens in an echinoid-dominated interval in the Zeven Wegen Chalk Member (IIIa), 16.5 m below the Froidmont Horizon, Gulpen Formation (Textfigure 6).

Level 2 : Fossil grit lens in a poriferan-dominated interval in the Zeven Wegen Chalk Member (IIIa), 14.5 m below the Froidmont Horizon, Gulpen Formation (Textfigure 6).

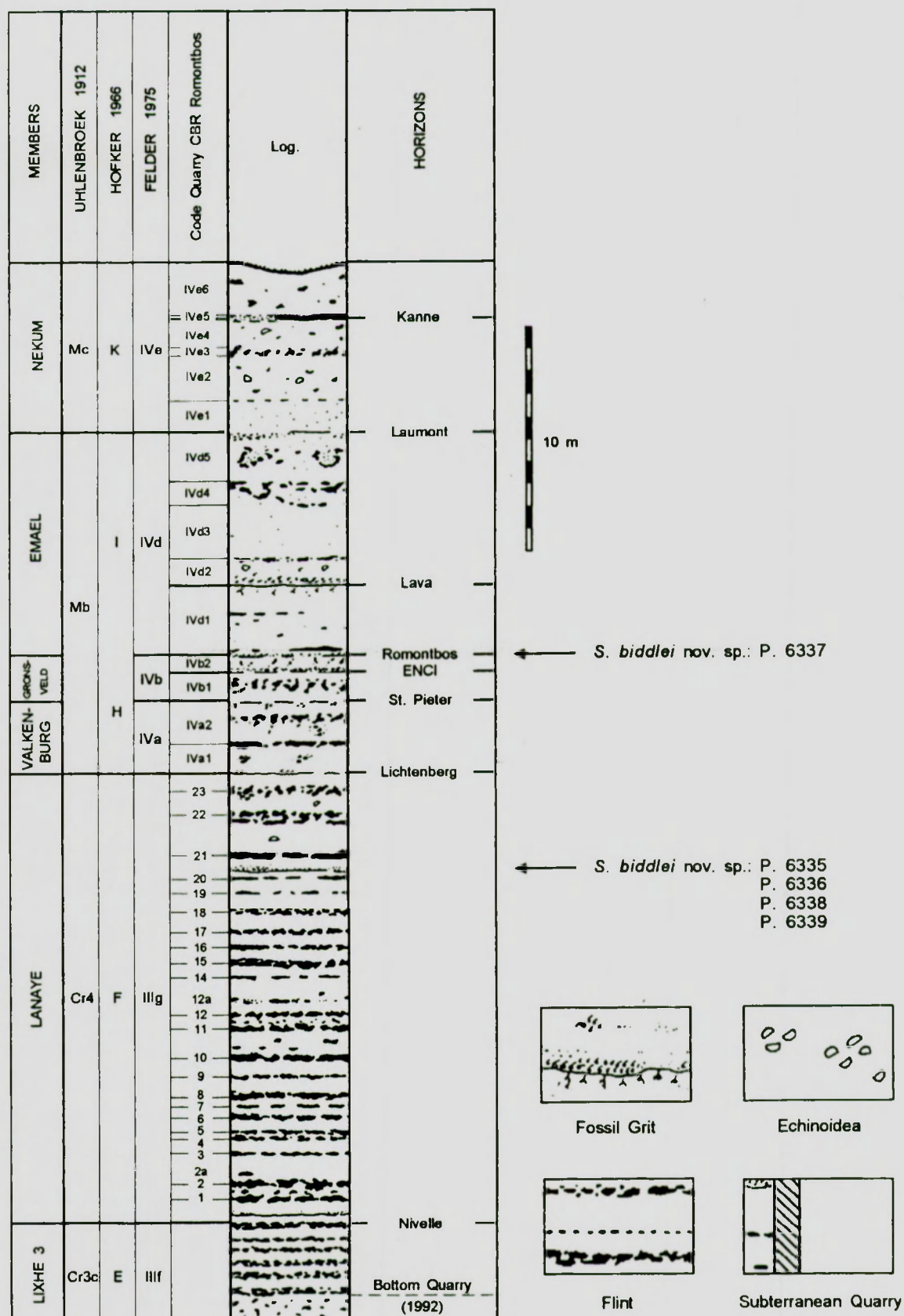


**Textfigure 1.** Sketch map of the localities C.B.R. Romontbos (1), E.N.C.I. (2), Nekami (3) and C.P.L. (4).

FORMATIONS	MEMBERS	CHRONO-STRAT.
MAASTRICHT	Meerssen	LATE MAASTRICHTIAN
	Nekum	
	Emael	
	Gronsveld	
	Schiepersberg	
	Valkenburg	
GULPEN	Lanaye	EARLY MAASTR.
	Lixhe 1-3	
	Vijlen	
	Beutenaken	LATE CAMP.
	Zevenwegen	
VAALS	Terstraeten	EARLY CAMPANIAN
	Beusdal	
	Vaalsbroek	
	Gemmenich	
	Cottessen	
	Raeren	
AACHEN	Hauset	SANTONIAN
	Aachen	
	Hergenrath	

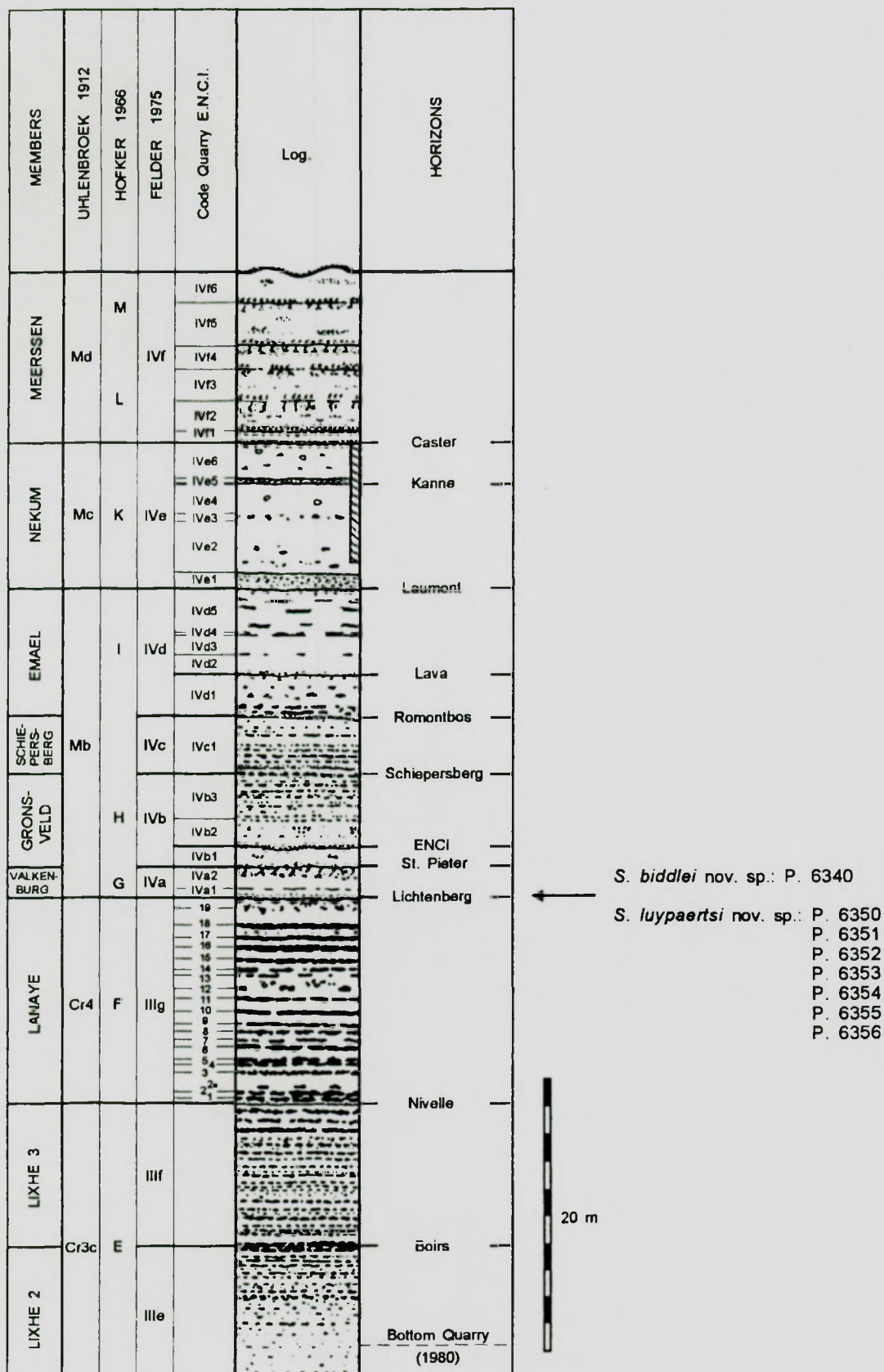
**Textfigure 2.** Lithostratigraphy and Chronostratigraphy of the Late Cretaceous in South Limburg (The Netherlands) and adjacent areas. From Duffin & Reynders (this volume).



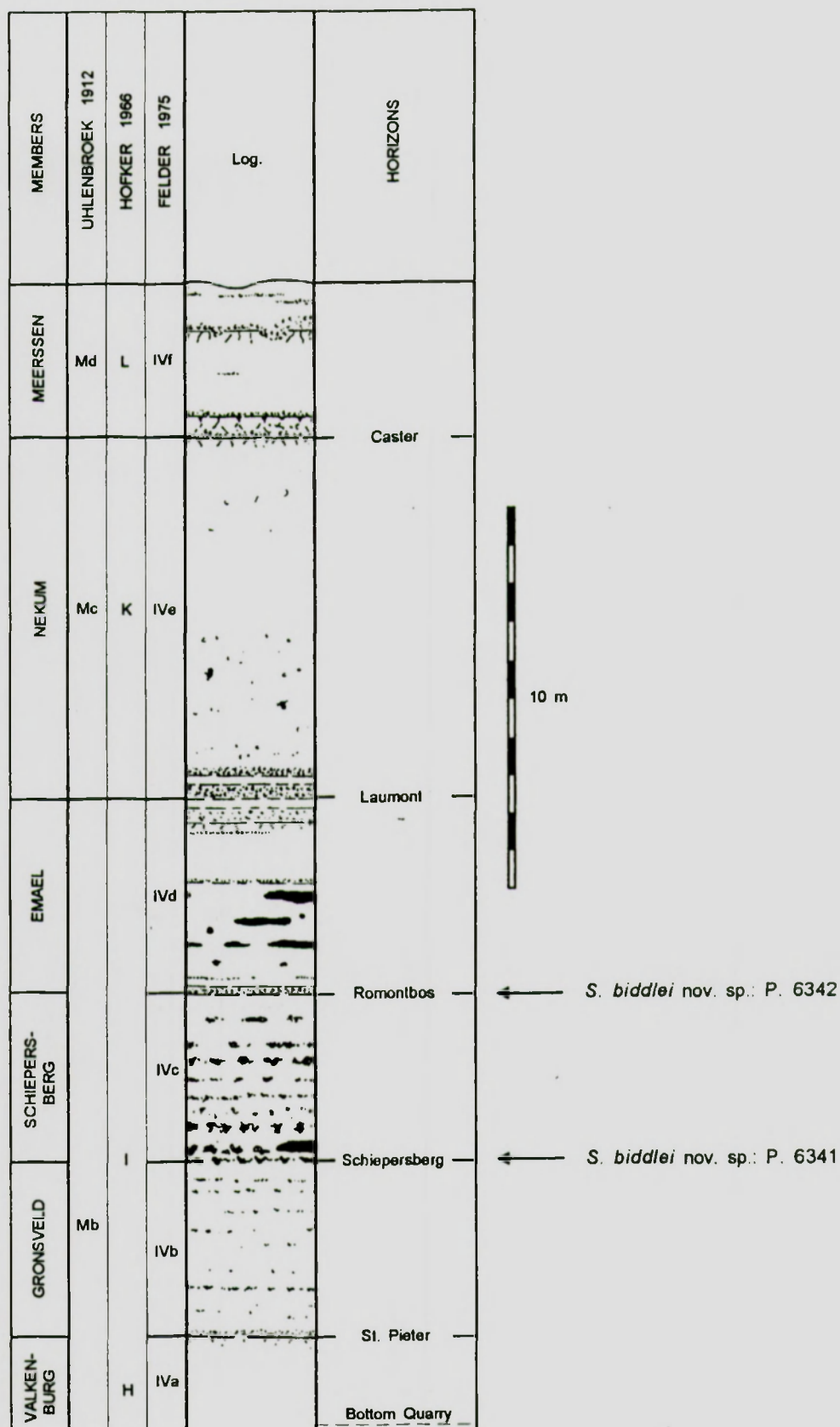


**Textfigure 3.** Lithological section of the quarry C.B.R. Romontbos, Eben-Emael, Belgium. Redrawn after Duffin & Reynders (this volume). The arrows indicate provenance of *Scyliorhinus biddlei* sp. nov. (I.R.S.N.B. P 6335, 6336, 6337, 6338, 6339).

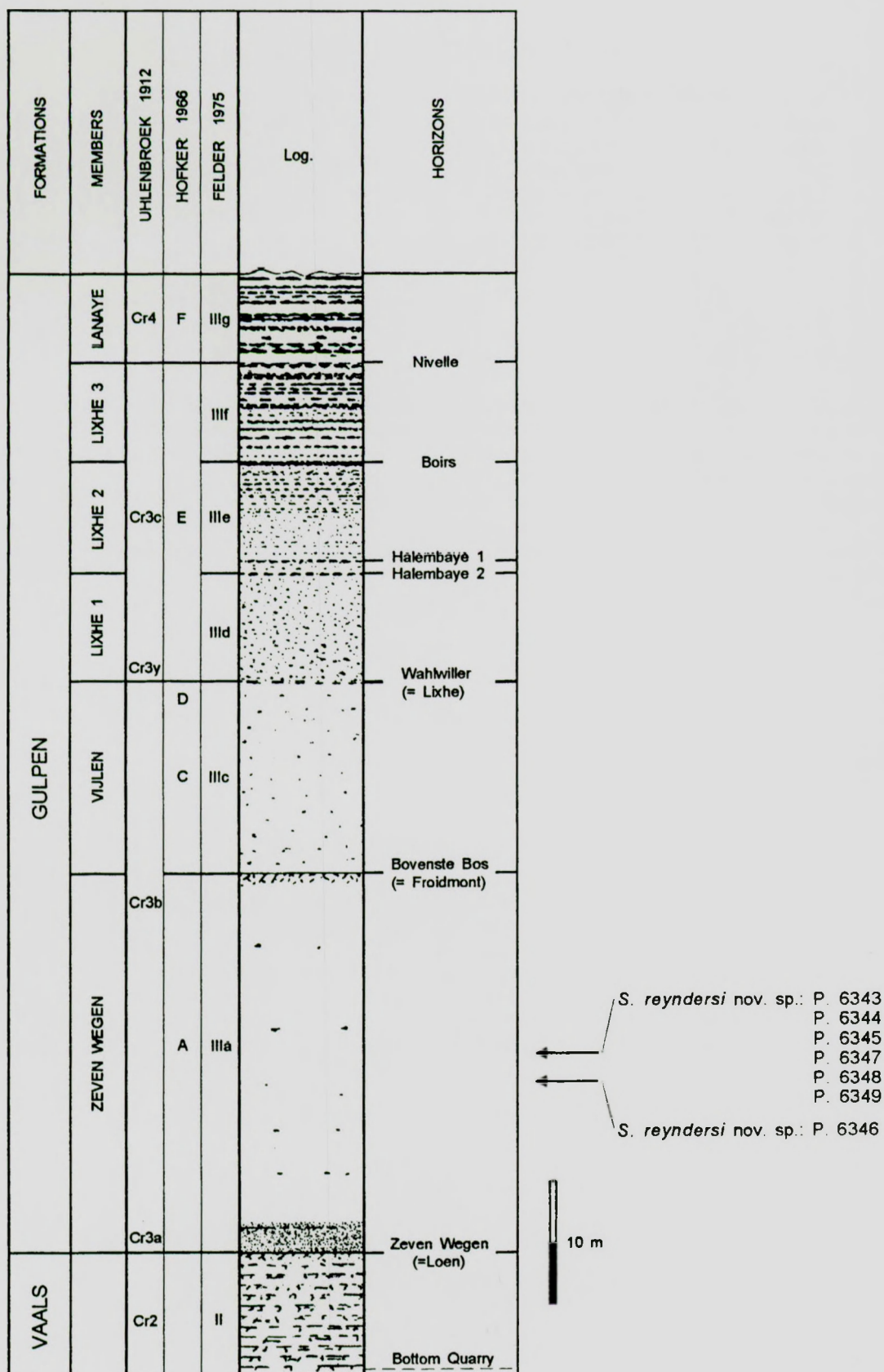




**Textfigure 4.** Lithological section of the quarry E.N.C.I., Maastricht, The Netherlands. Redrawn after Duffin & Reynders (this volume). The arrows indicate provenance of *Scyliorhinus biddlei* sp. nov. (I.R.S.N.B. P 6340) and *Scyliorhinus luypaertsii* sp. nov. (I.R.S.N.B. P 6350, 6351, 6352, 6353, 6354, 6355, 6356). For explanations see Textfigure 2.



**Textfigure 5.** Lithological section of the quarry Nekami, t' Rooth, The Netherlands. Redrawn after Felder et al. (1978). The arrows indicate provenance of *Scyliorhinus biddlei* sp. nov. (I.R.S.N.B. P 6341, 6342). For explanations see Textfigure 2.





## SYSTEMATIC PALAEONTOLOGY

CLASS	CHONDRICHTHYES HUXLEY, 1880
SUBCLASS	ELASMOBRANCHII BONAPARTE, 1838
SUBCOHORT	EUSELACHII HAY, 1902
COHORT	NEOSELACHII COMPAGNO, 1977
SUPERORDER	GALEOMORPHII COMPAGNO, 1973
ORDER	CARCHARHINIFORMES sensu COMPAGNO, 1988
FAMILY	SCYLIORHINIDAE GILL, 1862

### Discussion:

The family Scyliorhinidae (Catsharks) is by far the largest family of sharks. These sharks are small with a maximum length of 1.5 m but mostly no longer than 80 cm. With the exception of *Pentanchus* (SMITH & RADCLIFFE, 1912), they have two spineless dorsal fins; the first of which is small and not keel-like. Its base lies opposite or behind the pelvic origin. Catsharks show five gill slits of which either the 5th, or the 4th and 5th are placed over or behind the pectoral origin. An anal fin is present. Each jaw has numerous small teeth with several functional series. Catsharks occur worldwide from tropical to arctic waters, but the range of the individual species is mostly localized. They occur in coastal waters, although some deepwater species are found down the slopes of the continental and insular shelves up to depths greater than 2000 m. They generally live at or near the bottom. The family Scyliorhinidae is divided into 15 extant and 5 extinct genera.

### Referred genera :

#### Extant:

<i>Apristurus</i>	GARMAN (1913)
<i>Asymbolus</i>	WHITLEY (1939)
<i>Atelomycterus</i>	GARMAN (1913)
<i>Aulohalaelurus</i>	FOWLER (1934)
<i>Cephaloscyllium</i>	GILL (1862)
<i>Cephalurus</i>	BIGELOW & SCHROEDER (1941)
<i>Galeus</i>	RAFINESQUE (1810)
<i>Halaelurus</i>	GILL (1862)
<i>Haploblepharus</i>	GARMAN (1913)
<i>Macrourogaleus</i>	FOWLER (1947)
<i>Parmaturus</i>	GARMAN (1906)
<i>Pentanchus</i>	SMITH & RADCLIFFE in SMITH (1912)
<i>Poroderma</i>	SMITH (1837)
<i>Schroederichthys</i>	SPRINGER (1966)
<i>Scyliorhinus</i>	BLAINVILLE (1816)

#### Extinct:

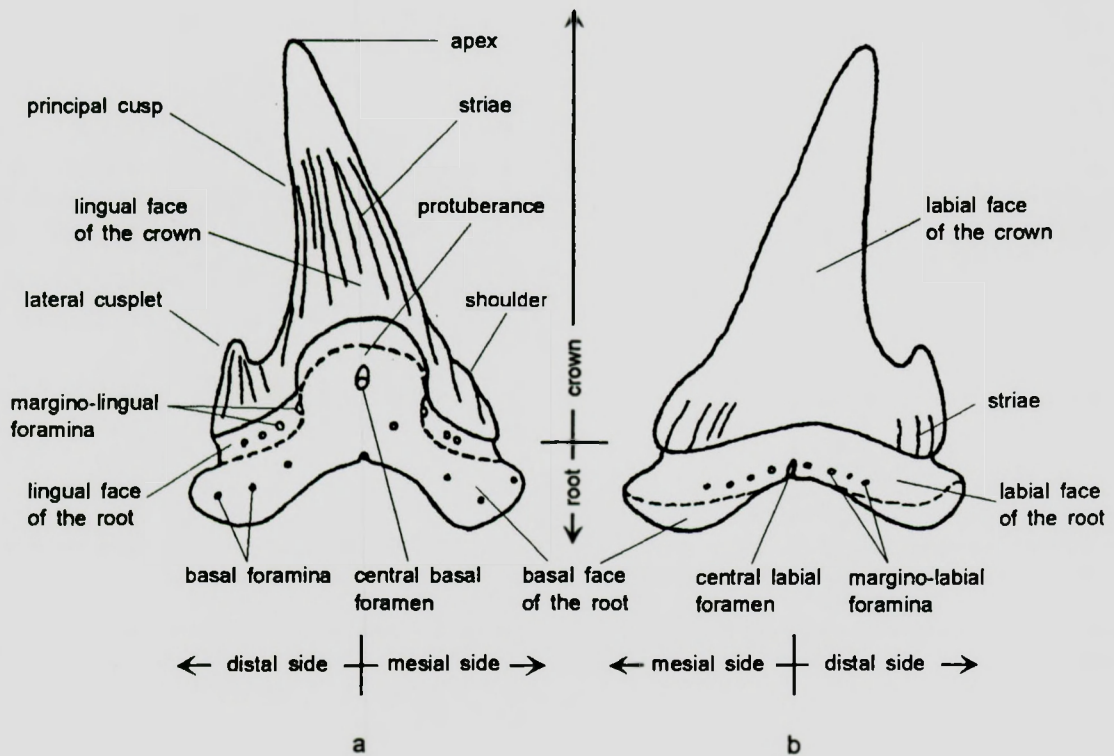
<i>Megascyliorhinus</i>	CAPPETTA & WARD (1977)
<i>Parasymbolus</i>	CANDONI (1993)
<i>Protoscyliorhinus</i>	HERMAN (1977)
<i>Pseudoscyliorhinus</i>	MÜLLER & DIEDRICH (1991)
<i>Pteroscylidium</i>	CAPPETTA (1980)

Genus: *Scyliorhinus* BLAINVILLE, 1816

Type species: *Squalus canicula* LINNAEUS (1758: 234); extant.

The following 13 extant species belong to the genus *Scyliorhinus* (COMPAGNO, 1988):

<i>Scyliorhinus besnardi</i>	SPRINGER & SADOWSKY, 1970
<i>Scyliorhinus boa</i>	GOODE & BEAN, 1896
<i>Scyliorhinus canicula</i>	(LINNAEUS, 1758)
<i>Scyliorhinus capensis</i>	(SMITH, 1838)
<i>Scyliorhinus cervigoni</i>	MAURIN & BONNET, 1970
<i>Scyliorhinus garmani</i>	(FOWLER, 1934)
<i>Scyliorhinus haeckeli</i>	(RIBEIRO, 1907)
<i>Scyliorhinus hesperius</i>	SPRINGER, 1966
<i>Scyliorhinus meadi</i>	SPRINGER, 1966
<i>Scyliorhinus retifer</i>	(GARMAN, 1881)
<i>Scyliorhinus stellaris</i>	(LINNAEUS, 1758)
<i>Scyliorhinus torazame</i>	(TANAKA, 1908)
<i>Scyliorhinus torrei</i>	HOWELL-RIVERO, 1936



Textfigure 7. *Scyliorhinus biddlei* sp. nov.; a) lingual view, b) labial view. The dental terminology is based on Cappetta (1987).

### Generic diagnosis:

The odontological differences among the living species of *Scyliorhinus* sensu stricto are minor (HERMAN, HOVESTADT-EULER & HOVESTADT, 1990). Therefore, this generic diagnosis is based on *Scyliorhinus canicula* (LINNAEUS, 1758), figured in HERMAN, HOVESTADT-EULER & HOVESTADT (1990: 190, pl. 31, 32).

The teeth of *Scyliorhinus canicula* have a maximum height of 2.0 mm and width of 1.5 mm. The teeth have a tall and elongated principal cusp, becoming lower towards the commissure. The principal cusp is slightly inclined towards the commissure, and commonly one pair of lateral cusplets is present in upper lateral and posterior teeth and in the lower teeth. Upper lateral and lower antero-lateral teeth show a mesial shoulder and a distal lateral cusplet. Upper anterior teeth have a mesial and distal shoulder.

The labial face of the principal cusp and lateral cusplets is flat or weakly convex and shows basal striae. These striae are absent in lower symphyseal, anterior and antero-lateral teeth. A reticulated microornamentation is present in posterior and lower lateral teeth.

The lingual face of the principal cusp and lateral cusplets is strongly convex and presents striae that are slightly less distinct than the basal striae on the labial face of the crown. They run from the base to the apex of the crown and cusplets in a more or less regular way. Their density varies from 5 to 15 on the principal cusp and from 3 to 4 on lateral cusplets. The striae do not fully reach the apex of the principal cusp.

The root is always secondary hemiaulacorhize with a completely closed median groove. The root is bilobate with lobes that are relatively long and narrow. The labial face of the root presents up to nine well-developed foramina. The basal face of the root is flat to slightly concave and shows some randomly scattered foramina.

### Heterodonty:

*Scyliorhinus canicula* shows a strong monognathic and a weak dignathic heterodonty. An ontogenetic heterodonty is not observable because of the lack of comparative tooth material from juvenile specimens.

#### (1) Dignathic heterodonty:

Upper teeth show prominent basal striae. The base of the labial face of the crown slightly overhangs the crown-root-junction. Lower teeth have basal striae, which are less prominent, only in lateral and posterior teeth; the base of the labial face of the crown strongly overhangs the crown-root-junction.

#### (2) Monognathic heterodonty:

(a) Increasing tooth height and width from symphyseal to anterior and antero-lateral teeth; then decreasing again to posterior teeth.

(b) Symphyseal and lower anterior teeth show one pair of lateral cusplets; upper anterior teeth have a mesial and distal shoulder; upper lateral and lower antero-lateral teeth have a mesial shoulder and a distal lateral cusplet; posterior, commissural and lower lateral teeth have one pair of lateral cusplets.

(c) Reticulated microornamentation at the base of the labial face of the crown in posterior and latero-posterior teeth.



## FOSSIL RECORD OF THE GENUS *SCYLIORHINUS*

The following fossil species have so far been included in the genus *Scyliorhinus*. Species preceded by a question mark do not belong to the genus *Scyliorhinus* sensu stricto:

- Scyliorhinus antiquus* (AGASSIZ, 1843: 378, pl. 38, fig. 1, 3 (non fig. 2)), CAPPETTA (1977: 481; pl. 1, fig. 3 - 4 ) from the Turonian, Late Cretaceous of England and France HERMAN (1977: 251; pl. 11, fig. 1a, b, c, d, e, f).
- ?*Scyliorhinus arambourgi* CAPPETTA (1980: 126-127; fig. 27; pl. 19, fig. 1-4) from the Cenomanian, Late Cretaceous of Lebanon.
- ?*Scyliorhinus bloti* CAPPETTA (1980: 127-129; fig. 28; pl. 18) from the Cenomanian, Late Cretaceous of Lebanon.
- ?*Scyliorhinus burnhamensis* CAPPETTA (1976: 558; pl. 3, fig. 1-2) from the Ypresian, Early Eocene of England.
- ?*Scyliorhinus cabindensis* (LERICHE, 1927: 399; fig. 1-3), DARTEVELLE & CASIER (1943: pl. 3, fig. 41-44) from the Palaeocene of Cabinda.
- ?*Scyliorhinus casieri* CAPPETTA (1976: 558-559; pl. 3, fig. 3-6) from the Ypresian, Early Eocene of England.
- ?*Scyliorhinus cepaeformis* HALTER (1990: 223, 225-228; fig. 4; pl. 2, fig. 3; pl. 3) from the Late Maastrichtian, Late Cretaceous of Belgium and The Netherlands.
- Scyliorhinus coupatezi* HERMAN (1974: 23-24; pl. 2, fig. 4) from the Pliocene of Belgium.
- ?*Scyliorhinus destombesi* CAPPETTA (1977: 968; pl. 1, fig. 3-6) from the Late Albian, Early Cretaceous of France.
- ?*Scyliorhinus distans* (PROBST, 1879: 170-171; pl. 3, fig. 23-26) from the Early Miocene of Germany.
- ?*Scyliorhinus dubius* (WOODWARD, 1889: 341; pl. 16, fig. 7-8), CAPPETTA (1977: 481; pl. 1, fig. 5-6) from the Lower Chalk, Late Cretaceous of England.
- Scyliorhinus elongatus* (DAVIS, 1887: 473; pl. 14, fig. 2-3), CAPPETTA (1980: 129-133; fig. 29-30; pl. 21; pl. 22; pl. 23, fig. 1-6) from the Late Santonian, Late Cretaceous of Lebanon and from the Campanian, Late Cretaceous of Belgium HERMAN (1977: 252-253; pl. 11, fig. 1g, i, j non fig. 1a, b, c, d, e, f, h).
- Scyliorhinus fossilis* (LERICHE, 1927: 54-55; pl. 5, fig. 11-15 non PROBST 1879) from the Miocene of Switzerland, ANTUNES & JONET (1970: 159-162; fig. 6; pl. 10, fig. 53-57) from the Late Helvétian and Tortonian, Middle and Upper Miocene of Portugal, CAPPETTA (1970: 43-45; pl. 10, fig. 1-17) from the Langhian, Middle Miocene of France.
- ?*Scyliorhinus germanicus* HERMAN (1982: 141-142; pl. 2, fig. 10; pl. 4, fig. 4-5) from the Maastrichtian, Late Cretaceous of Germany.
- ?*Scyliorhinus gilberti* (CASIER, 1946: 58; pl. 1, fig. 14) from the Ypresian, Early Eocene of Belgium.
- ?*Scyliorhinus moosi* HERMAN (1975: 299-300; pl. 1, fig. 2) from the Campanian, Late Cretaceous of Germany.
- ?*Scyliorhinus musteliformis* HERMAN (1977: 254-255; pl. 11, fig. 3) from the Campanian, Late Cretaceous of Belgium.
- ?*Scyliorhinus pattersoni* CAPPETTA (1976: 559-560; pl. 4, fig. 1-5) from the Ypresian, Early Eocene of England.
- ?*Scyliorhinus reussi* HERMAN (1977: 253-254; pl. 11, fig. 2) from the Turonian, Late Cretaceous of France.
- ?*Scyliorhinus riegrafi* MÜLLER (1989: 48-49; pl. 14, fig. 2-10) from the from the Campanian, Late Cretaceous of Germany.
- ?*Scyliorhinus subulidens* ARAMBOURG (1952: 121-122; fig. 22; pl. 23, fig. 1-19) from the Palaeocene and Early Eocene of Morocco.
- ?*Scyliorhinus tensleepensis* CASE (1987: 13-14; fig. 3) from the Campanian, Late Cretaceous of the USA.
- ?*Scyliorhinus wardi* HALTER (1990: 228, 230-232; fig. 6; pl. 1; pl. 2, fig. 1-2) from the Late Maastrichtian, Late Cretaceous of Belgium and The Netherlands.

### Differential diagnosis:

The teeth of living and fossil species of the genus *Scyliorhinus* sensu stricto can be distinguished from all other genera of the family Scyliorhinidae by a combination of the following characteristics:

(a) Anterior and antero-lateral teeth with an elongated and biconvex principal cusp, which is upright or slightly bent towards the commissure.

(b) Lateral cusplets, if present, are generally low and poorly developed.

(c) Anterior and sometimes antero-lateral teeth with a pair of shoulders or a lateral cusplet and a shoulder. Lateral, latero-posterior and posterior teeth with one mesial shoulder and one distal lateral cusplets, one pair or sometimes two pairs, of lateral cusplets.

(d) A strongly convex lingual face of the crown with a varying number of striae. A convex to concave labial face of the crown. Lateral teeth may show a suberect crown.

(e) The root vascularization is generally secondary hemiaulacorrhize with a completely or partially closed median groove. In anterior teeth the median groove may be open. Anterior and antero-lateral teeth show a prominent and massive protuberance.

### Discussion:

The comparison of teeth from the living species *Scyliorhinus canicula* (LINNAEUS, 1758) and *Scyliorhinus torazame* (TANAKA, 1908), figured in HERMAN, HOVESTADT-EULER & HOVESTADT (1990: pl. 33, 34), with the aforementioned fossil species leads to the conclusion that *Scyliorhinus antiquus* (AGASSIZ, 1843) from the Turonian of France HERMAN (1977) and England CAPPETTA (1976), *Scyliorhinus elongatus* (DAVIS, 1887) from the Late Santonian of Lebanon CAPPETTA (1980) and the Campanian of Belgium HERMAN (1977), *Scyliorhinus fossilis* (LERICHE, 1927), ANTUNES & JONET (1970), CAPPETTA (1970) from the Miocene of Switzerland, Portugal and France, and *Scyliorhinus coupatezi* HERMAN (1974) from the Pliocene of Belgium are representatives of the genus *Scyliorhinus* sensu stricto.

All these species show a combination of the characteristics listed in the differential diagnosis. The most important characteristic that separates the species of *Scyliorhinus* sensu stricto from other genera of the family Scyliorhinidae figured in HERMAN, HOVESTADT-EULER & HOVESTADT (1990: pl. 1-30) is that anterior and sometimes antero-lateral teeth show a pair of shoulders or one lateral cusplet and a shoulder.

All species listed above which are preceded by a question mark do not have anterior teeth of this type, and therefore belong to other genera of the family Scyliorhinidae.

*Scyliorhinus antiquus* (AGASSIZ, 1843) has anterior teeth with poorly developed lateral cusplets HERMAN (1977: pl. 11, fig 1c, d). Some anterior teeth of *S. antiquus* from the same locality as the teeth figured in HERMAN (1977) in the collection of the author show a mesial shoulder and a poorly developed distal lateral cusplet. Therefore, *S. antiquus* is assigned to *Scyliorhinus* sensu stricto.

*Scyliorhinus elongatus* (DAVIS, 1887) has anterior teeth with poorly developed lateral cusplets CAPPETTA (1980: 131, fig. 30; pl. 22, fig. 4), HERMAN (1977: pl. 11, fig 1i, j). Several anterior and antero-lateral teeth of *S. elongatus* from the Campanian of Obourg, Belgium in the collection of Mr. J.P.H. Reynders (Houthalen, Belgium) have a mesial and distal shoulder or a mesial shoulder and a distal lateral cusplet. Therefore, *S. elongatus* is assigned to *Scyliorhinus* sensu stricto.

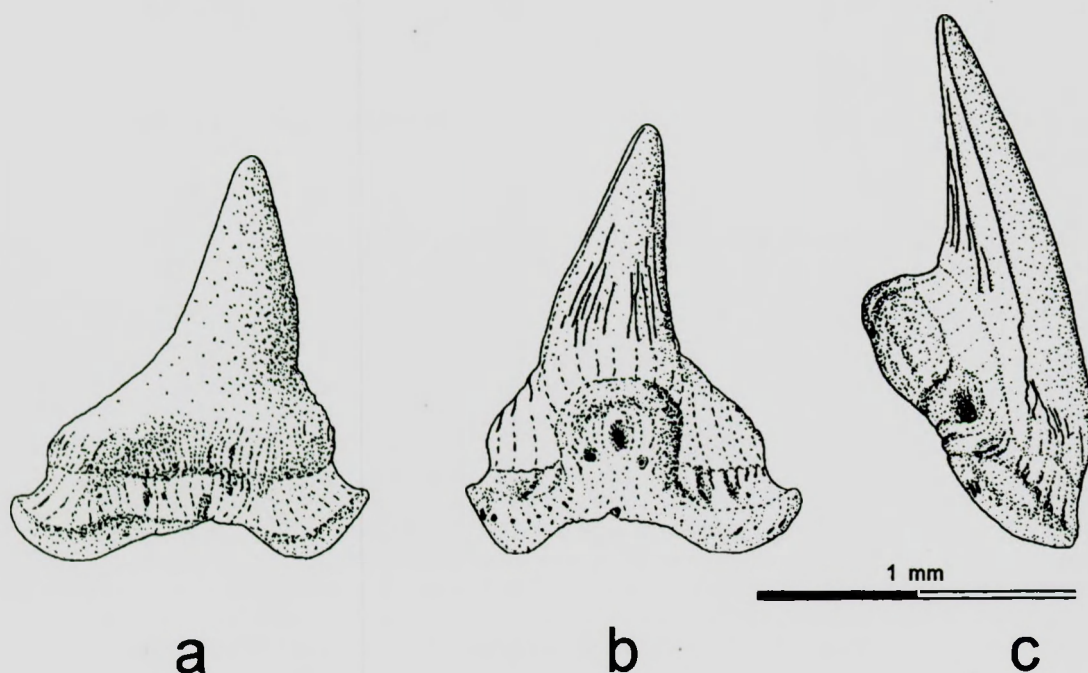
The figured antero-lateral tooth of ?*Scyliorhinus moosi* HERMAN (1975) has an elongated cusp and two pairs of low lateral cusplets. No other teeth have been figured, thus, although there are certain similarities, it is impossible to assign this species to *Scyliorhinus* sensu stricto.

The occurrence of *Scyliorhinus antiquus* (AGASSIZ, 1843) in the Turonian of France gives evidence that the genus *Scyliorhinus* sensu stricto is at least of a Late Cretaceous origin, and therefore much older than proposed by CANDONI (1993: 148), who argued that *Scyliorhinus fossilis* (synonym: *S. joleaudi* CAPPETTA (1970: 43-45; pl. 9, fig. 19-29)) from the Miocene is the first representative of *Scyliorhinus* sensu stricto.

With the description of the new species, *Scyliorhinus* sensu stricto is well documented throughout the Late Cretaceous (five species) and Tertiary (three species).

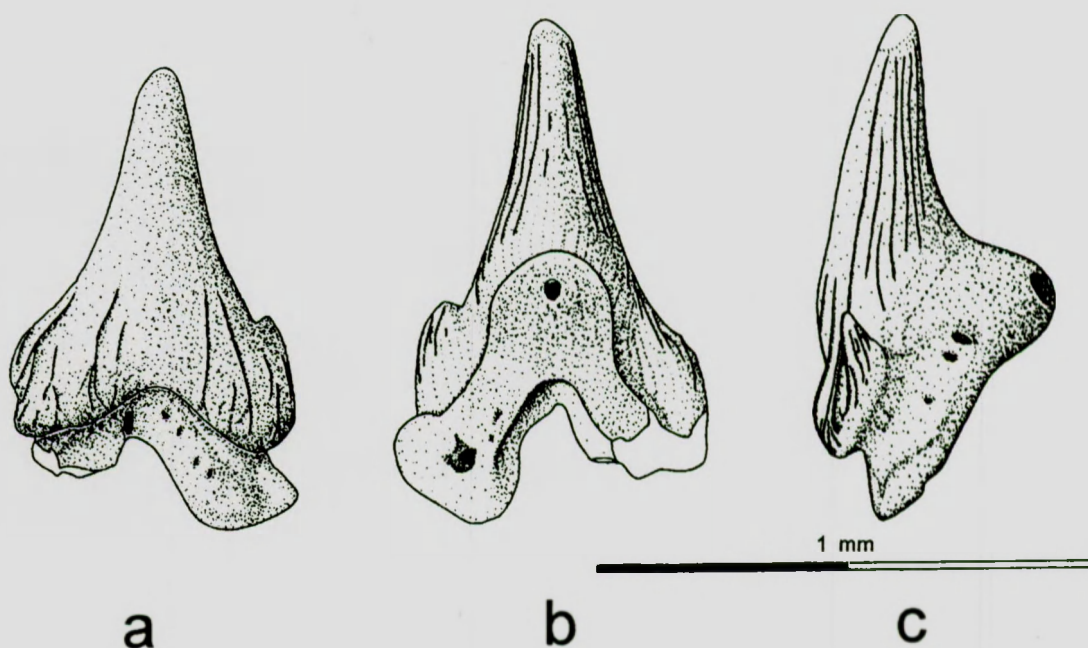
*Scyliorhinus biddlei* sp. nov.

Plate 1-5; Textfigure 8-10



**Textfigure 8.** *Scyliorhinus biddlei* sp. nov., Holotype (I.R.S.N.B. P 6335); a) labial view, b) lingual view, c) distal lateral view.





**Textfigure 9.** *Scyliorhinus biddlei* sp. nov., Paratype 5 (I.R.S.N.B. P 6340); a) labial view, b) lingual view, c) distal lateral view.

**Derivatio nominis:** named after Mr. Jean-Pierre Biddle (Bonnelles, France) in recognition of his scientific work on cretaceous elasmobranchs of France.

**Stratum typicum:** Quarry C.B.R. Romontbos (Eben-Emael, Belgium); crinoid-dominated fossil grit layer between flint stone layers 20 and 21 of the Lanaye Chalk Member (IIIg), Gulpden Formation, Late Maastrichtian (Textfigure 1, 3).

**Material:**

More than 60 teeth in the collections of the author and Mr. J.P.H. Reynders.

The Paratypes 2, 5, 6 and 7 of *Scyliorhinus biddlei* sp. nov. were collected by the author and his father R.P. Halter from 1986 to 1993. The material from the three horizons (Textfigure 3, 4, 5) was sieved down to 300  $\mu$ m. The teeth of the new species were found in the fractions of 400  $\mu$ m to 1000  $\mu$ m. The Holotype and Paratypes 1, 3 and 4 (Textfigure 3) have been provided by Mr. J.P.H. Reynders and were collected in 1989 and 1990.

**Type series:**

- Holotype: I.R.S.N.B. P 6335, Locality 1, Horizon 1.
- Paratype 1: I.R.S.N.B. P 6336, Locality 1, Horizon 1.
- Paratype 2: I.R.S.N.B. P 6337, Locality 1, Horizon 2.
- Paratype 3: I.R.S.N.B. P 6338, Locality 1, Horizon 1.
- Paratype 4: I.R.S.N.B. P 6339, Locality 1, Horizon 1.
- Paratype 5: I.R.S.N.B. P 6340, Locality 2.
- Paratype 6: I.R.S.N.B. P 6341, Locality 3, Horizon 1.
- Paratype 7: I.R.S.N.B. P 6342, Locality 3, Horizon 2.

Age: Late Cretaceous, Late Maastrichtian.

### Specific diagnosis:

*Scyliorhinus* with teeth up to 2.0 mm in height and 1.5 mm in width.

Anterior and antero-lateral teeth are taller than they are wide. Lateral and posterior teeth are approximately as tall as they are wide.

The principal cusp is elongated, slender, biconvex, bent lingually, upright or slightly bent towards the commissure in anterior and antero-lateral teeth, becoming progressively lower and more inclined in lateral and posterior teeth. Lateral cusplets, if present, are generally low and poorly developed. Anterior and antero-lateral teeth either have a pair of shoulders or, like lateral and posterior teeth, have a mesial shoulder and a distal lateral cusplet. Only a few lateral teeth show one pair of lateral cusplets.

The labial face of the crown is slightly convex. Its base has a strongly concave outline in anterior, antero-lateral and lateral teeth. A few weak striae may be present, generally limited to the very base of the crown. Only posterior and juvenile teeth show striae on the lower half of the labial face of the crown. A reticulated microornamentation may be present in posterior teeth. The very base of the labial face of the crown that overhangs the crown-root-junction may show several weak depressions in anterior to lateral teeth.

The lingual face of the principal cusp is strongly convex and can show up to ten striae, generally limited to its middle part. The striae can reach the apex of the principal cusp in posterior and juvenile teeth.

The lingual face of the lateral cusplets and shoulders shows a few weak and short striae. The striae on the shoulders turn towards the apex of the principal cusp forming a cutting edge, which is rugged to varying degrees.

The root is bilobate with a well developed protuberance and lobes that are relatively long and narrow. The vascularization is always secondary hemiaulacorhize with a median groove partially to completely closed. The central labial foramen is situated at the base of the labial face of the root. The lingual face of the root shows up to five pairs of margino-lingual foramina. The basal face of the root is slightly concave in anterior and antero-lateral to flat or slightly convex in lateral and posterior teeth. The basal face of the root shows several randomly scattered foramina. The labial face of the root shows up to five pairs of margino-labial foramina.

### Differential diagnosis:

The differential diagnosis is based on teeth from mature individuals. In each case the characters cited belong to the aforementioned species.

*S. antiquus* differs from *S. biddlei* sp. nov. by the following: larger size; anterior teeth show one pair of poorly developed lateral cusplets or one lateral cusplet and a shoulder; antero-lateral and lateral teeth have one pair of lateral cusplets; posterior teeth have one or two pairs of lateral cusplets; prominent basal striae are present on the labial face of the crown and numerous well developed striae on the lingual face of the crown, both reaching from the base to the apex of the principal cusp.

*S. canicula* differs from *S. biddlei* sp. nov. by the following: the root has a very large central basal foramen; the striae on the lingual face of the crown are more well developed; upper anterior teeth show prominent basal striae on the labial face of the crown.

*S. coupatezi* differs from *S. biddlei* sp. nov. by the following: larger size; antero-lateral and posterior teeth have two lateral cusplets and sometimes a third, tiny mesial or distal lateral cusplet; very prominent basal striae are present on the labial face of the crown in antero-lateral and lateral teeth.

*S. elongatus* differs from *S. biddlei* sp. nov. by the following: larger size; anterior teeth show two shoulders, one pair of lateral cusplets, or one lateral cusplet and a shoulder; antero-lateral to posterior teeth have one pair of lateral cusplets; prominent basal striae are present on the labial face of the crown and numerous well developed striae on the lingual face of the crown, both generally reaching from the base to the apex of the principal cusp.



*S. fossilis* differs from *S. biddlei* sp. nov. by the following: larger size; antero-lateral and posterior teeth have two pairs of lateral cusplets; prominent basal striae are present on the labial face of the crown in antero-lateral and lateral teeth.

*S. woodwardi* differs from *S. biddlei* sp. nov. by the following: anterior and antero-lateral teeth have two pairs of poorly developed lateral cusplets and prominent basal striae on the labial face of the crown. (Lateral and posterior teeth have never been figured.)

#### **Description:**

**Holotype:** I.R.S.N.B. P 6335; antero-lateral tooth (Plate 1)

Condition: Excellent.

Principal Cusp: Tall, lingually bent, slightly inclined towards the commissure; lingual face is strongly convex with 11 striae limited to the middle part of the cusp.

Crown: Mesial and distal shoulder; lingual face of mesial shoulder shows three short striae; distal shoulder shows two striae, limited to the crest of shoulder; distal shoulder is less steep but wider than mesial shoulder; labial face of the crown is convex, shows a few poorly developed striae at its base near the mesial and distal edges; very base of labial face slightly overhangs the crown-root-junction.

Root: Strongly bilobate with a prominent protuberance, vascularization is secondary hemiaulacorhize with partially closed median groove; labial face shows three margino-labial foramina; basal face is slightly concave with numerous small and randomly scattered foramina; lingual face shows four pairs of margino-lingual foramina.

**Paratype 1:** I.R.S.N.B. P 6336; anterior tooth (Plate 2, Fig. 1)

Condition: Very good; principal cusp shows little functional wear.

Principal Cusp: Tall, lingually bent, slightly inclined towards the commissure; lingual face is strongly convex without striae.

Crown: Almost symmetrical; mesial and distal shoulder; lingual face of mesial and distal shoulder shows four poorly developed striae each, limited to crest of shoulder; labial face of the crown is convex, shows a couple of short and poorly developed striae near the mesial edge; very base of labial face strongly overhangs the crown-root-junction and shows several weak depressions.

Root: Strongly bilobate with a prominent protuberance, vascularization is secondary hemiaulacorhize with partially closed median groove; labial face shows five margino-labial foramina; basal face is slightly concave with numerous small foramina; lingual face shows five pairs of margino-lingual foramina.

**Paratype 2:** I.R.S.N.B. P 6337; antero-lateral tooth (Plate 2, Fig. 2)

Condition: Good; root slightly corroded.

Principal Cusp: Elongated, lingually bent, slightly inclined towards the commissure; lingual face is strongly convex with a couple of poorly developed striae near its distal cutting edge.

Crown: Mesial and distal shoulder is steep with a couple of poorly developed striae; labial face is strongly convex; very base of labial face strongly overhangs the crown-root-junction and shows several weak depressions.

Root: Strongly bilobate; vascularization is secondary hemiaulacorhize.



**Paratype 3:** I.R.S.N.B. P 6338; lateral tooth (Plate 3, Fig. 1)

- Condition:** Poor; lacks the entire root; principal cusp and lateral cusplets show little functional wear.
- Principal Cusp:** Lower than in the teeth described above, slightly inclined towards the commissure; lingual face (not figured) is strongly convex.
- Crown:** Unlike the Holotype, Paratype 1 and 2, the crown has a pair of poorly developed lateral cusplets; labial face is slightly convex and shows four striae at its base near the mesial and distal edge; weak depressions at the very base of the labial face are less developed than in the teeth described above; base of the labial face has a strongly concave outline.

**Paratype 4:** I.R.S.N.B. P 6339; latero-posteral tooth (Plate 3, Fig. 2)

- Condition:** Good; root is slightly corroded; principal cusp shows functional wear.
- Principal Cusp:** Lower than in the teeth described above, slightly inclined towards the commissure; lingual face is strongly convex with a couple of striae near the mesial and distal cutting edge.
- Crown:** Distal lateral cusplet and a mesial shoulder; mesial shoulder has a rugged cutting edge with four striae on its lingual face; lingual face of distal lateral cusplet shows three striae; labial face is convex with a few short basal striae; very base of labial face strongly overhangs the crown-root junction and shows several weak depressions.
- Root:** Strongly bilobate with a median groove that was formerly completely closed; vascularization is secondary hemiaulacorhize; lingual face shows two pairs of margino-lingual foramina; basal face is flat; labial face has four margino-labial foramina.

**Paratype 5:** I.R.S.N.B. P 6340; juvenile antero-lateral tooth (Plate 4, Fig. 1)

- Condition:** Good; root slightly rolled; lower half of mesial root lobe is broken off; principal cusp shows little functional wear.
- Principal Cusp:** Elongated, slender, upright, slightly lingually bent, slightly inclined towards the commissure; lingual face is strongly convex and shows eight striae that reach up to the apex.
- Crown:** Mesial shoulder has five striae on its lingual face; poorly developed distal lateral cusplet shows four striae on its lingual side; labial face is convex and shows several striae on its lower half that reach up higher than in the teeth described above; very base of labial face strongly overhangs the crown-root junction.
- Root:** Strongly bilobate with relatively long and narrow lobes; vascularization is secondary hemiaulacorhize with a completely closed median groove; labial face shows nine margino-labial foramina; basal face is slightly concave; lingual face shows four pairs of margino-lingual foramina.

**Paratype 6:** I.R.S.N.B. P 6341; posterior tooth (Plate 4, Fig. 2)

- Condition:** Excellent; principal cusp shows functional wear.
- Principal Cusp:** Lower than in the teeth described above, strongly inclined towards the commissure; lingual face is strongly convex and shows eight striae that reach up to the apex.
- Crown:** Mesial shoulder has four striae; distal lateral cusplet has two striae; cutting edge of the shoulder and the principal cusp form an almost straight line; labial face is slightly convex, shows several short basal striae; very base of labial face slightly overhangs the crown-root junction.
- Root:** Slightly bilobate, prominent protuberance; vascularization is secondary hemiaulacorhize with a partially closed median groove; labial face shows ten margino-labial foramina; basal face is slightly convex and has a few small foramina; lingual face shows four mesial margino-lingual foramina and two distal margino-lingual foramina.

**Paratype 7:** I.R.S.N.B. P 6342; posterior tooth (Plate 5)

- Condition: Good; mesial shoulder shows little functional wear.
- Principal cusp: Low and not as strongly inclined as Paratype 6; lingual face is strongly convex without striae; lack of striae might be caused by a slight corrosion of the enamel.
- Crown: Mesial shoulder and poorly developed distal lateral cusplet; mesial shoulder has several striae; labial face is slightly convex and shows several striae at its base that merge and reach up half way to the apex; a reticulated microornamentation is present; very base of labial face slightly overhangs the crown-root-junction.
- Root: Strongly bilobate with long and relatively narrow lobes; vascularization is secondary hemiaulacorhize with a median groove completely closed; labial face shows five margino-labial foramina; basal face is slightly convex; lingual face has four margino-lingual foramina.

### **Heterodonty:**

The teeth of *Scyliorhinus biddlei* sp. nov. show a strong monognathic, weak dignathic and weak ontogenetic heterodonty.

#### **(1) Dignathic heterodonty:**

The very base of the labial face of the crown slightly overhangs the crown-root-junction in one tooth series and strongly overhangs the crown-root-junction in the other tooth series. Possibly, the presence or lack of a reticulated microornamentation on the base of the labial face of the crown is another characteristic of the dignathic heterodonty. It is impossible, in comparison with living representatives of *Scyliorhinus* sensu stricto, to determine which of the two different tooth series belongs to the upper and which to the lower jaw.

#### **(2) Monognathic heterodonty:**

(a) Successive decrease in height combined with an increase in width from anterior to posterior teeth.

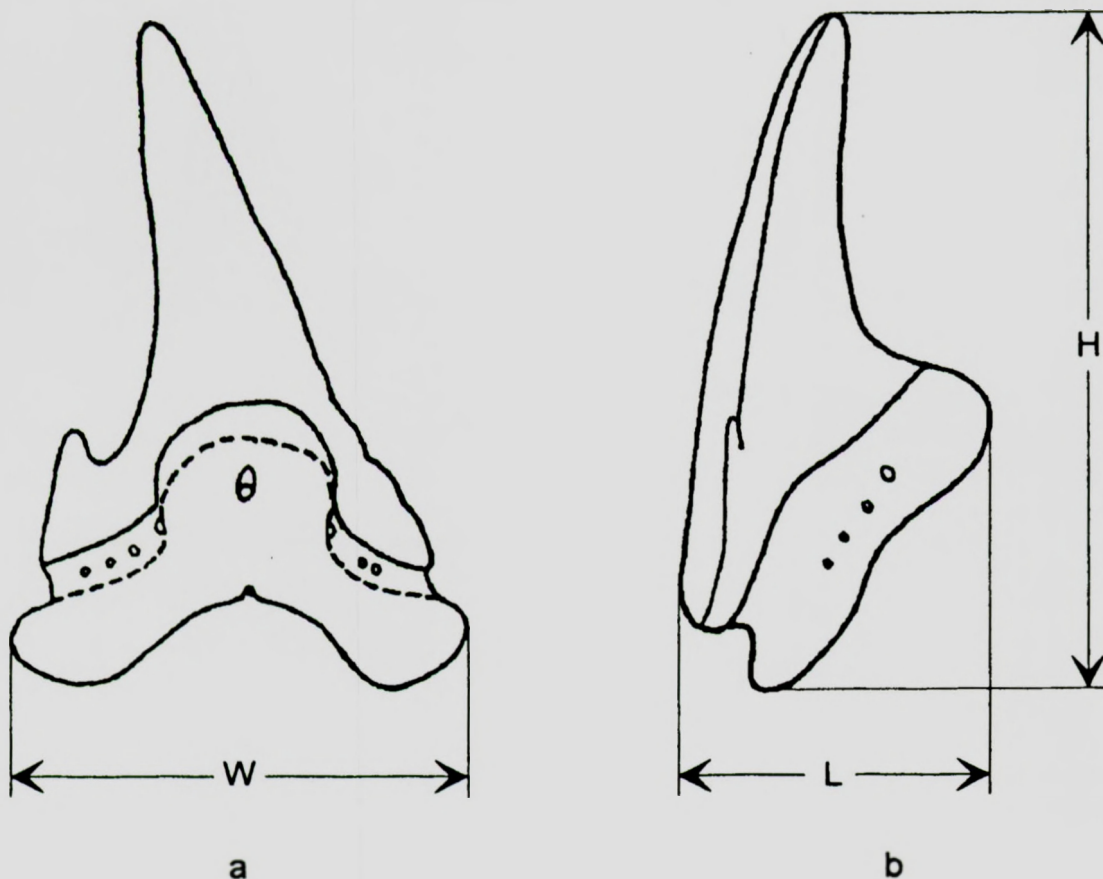
(b) Anterior and antero-lateral teeth have a mesial and distal shoulder; lateral, posterior and a few antero-lateral teeth show a mesial shoulder and a distal lateral cusplet; a few lateral teeth have one pair of lateral cusplets.

(c) Posterior teeth show a reticulated microornamentation at the base of the labial face of the crown.

(d) Basal face of the root is slightly concave in anterior and antero-lateral to flat or slightly convex in lateral and posterior teeth.

#### **(3) Ontogenetic heterodonty:**

A decrease in number and length of basal striae on the labial face of the crown in anterior to lateral teeth with age. Furthermore, a decrease in number and length and possible loss of striae on the lingual face of the crown in anterior to antero-lateral teeth with age.



**Textfigure 10.** *Scyliorhinus biddlei* sp. nov., dimensions given; a) lingual view, b) labial view.

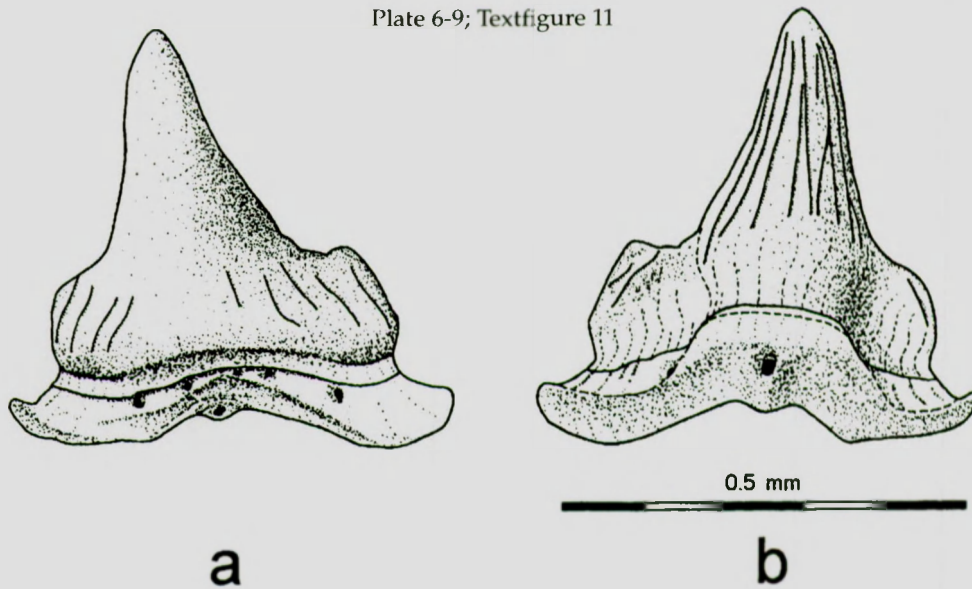
**Dimensions (in mm):**

		Height	Width	Length
Holotype:	I.R.S.N.B. P 6335	1.5	1.1	0.7
Paratype 1:	I.R.S.N.B. P 6336	1.8	1.2	0.9
Paratype 2:	I.R.S.N.B. P 6337	1.8	1.2	-
Paratype 3:	I.R.S.N.B. P 6338	1.3	1.1	-
Paratype 4:	I.R.S.N.B. P 6339	1.1	1.0	0.7
Paratype 5:	I.R.S.N.B. P 6340	1.0	0.6	0.5
Paratype 6:	I.R.S.N.B. P 6341	0.8	0.9	0.5
Paratype 7:	I.R.S.N.B. P 6342	0.8	0.9	0.4



*Scyliorhinus reyndersi* sp. nov.

Plate 6-9; Textfigure 11



**Textfigure 11.** *Scyliorhinus reyndersi* sp. nov., Holotype (I.R.S.N.B. P 6343); a) labial view, b) lingual view.

**Derivatio nominis:** named after Mr. Jozef P.H. Reynders (Houthalen, Belgium) who generously provided the presented specimen.

**Stratum typicum:** Quarry C.P.L. (Halembaye, Belgium); fossil grit lens in a poriferan-dominated interval in the Zeven Wegen Chalk Member (IIIa), 14.5 m below the Froidmont Horizon, Gulpen Formation, Late Campanian (Textfigure 1, 6).

**Material:**

More than 50 teeth in the collection of Mr. J.P.H. Reynders.

The teeth of *Scyliorhinus reyndersi* sp. nov. described in this publication were collected in 1990. The material of the lenses (Textfigure 6) was sieved down to 300  $\mu$ m.

**Type series:**

- Holotype: I.R.S.N.B. P 6343, Locality 4, Level 2.  
Paratype 1: I.R.S.N.B. P 6344, Locality 4, Level 2.  
Paratype 2: I.R.S.N.B. P 6345, Locality 4, Level 2.  
Paratype 3: I.R.S.N.B. P 6346, Locality 4, Level 1.  
Paratype 4: I.R.S.N.B. P 6347, Locality 4, Level 2.  
Paratype 5: I.R.S.N.B. P 6348, Locality 4, Level 2.  
Paratype 6: I.R.S.N.B. P 6349, Locality 4, Level 2.

Age: Late Cretaceous, Late Campanian.

#### Specific diagnosis:

*Scyliorhinus* with teeth up to 0.8 mm in height and 0.8 mm in width. Symphysial, anterior and antero-lateral teeth are taller than they are wide. Lateral and posterior teeth are approximately as tall as they are wide.

The principal cusp is slender, upright or slightly bent towards the commissure. The teeth become progressively lower and wider towards the commissure. The crown is suberect in lateral and latero-posteral teeth.

Anterior teeth have a mesial and distal shoulder; antero-lateral teeth have a distal shoulder and a mesial lateral cusplet; lateral teeth have either one pair of lateral cusplets or two mesial and one distal lateral cusplet; posterior teeth have two pairs of lateral cusplets. A third distal lateral cusplet may be present in posterior teeth.

The labial face of the crown is slightly convex in anterior and antero-lateral teeth and flat or concave in lateral and posterior teeth. The ornamentation on the base of the labial face of the crown ranges from a few poorly developed striae to massive folds. In posterior teeth these striae reach up higher but do not fully reach the apex. Juvenile anterior and antero-lateral teeth show striae that reach from the base to the apex of the principal cusp. The very base of the labial face of the crown overhangs the crown-root-junction to varying degrees. The lingual face of the principal cusp is strongly convex and shows up to eight striae, reaching from the base to the apex. The lingual face of lateral cusplets and shoulders generally shows a few striae.

The root is slightly to strongly bilobate with a prominent protuberance and massive lobes. The vascularization is always secondary hemiaulacorhize with a median groove completely closed. The median groove is generally limited to the protuberance in anterior to lateral teeth; thus there is no central labial foramen, but a second main foramen on the labial face of the root. Posterior teeth have a longer median groove with the second main foramen near the labial-basal-junction. The basal face of the root is slightly concave in anterior and antero-lateral teeth and flat or slightly convex in lateral and posterior teeth. The lingual face of the root presents up to five pairs of marginolingual foramina. The basal face of the root shows several randomly scattered foramina. The labial face of the root shows up to five pairs of marginolabial foramina.

#### Differential diagnosis:

The differential diagnosis is based on teeth of mature individuals. In each case the characters cited belong to the aforementioned species.

*S. antiquus* differs from *S. reyniersi* sp. nov. by the following: larger size; anterior teeth have one pair of poorly developed lateral cusplets or one lateral cusplet and a shoulder; antero-lateral and lateral teeth show one pair of lateral cusplets; prominent basal striae are present on the labial face of the crown, reaching from the base to the apex of the principal cusp; root has a central labial foramen.

*S. biddlei* sp. nov. differs from *S. reyniersi* sp. nov. by the following: larger size; lateral and posterior teeth have one pair of lateral cusplets; a smaller number of weak striae limited to the middle portion of the lingual face of the crown; labial face of the crown shows weak basal striae; posterior teeth have a reticulated microornamentation at the base of the labial face of the crown; root is strongly bilobate with relatively long and narrow lobes in anterior and antero-lateral teeth; root shows a very large central basal foramen and central labial foramen.

*S. canicula* differs from *S. reyniersi* sp. nov. by the following: larger size; lateral to posterior teeth with one pair of lateral cusplets; posterior teeth show a reticulated microornamentation; root is strongly bilobate with relatively long and narrow lobes in anterior and antero-lateral teeth; root with a very large central basal foramen and a labial foramen.

*S. coupatezi* differs from *S. reyniersi* sp. nov. by the following: larger size; antero-lateral and lateral teeth have two pairs of lateral cusplets and sometimes a third, tiny mesial or distal lateral cusplet; numerous basal striae are present on the labial face of the crown in antero-lateral and lateral teeth; root is strongly bilobate with relatively long and narrow lobes in anterior teeth.

*S. elongatus* differs from *S. reyndersi* sp. nov. by the following: larger size; anterior teeth show two shoulders, one pair of lateral cusplets or one lateral cusplet and a shoulder; base of labial face of the crown has a strongly concave outline; very prominent basal striae are present on the labial face of the crown, reaching from the base to the apex of the principal cusp; root has a labial foramen.

*S. fossilis* differs from *S. reyndersi* sp. nov. by the following: larger size; anterior and antero-lateral teeth have a more elongated principal cusp; base of the labial face of the crown has a strongly concave outline in anterior and antero-lateral teeth; root has a labial foramen.

#### **Description:**

**Holotype:** I.R.S.N.B. P 6343; antero-lateral tooth (Plate 6, Fig. 1)

Condition: Excellent.

Principal Cusp: Elongated, biconvex, slightly inclined towards the commissure; lingual face is strongly convex and shows eight striae, reaching from the base to the apex.

Crown: Mesial lateral cusplet and distal shoulder; lingual face of the shoulder and lateral cusplet show a couple striae; labial face is slightly convex with eight basal striae; very base of labial face slightly overhangs the crown-root-junction.

Root: Slightly bilobate with massive protuberance and lobes; vascularization is secondary hemiaulacorhize with a completely closed median groove, limited to the protuberance; second main foramen is situated in the center of the basal face which is slightly concave; labial face shows five margino-labial foramina; lingual face has two pairs of margino-lingual foramina.

**Paratype 1:** I.R.S.N.B. P 6344; anterior tooth (Plate 6, Fig. 2)

Condition: Excellent; principal cusp shows little functional wear.

Principal Cusp: Slender, elongated, biconvex, upright; lingual face of the principal cusp is strongly convex and shows eight striae, reaching from the base to the apex.

Crown: Mesial and distal shoulder, without striae on the lingual face; labial face is slightly convex with a few poorly developed basal striae; very base of labial face slightly overhangs the crown-rootjunction.

Root: Slightly bilobate with massive protuberance and lobes; vascularization is secondary hemiaulacorhize with a completely closed median groove, limited to the protuberance; second main foramen is situated in the center of the basal face which is slightly concave; labial face has seven margino-labial foramina; lingual face shows two pairs of margino-lingual foramina.

**Paratype 2:** I.R.S.N.B. P 6345; latero-posterior tooth (Plate 7, Fig. 1)

Condition: Good; principal cusp and lateral cusplets show little functional wear; basal face of the root is corroded.

Principal Cusp: Suberect, slightly bent towards the commissure; lingual face is strongly convex and shows five striae, reaching from the base to the apex.



- Crown:** One distal and two mesial lateral cusplet are present; labial face of the crown is strongly concave with a few prominent basal striae; very base of labial face strongly overhangs the crown-rootjunction.
- Root:** Bilobate with massive protuberance and lobes; vascularization is secondary hemiaulacorhize; basal face is flat; labial face shows four margino-labial foramina; lingual face shows four mesial and two distal margino-lingual foramina.

**Paratype 3:** I.R.S.N.B. P 6346; juvenile antero-lateral tooth (Plate 7, Fig. 2)

- Condition:** Excellent; principal cusp shows little functional wear.
- Principal Cusp:** Broad, biconvex, upright; lingual face is strongly convex and shows eight striae, reaching from the base to the apex.
- Crown:** Mesial lateral cusplet and distal shoulder lacking striae; labial face is slightly convex with seven well-developed striae, reaching from the base to the apex; very base of labial face strongly overhangs the crown-root-junction.
- Root:** Slightly bilobate with massive protuberance and lobes; vascularization is secondary hemiaulacorhize with a completely closed median groove, limited to the protuberance; second main foramen is situated in the center of the basal face which is slightly concave; labial face shows five margino-labial foramina; lingual face shows two pairs of margino-lingual foramina.

**Paratype 4:** I.R.S.N.B. P 6347; lateral tooth (Plate 8, Fig. 1)

- Condition:** Very good; principal cusp and mesial cusplet show little functional wear.
- Principal Cusp:** Suberect, broad at its base and slightly bent towards the commissure; lingual face of the principal cusp is strongly convex and shows seven striae.
- Crown:** One pair of lateral cusplets; labial face is flat to slightly concave with a few weak basal striae; very base of labial face strongly overhangs the crown-root-junction.
- Root:** Bilobate with massive protuberance and lobes; vascularization is secondary hemiaulacorhize with a completely closed median groove, limited to the protuberance; second main foramen is situated in the center of the basal face which is flat; labial face shows five margino-labial foramina; lingual face has six margino-lingual foramina.

**Paratype 5:** I.R.S.N.B. P 6348; latero-posteral tooth (Plate 8, Fig. 2)

- Condition:** Good; principal cusp and lateral cusplets show little functional wear; basal face of the root is partly corroded.
- Principal Cusp:** Suberect, slightly bent towards the commissure; lingual face of the principal cusp is strongly convex and shows seven striae, reaching from the base to the apex.
- Crown:** Two pairs of lateral cusplets present, but the outer one is poorly developed; a couple of striae are present on the lingual face of the lateral cusplets; labial face is strongly concave with several prominent basal striae; very base of labial face slightly overhangs the crown-rootjunction.
- Root:** Slightly bilobate with massive protuberance and lobes; vascularization is secondary hemiaulacorhize with a completely closed median groove, limited to the protuberance; second main foramen is situated near the labial-basal-junction of the basal face which is flat; labial face shows four margino-labial foramina; lingual face has three pairs of margino-lingual foramina.

**Paratype 6:** I.R.S.N.B. P 6349; commissural tooth (Plate 9, Fig. 1)

- Condition: Very good; principal cusp shows little functional wear.
- Principal Cusp: Broad at its base, slightly bent towards the commissure; lingual face of the principal cusp is strongly convex and shows five striae, reaching from the base to the apex.
- Crown: Two mesial and three distal lateral cusplets are present; however, the third outer lateral cusplet is poorly developed; labial face of the crown is flat to slightly concave with striae reaching up to the lateral cusplets and half way up to the apex; very base of labial face slightly overhangs the crown-rootjunction.
- Root: Slightly bilobate with massive protuberance and lobes; vascularization is secondary hemiaulacorhize with a completely closed median groove, limited to the protuberance; second main foramen is situated near the labial-basal-junction of the basal face which is slightly convex; labial face shows five margino-labial foramina; lingual face shows four mesial and three distal margino-lingual foramina.

**Heterodonty:**

The teeth of *S. reyndersi* sp. nov. show a strong monognathic and weak ontogenetic heterodonty. A dignathic heterodonty cannot be observed.

(1) Monognathic heterodonty:

(a) A successive decrease in height combined with an increase in width from anterior to posterior and commissural teeth.

(b) Anterior teeth have a mesial and distal shoulder; antero-lateral teeth show a mesial shoulder and a distal lateral cusplet; lateral teeth have either one pair of lateral cusplets or two mesial and one distal lateral cusplet; posterior and commissural teeth show two pairs of lateral cusplets.

(c) The root is slightly bilobate with a slightly concave basal face in anterior to antero-lateral teeth and bilobate to strongly bilobate with a flat or slightly convex basal face in lateral to posterior teeth.

(2) Ontogenetic heterodonty:

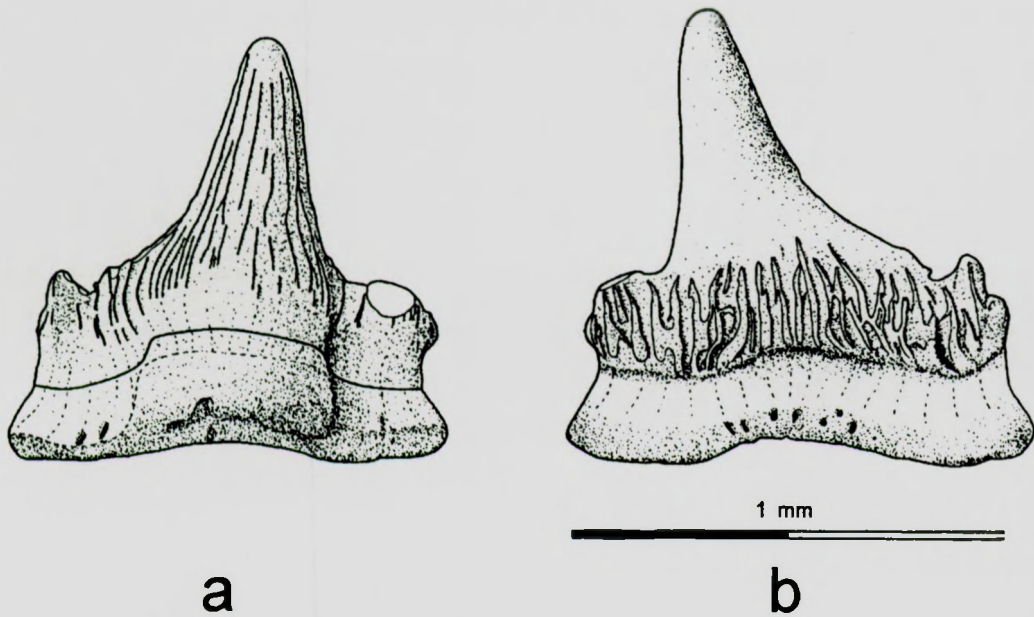
A decrease in length of striae on the labial face of the crown in anterior to lateral teeth with age.

**Dimensions (in mm):**

		Height	Width
Holotype:	I.R.S.N.B. P 6343	0.7	0.6
Paratype 1:	I.R.S.N.B. P 6344	0.7	0.6
Paratype 2:	I.R.S.N.B. P 6345	0.5	0.7
Paratype 3:	I.R.S.N.B. P 6346	0.4	0.4
Paratype 4:	I.R.S.N.B. P 6347	0.7	0.8
Paratype 5:	I.R.S.N.B. P 6348	0.5	0.8
Paratype 6:	I.R.S.N.B. P 6349	0.4	0.8

*Scyliorhinus luypaertsii* sp. nov.

Plate 9-12; Textfigure 12



**Textfigure 12.** *Scyliorhinus luypaertsii* sp. nov., Holotype (I.R.S.N.B. P 6350); a) labial view, b) lingual view, c) mesial lateral view.

**Derivatio nominis:** named after Mr. Jean-Pierre Luypaerts (Wezembeek-Oppem, Belgium). Meeting Jean-Pierre in the summer of 1985 started a decade of systematic collecting of fossil elasmobranchs together with many good friends in Belgium, France, England and The Netherlands.

**Stratum typicum:** Quarry E.N.C.I. (Maastricht, The Netherlands); crinoid-dominated fossil grit layer at the base of the Valkenburg Chalk Member (IVa), Lichtenberg Horizon, Maastricht Formation, Late Maastrichtian (Textfigure 1, 4).

**Material:**

More than 80 teeth in the collection of the author.

The teeth of *Scyliorhinus luypaertsii* sp. nov. described in this publication were collected by the author and his father R.P. Halter in 1988 and 1989. The material from the horizon (Textfigure 4) was sieved down to 300  $\mu$ m. The teeth of the new species were found in fractions between 300  $\mu$ m to 1000  $\mu$ m.

**Type series:**

- Holotype: I.R.S.N.B. P 6350, Locality 2.
- Paratype 1: I.R.S.N.B. P 6351, Locality 2.
- Paratype 2: I.R.S.N.B. P 6352, Locality 2.
- Paratype 3: I.R.S.N.B. P 6353, Locality 2.
- Paratype 4: I.R.S.N.B. P 6354, Locality 2.
- Paratype 5: I.R.S.N.B. P 6355, Locality 2.
- Paratype 6: I.R.S.N.B. P 6356, Locality 2.

Age: Late Cretaceous, Late Maastrichtian.



### Specific diagnosis:

*Scyliorhinus* with teeth up to 2.0 mm in height and 1.5 mm in width. Anterior and antero-lateral teeth are taller than they are wide, becoming progressively lower and wider towards the commissure.

The principal cusp is slender, biconvex, upright or slightly bent towards the commissure. It is suberect in lateral teeth.

Lateral cusplets, if present, are generally low and poorly developed. Anterior and antero-lateral teeth have either shoulders or a pair of lateral cusplets. Lateral teeth have either a mesial shoulder and one distal lateral cusplet or one pair of lateral cusplets. Posterior teeth have a mesial shoulder and a distal lateral cusplet. A few lateral teeth show a second pair of small lateral cusplets.

The labial face of the crown is slightly convex. Its base either shows numerous prominent folds or is incised by several grooves. In posterior teeth these folds reach half way up to the apex of the principal cusp. The folds have a rugged surface in lateral to posterior teeth.

The lingual face of the principal cusp, shoulder and lateral cusplets can show numerous well-developed striae. The striae on the principal cusp reach from the base to the apex.

The root is strongly bilobate with a well developed protuberance. The root vascularization is always secondary hemiaulacorhize with a median groove partially to completely closed. The lingual face of the root has up to three pairs of margino-lingual foramina. The basal face of the root shows several randomly scattered foramina. The labial face of the root has up to seven margino-labial foramina situated near the labial-basal-junction.

### Differential diagnosis:

The differential diagnosis is based on teeth of mature individuals. In each case the characters cited belong to the aforementioned species.

*S. antiquus* differs from *S. luypaertsi* sp. nov. by the following: larger size; anterior teeth have one pair of lateral cusplets or one lateral cusplet and a shoulder; prominent striae are present on the labial face of the crown, reaching from the base to the apex of the principal cusp.

*S. biddlei* sp. nov. differs from *S. luypaertsi* sp. nov. by the following: antero-lateral teeth have a mesial and distal shoulder; weak striae are present on the lingual face of the crown; labial face of the crown shows weak basal striae; posterior teeth have a reticulated microornamentation at the base of the labial face of the crown.

*S. canicula* differs from *S. luypaertsi* sp. nov. by the following: upper anterior teeth show less prominent basal striae; posterior teeth have a reticulated microornamentation at the base of the labial face of the crown; the root has a very large central basal foramen.

*S. coupatezi* differs from *S. luypaertsi* sp. nov. by the following: larger size; antero-lateral teeth have two pairs of lateral cusplets and sometimes a third, tiny mesial or distal lateral cusplet; very prominent basal striae are present on the labial face of the crown in antero-lateral and lateral teeth.

*S. elongatus* differs from *S. luypaertsi* sp. nov. by the following: larger size; lateral teeth have one or two pairs of lateral cusplets; base of labial face of the crown has a strongly concave outline in anterior teeth; prominent striae are present on the labial face of the crown, reaching from the base to the apex of the principal cusp.

*S. fossilis* differs from *S. luypaertsi* sp. nov. by the following: larger size; antero-lateral and posterior teeth have two pairs of lateral cusplets; base of the labial face of the crown has a strongly concave outline in anterior and antero-lateral teeth.

*S. reyndersi* sp. nov. differs from *S. luypaertsi* sp. nov. by the following: smaller size; latero-posterior and posterior teeth with one or two pairs of lateral cusplets; root with a median groove limited to the protuberance.

#### **Description:**

**Holotype:** I.R.S.N.B. P 6350, lateral tooth (Plate 9, Fig. 2)

**Condition:** Good; distal lateral cusplet shows little functional wear; basal face of the root is slightly corroded.  
**Principal Cusp:** Suberect, slender, biconvex, slightly bent towards the commissure; lingual face is strongly convex and shows numerous prominent striae, reaching from the base to the apex.  
**Crown:** One pair of lateral cusplets; mesial lateral cusplet is poorly developed; labial face is slightly convex, shows numerous prominent basal folds which have a rugged surface; very base of labial face strongly overhangs the crown-root-junction.  
**Root:** Bilobate; vascularization is secondary hemiaulacorrhize with a completely closed median groove; lingual face has three pairs of margino-lingual foramina; labial face shows six margino-labial foramina situated near the labial-basal-junction.

**Paratype 1:** I.R.S.N.B. P 6351, anterior tooth (Plate 10, Fig. 1)

**Condition:** Poor; entire root and mesial base of the crown are missing; principal cusp and the lateral cusplet show little functional wear.  
**Principal Cusp:** Tall, slender, biconvex, slightly bent towards the commissure; lingual face is strongly convex and shows two poorly developed striae close to the mesial and distal cutting edge.  
**Crown:** One poorly developed distal lateral cusplet; labial face is slightly convex with eight prominent basal folds.

**Paratype 2:** I.R.S.N.B. P 6352, anterior tooth (Plate 10, Fig. 2)

**Condition:** Poor; lacking the entire root.  
**Principal Cusp:** Elongated, slender, biconvex, upright; lingual face is strongly convex and shows 12 prominent striae, reaching from the base to the apex of the principal cusp.  
**Crown:** Almost symmetrical; steep mesial and distal shoulder; labial face is slightly convex, its base is incised by several small grooves.

**Paratype 3:** I.R.S.N.B. P 6353, antero-lateral tooth (Plate 10, Fig. 3)

- Condition: Poor; lacking the entire root.  
Principal Cusp: Tall, slender, biconvex, slightly bent towards the commissure; lingual face is strongly convex and shows numerous well-developed striae, reaching from the base to the apex.  
Crown: Almost symmetrical; one pair of poorly developed lateral cusplets; labial face is slightly convex, its base is incised by several prominent grooves.

**Paratype 4:** I.R.S.N.B. P 6354, lateral tooth (Plate 11, Fig. 1)

- Condition: Poor; principal cusp and the two mesial lateral cusplets completely worn off; basal face of the root corroded.  
Crown: Two pairs of lateral cusplets; labial face shows numerous prominent basal folds which have a rugged surface; very base of the labial face slightly overhangs the crown-root junction.  
Root: Bilobate; vascularization is secondary hemiaulacorhize with a partially closed median groove; lingual face shows three pairs of margino-lingual foramina; labial face shows seven margino-labial foramina situated near the labial-basal-junction.

**Paratype 5:** I.R.S.N.B. P 6355, lateral tooth (Plate 11, Fig. 2)

- Condition: Poor; lacking the entire root.  
Principal Cusp: Slender, biconvex, slightly bent towards the commissure; lingual face is strongly convex and shows numerous striae, reaching from the base to the apex.  
Crown: Broad mesial shoulder and a poorly developed distal lateral cusplet; labial face of the crown is slightly convex, its base is incised by several small grooves.

**Paratype 6:** I.R.S.N.B. P 6356, posterior tooth (Plate 12)

- Condition: Very good; principal cusp and distal lateral cusplet show little functional wear.  
Principal Cusp: Biconvex, slightly bent towards the commissure; lingual face is strongly convex and shows numerous prominent striae, reaching from the base to the apex.  
Crown: One distal lateral cusplet and a mesial shoulder with a tiny lateral cusplet at its end; reticulated ornamentation at the very base of the lingual face; labial face is slightly convex, shows numerous prominent folds which have a rugged surface and reach half way up to the apex; very base of labial face strongly overhangs the crown-root junction.  
Root: Bilobate; vascularization is secondary hemiaulacorhize with a completely closed median groove; lobes are relatively long and narrow; lingual face shows three pairs of margino-lingual foramina; labial face shows two margino-labial foramina.



**Heterodonty:**

The teeth of *Scyliorhinus luypaertsii* sp. nov. have a strong monognathic and dignathic heterodonty and a weak ontogenetic heterodonty.

**(1) Dignathic heterodonty:**

The base of the labial face of the crown has numerous prominent folds in one tooth series and is incised by a varying number of grooves in the other tooth series. It is impossible, in comparison with living representatives of *Scyliorhinus sensu stricto*, to determine which of the two different tooth series belongs to the upper and which to the lower jaw.

**(2) Monognathic heterodonty:**

- (a) Successive decrease in height combined with an increase in width from anterior to posterior teeth.
- (b) Anterior teeth having a mesial and distal shoulder or a pair of lateral cusplets; antero-lateral and lateral teeth show one pair of lateral cusplets; a few lateral teeth have a second pair of poorly developed lateral cusplets; posterior teeth have a mesial shoulder and a distal lateral cusplet.

**(3) Ontogenetic heterodonty:**

A decrease in number and length and a loss of striae on the lingual face of the crown with age.

**Dimensions (in mm):**

		Height	Width	Length
Holotype:	I.R.S.N.B. P 6350	1.5	1.1	0.7
Paratype 1:	I.R.S.N.B. P 6351	-	-	-
Paratype 2:	I.R.S.N.B. P 6352	-	-	-
Paratype 3:	I.R.S.N.B. P 6353	-	-	-
Paratype 4:	I.R.S.N.B. P 6354	-	1.0	0.7
Paratype 5:	I.R.S.N.B. P 6355	-	-	-
Paratype 6:	I.R.S.N.B. P 6356	0.9	0.9	0.6

**CONCLUSIONS**

The genus *Scyliorhinus sensu stricto* can odontologically be separated from the other genera of the family Scyliorhinidae by a unique type of anterior and sometimes antero-lateral teeth which have a pair of shoulders or a shoulder and a lateral cusplet. Therefore, along with the newly described species *Scyliorhinus biddlei* sp. nov., *Scyliorhinus reyndersi* sp. nov. and *Scyliorhinus luypaertsii* sp. nov., the formerly described species *Scyliorhinus antiquus* (AGASSIZ, 1843), *Scyliorhinus elongatus* (DAVIS, 1887), *Scyliorhinus woodwardi* CAPPETTA (1976), *Scyliorhinus fossilis* (LERICHE, 1927) and *Scyliorhinus coupatezi* HERMAN (1974) can be reassigned to the genus *Scyliorhinus sensu stricto*. This shows that the genus *Scyliorhinus sensu stricto* is at least of a Late Cretaceous (Turonian) origin, and therefore much older than proposed by CANDONI (1993: 148), who argued that *Scyliorhinus fossilis* (synonym: *S. joleaudi* CAPPETTA (1970: 43-45; pl. 9, fig. 19-29)) from the Miocene is the first representative of *Scyliorhinus sensu stricto*. The genus *Scyliorhinus sensu stricto* is well documented throughout the Late Cretaceous (five species) and Tertiary (three species).

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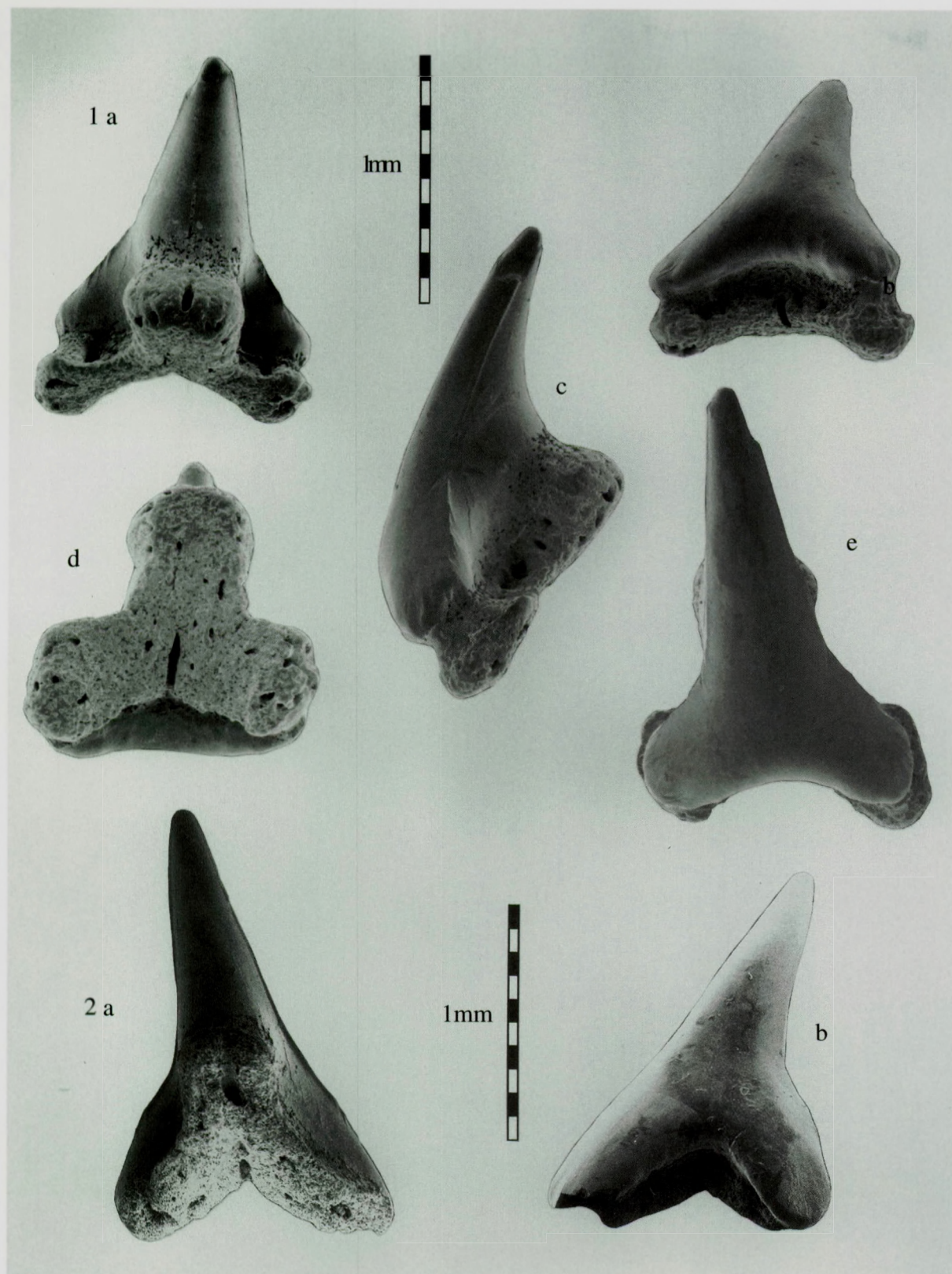
# Plates

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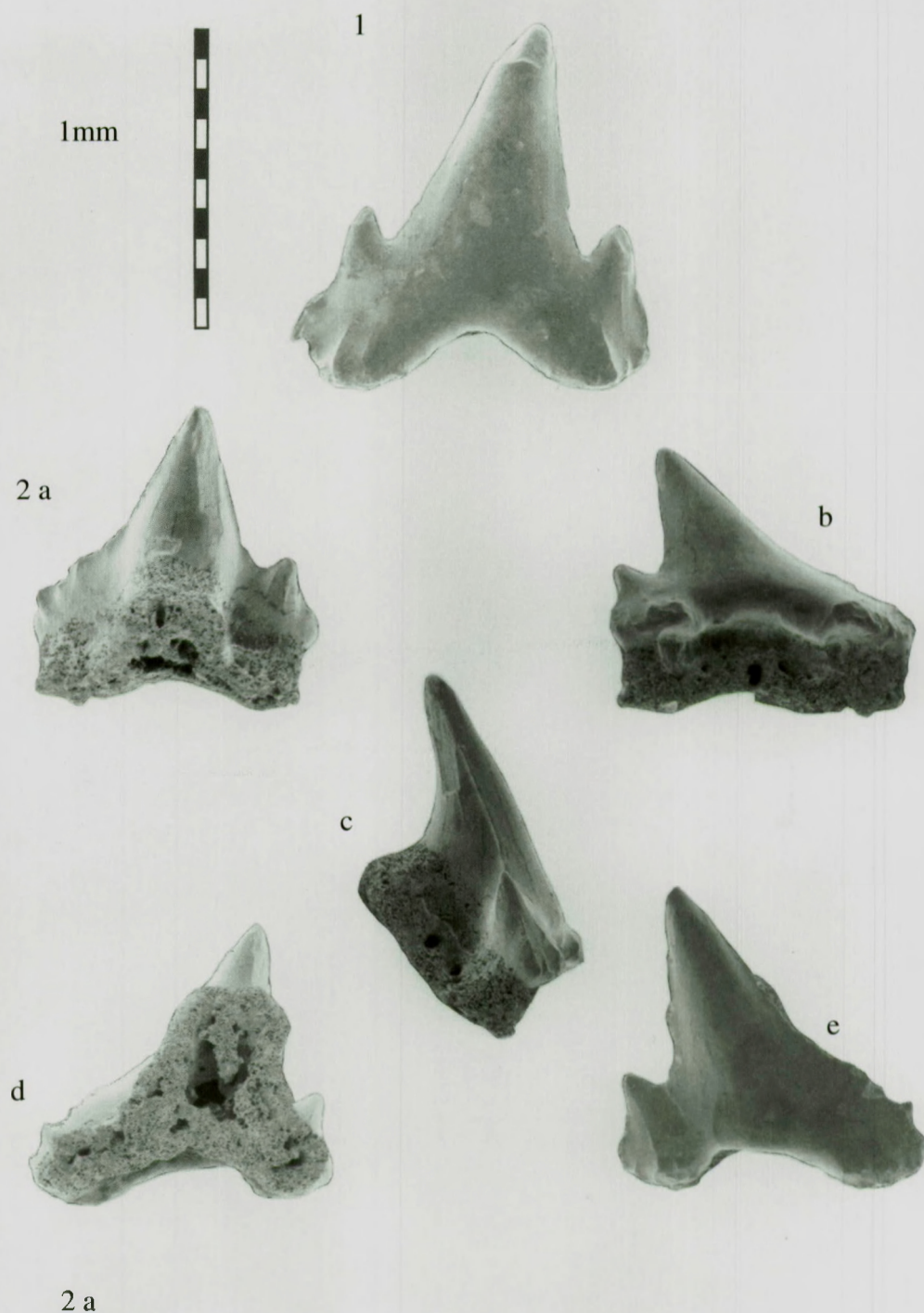


**Plate 1.** *Scyliorhinus biddlei* sp. nov.: 1. Holotype: I.R.S.N.B. P. 6335 (Locality 1, Horizon 1). **a:** lingual view, **b:** labial view, **c:** distal lateral view, **d:** basal view, **e:** occlusal view.





**Plate 2.** *Scyliorhinus biddlei* sp. nov.: 1. Paratype 1: I.R.S.N.B. P. 6336 (Locality 1, Horizon 1): a: lingual view, b: labial view, c: mesial lateral view, d: basal view, e: occlusal view. 2. Paratype 2: I.R.S.N.B. P. 6337 (Locality 1, Horizon 2): a: lingual view, b: labial view.



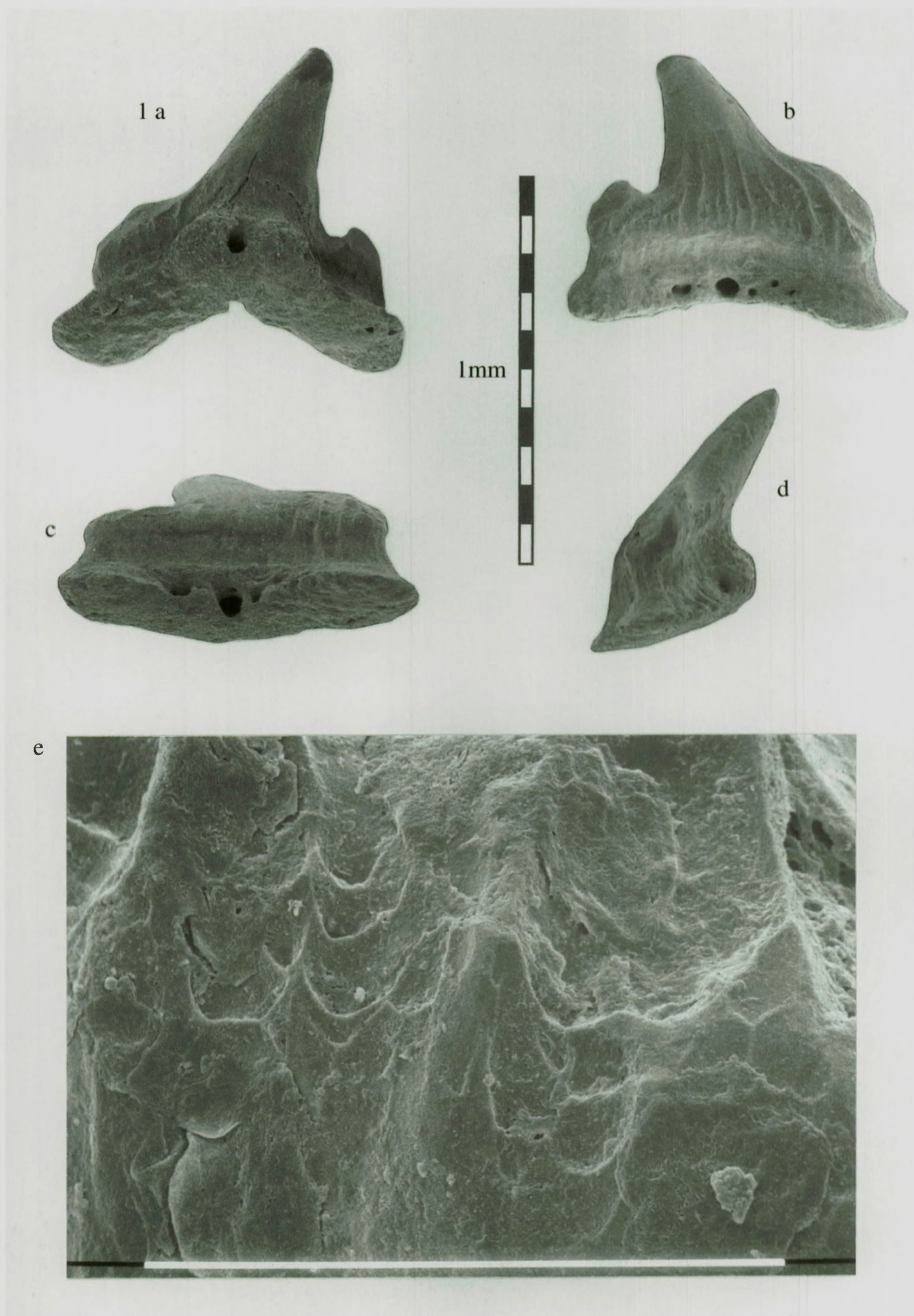
**Plate 3.** *Scyliorhinus biddlei* sp. nov.: 1. Paratype 3: I.R.S.N.B. P. 6338 (Locality 1, Horizon 1): labial view.  
2. Paratype 4: I.R.S.N.B. P. 6339 (Locality 1, Horizon 1): a: lingual view, b: labial view, c: distal lateral view, d: basal view, e: occlusal view.



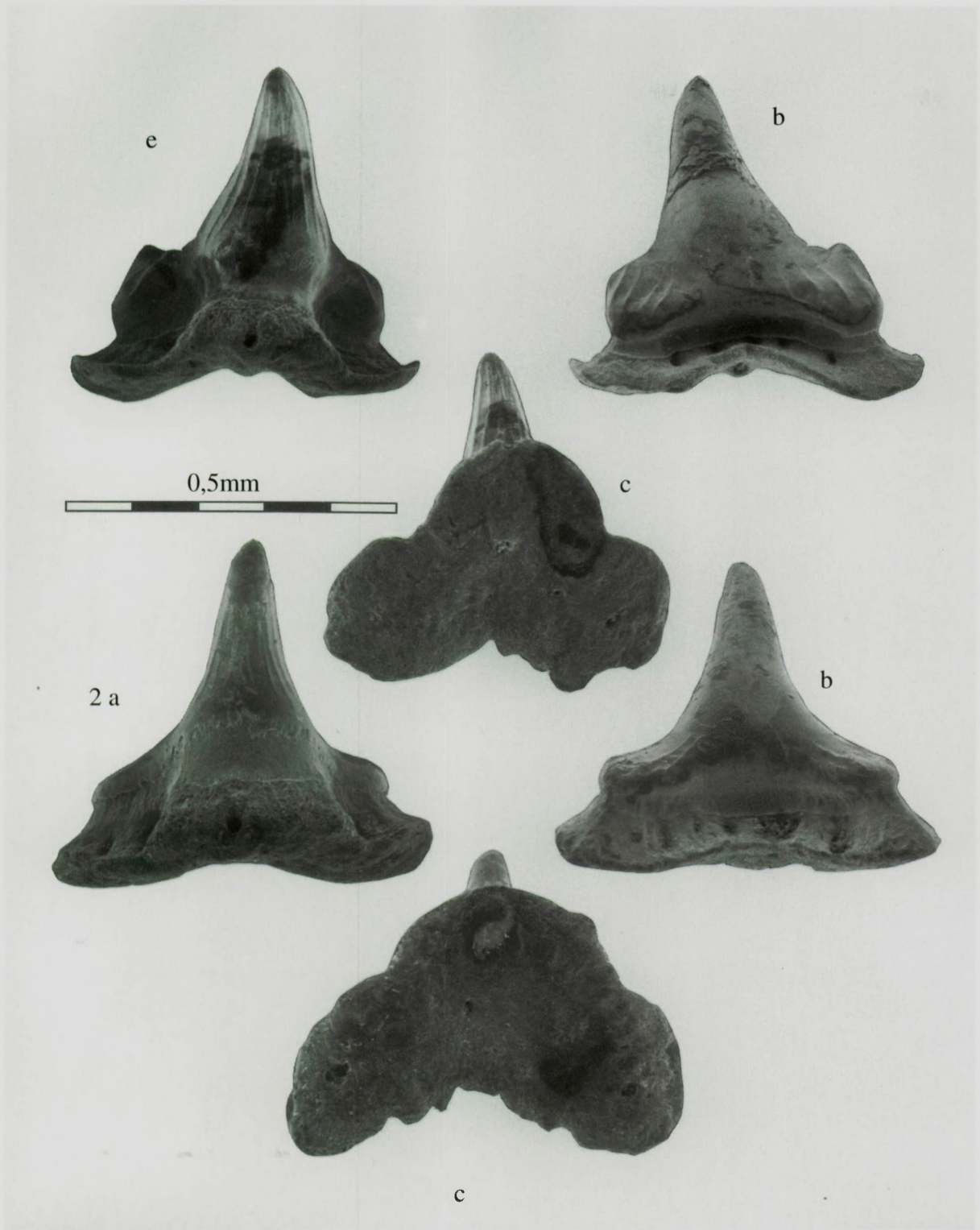


**Plate 4.** *Scyliorhinus biddlei* sp. nov.: 1. Paratype 5: I.R.S.N.B. P. 6340 (Locality 2): **a**: labial view, **b**: lingual view, **c**: distal lateral view. 2. Paratype 6: I.R.S.N.B. P. 6341 (Locality 3, Horizon 1): **a**: lingual view, **b**: labial view, **c**: basal view, **d**: occlusal view, **e**: distal lateral view.



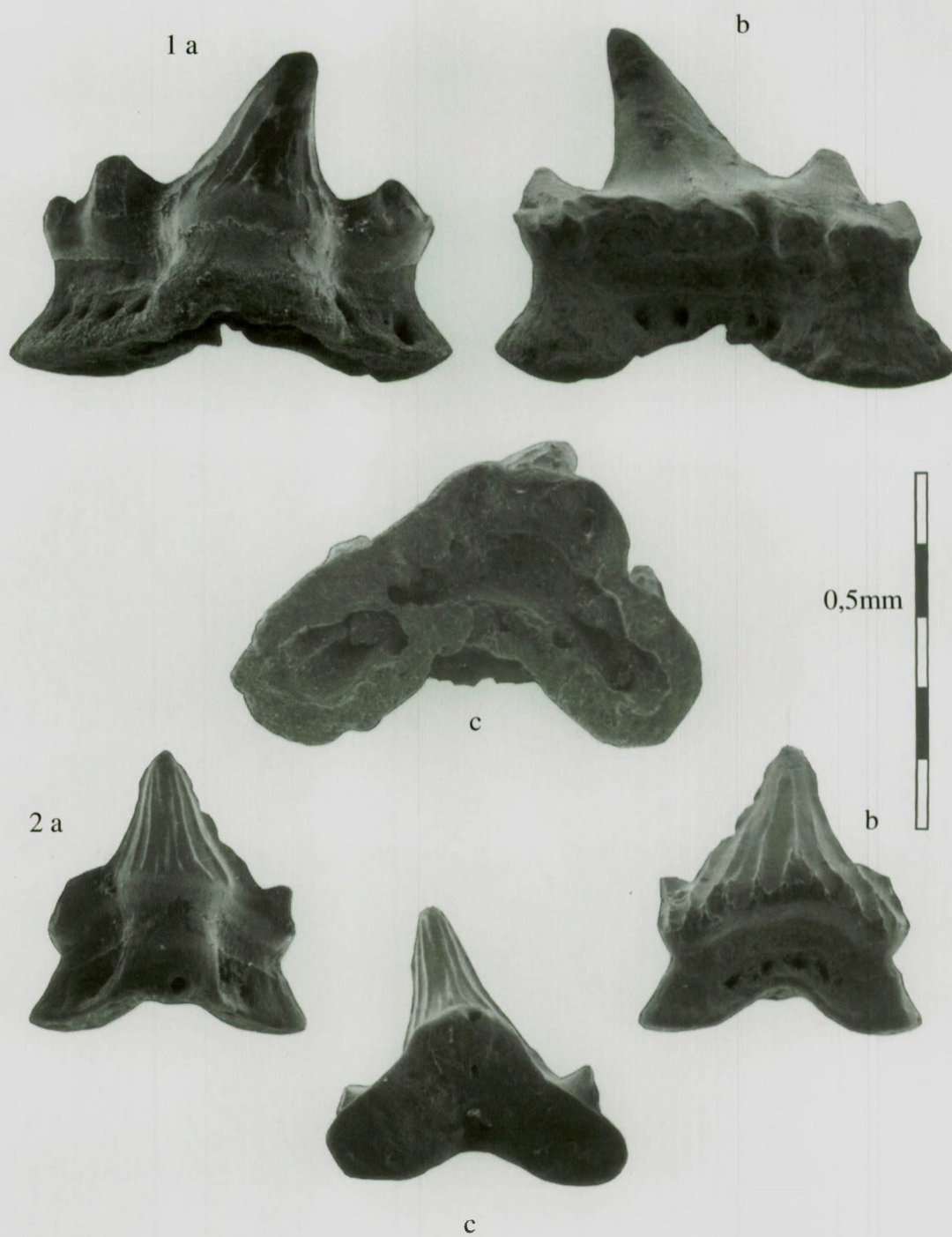


**Plate 5.** *Scyliorhinus biddlei* sp. nov.: 1. Paratype 7: I.R.S.N.B. P. 6342 (Locality 3, Horizon 2): **a:** lingual view, **b:** labial view, **c:** basal view, **d:** mesial lateral view; **e:** detail, showing the microornamentation at the base of the labial face of the crown (1b). Scale line 0.1 mm.



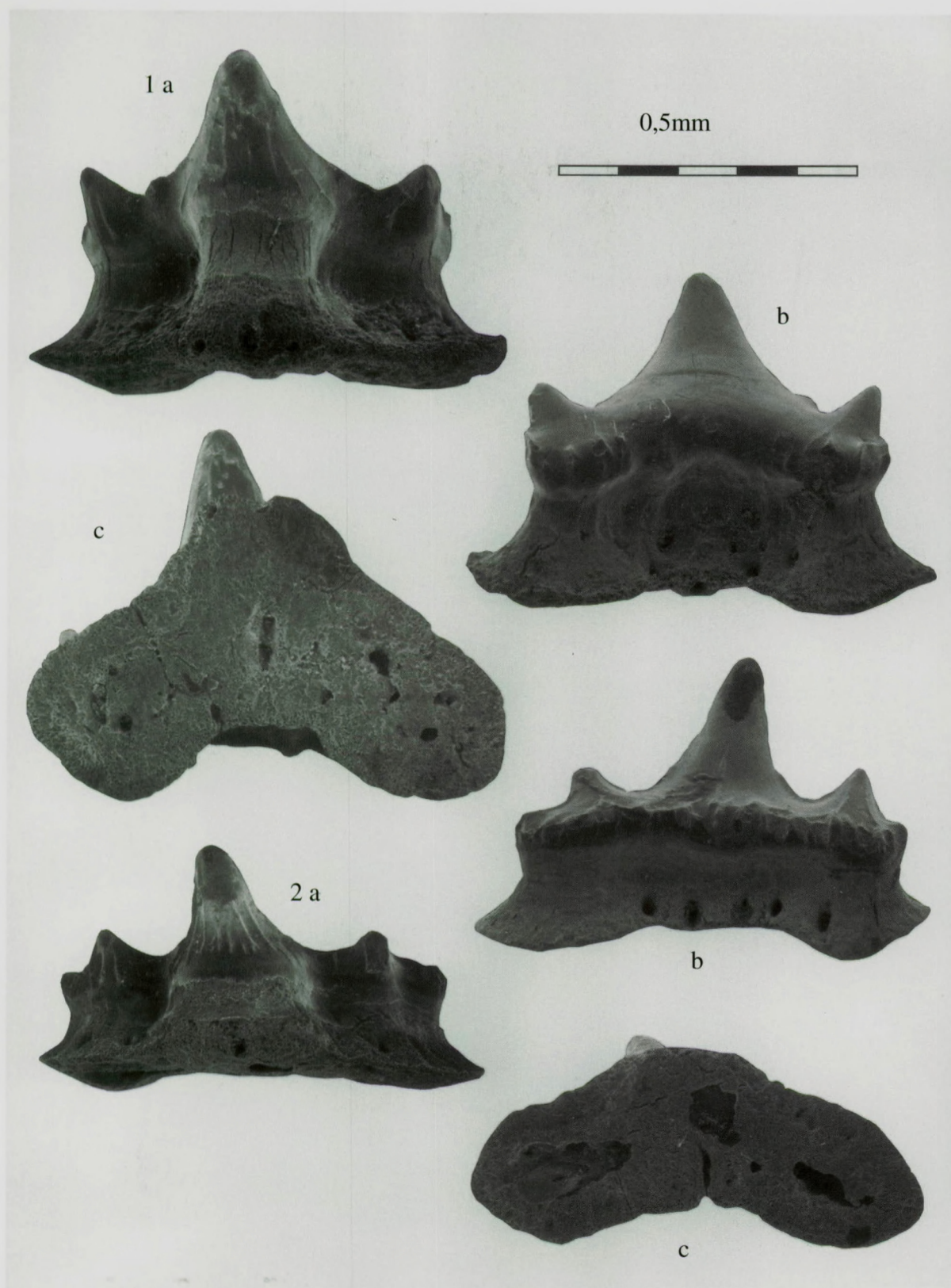
**Plate 6.** *Scyliorhinus reyniersi* sp. nov.: 1. Holotype: I.R.S.N.B. P. 6343 (Locality 4, Level 2): **a**: lingual view, **b**: labial view, **c**: basal view. 2. Paratype 1: I.R.S.N.B. P. 6344 (Locality 4, Level 2): **a**: lingual view, **b**: labial view, **c**: basal view.



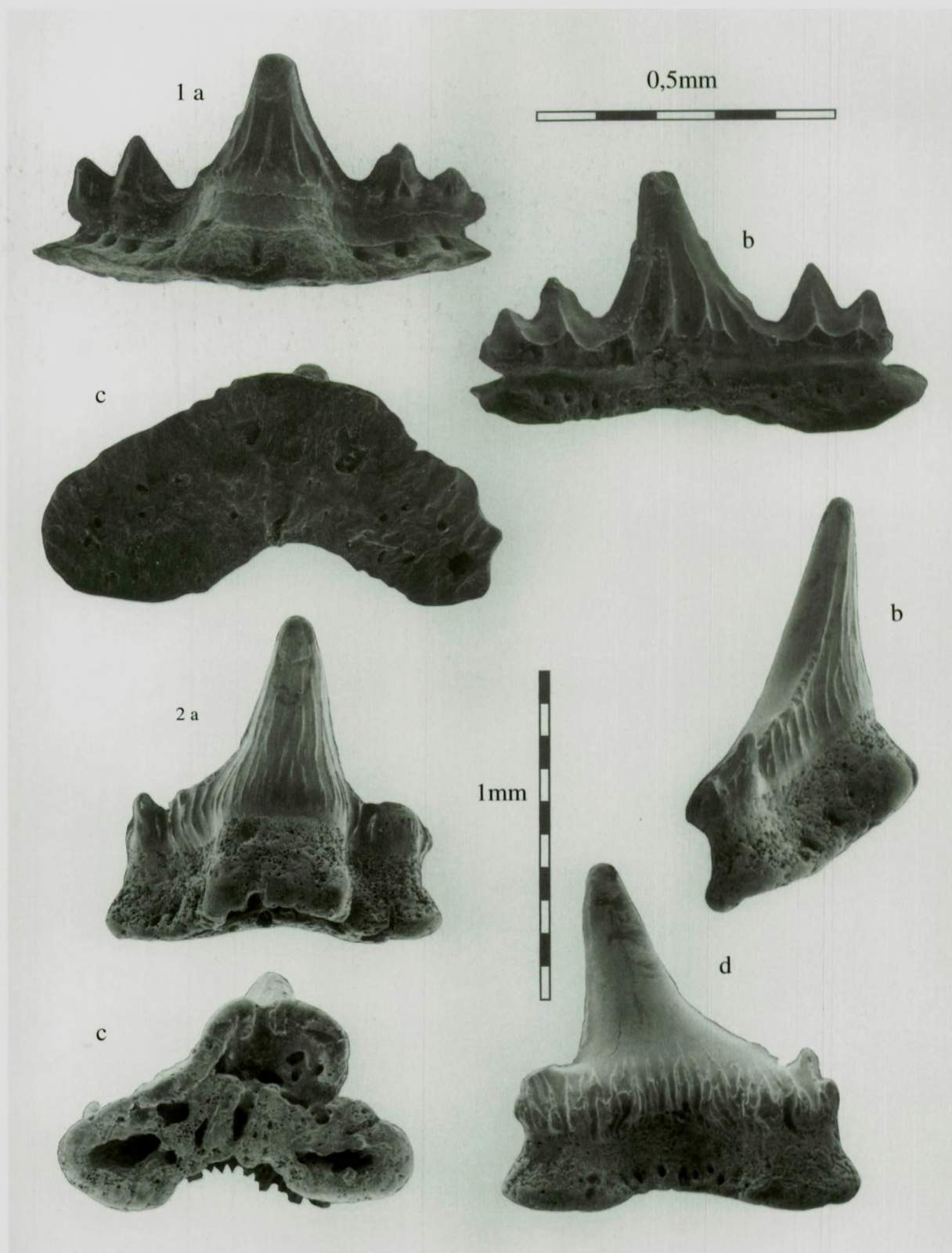


**Plate 7.** *Scyliorhinus reyniersi* sp. nov.: 1. Paratype 2: I.R.S.N.B. P. 6345 (Locality 4, Level 2): **a**: lingual view, **b**: labial view, **c**: basal view. 2. Paratype 3: I.R.S.N.B. P. 6346 (Locality 4, Level 1): **a**: lingual view, **b**: labial view, **c**: basal view.



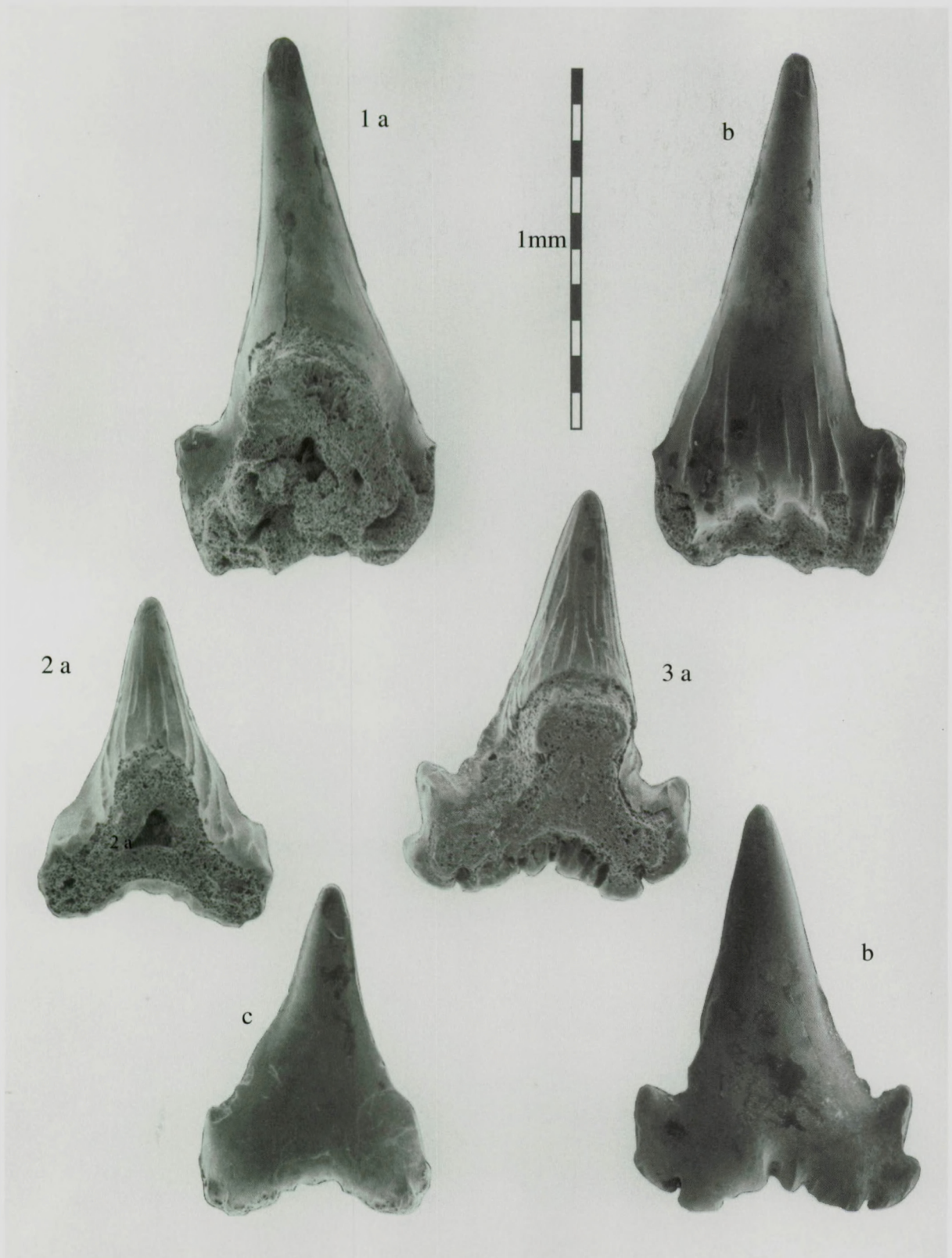


**Plate 8.** *Scyliorhinus reyniersi* sp. nov.: 1. Paratype 4: I.R.S.N.B. P. 6347 (Locality 4, Level 2): a: lingual view, b: labial view, c: basal view. 2. Paratype 5: I.R.S.N.B. P. 6348 (Locality 4, Level 2): a: lingual view, b: labial view, c: basal view.



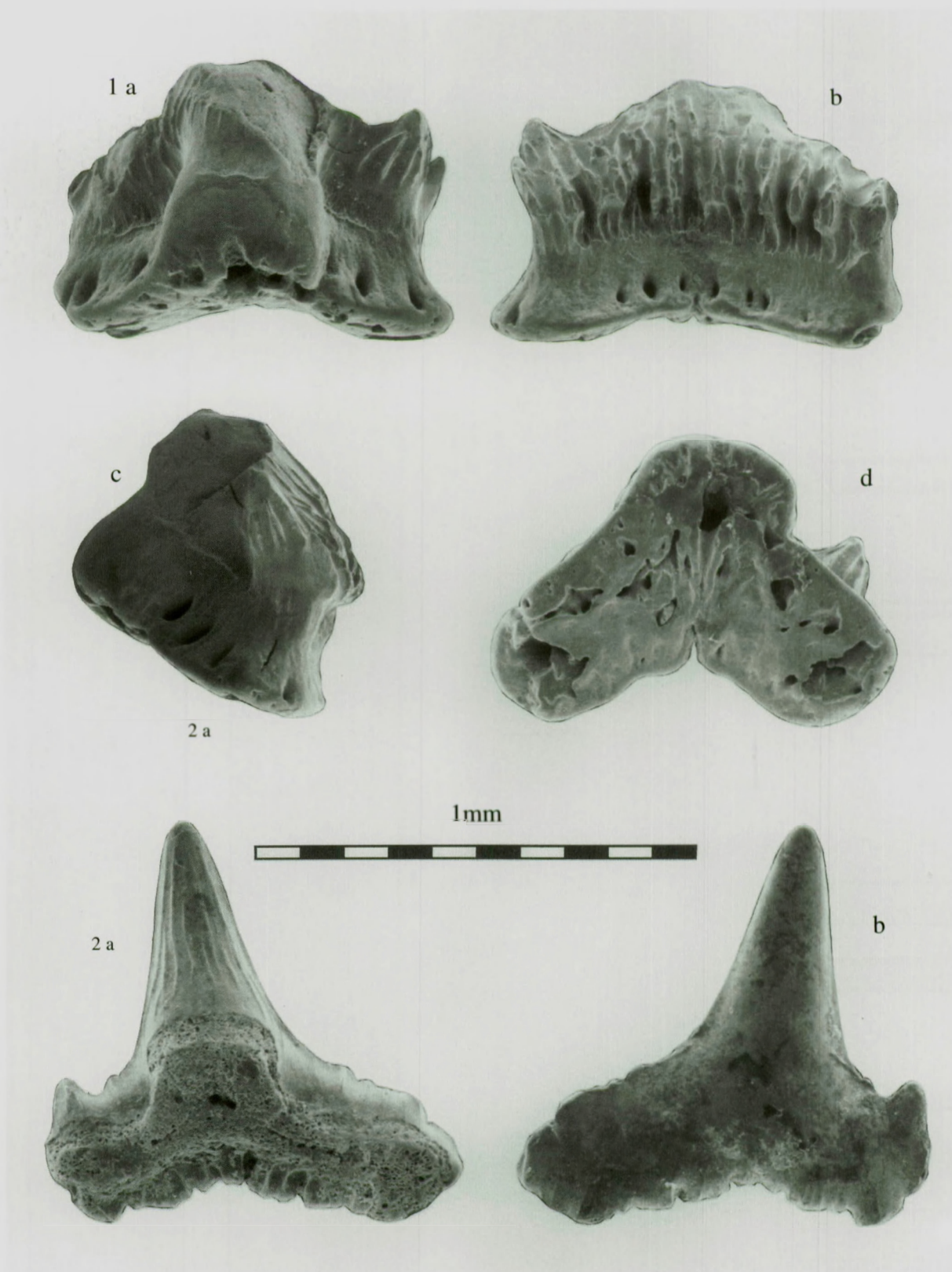
**Plate 9.** 1. *Scyliorhinus reyniersi* sp. nov.: Paratype 6: I.R.S.N.B. P. 6349 (Locality 4, Level 2): **a**: lingual view, **b**: labial view, **c**: basal view. 2. *Scyliorhinus luybaertsi* sp. nov.: Holotype: I.R.S.N.B. P. 6350 (Locality 2): **a**: lingual view, **b**: mesial lateral view, **c**: basal view, **d**: labial view.



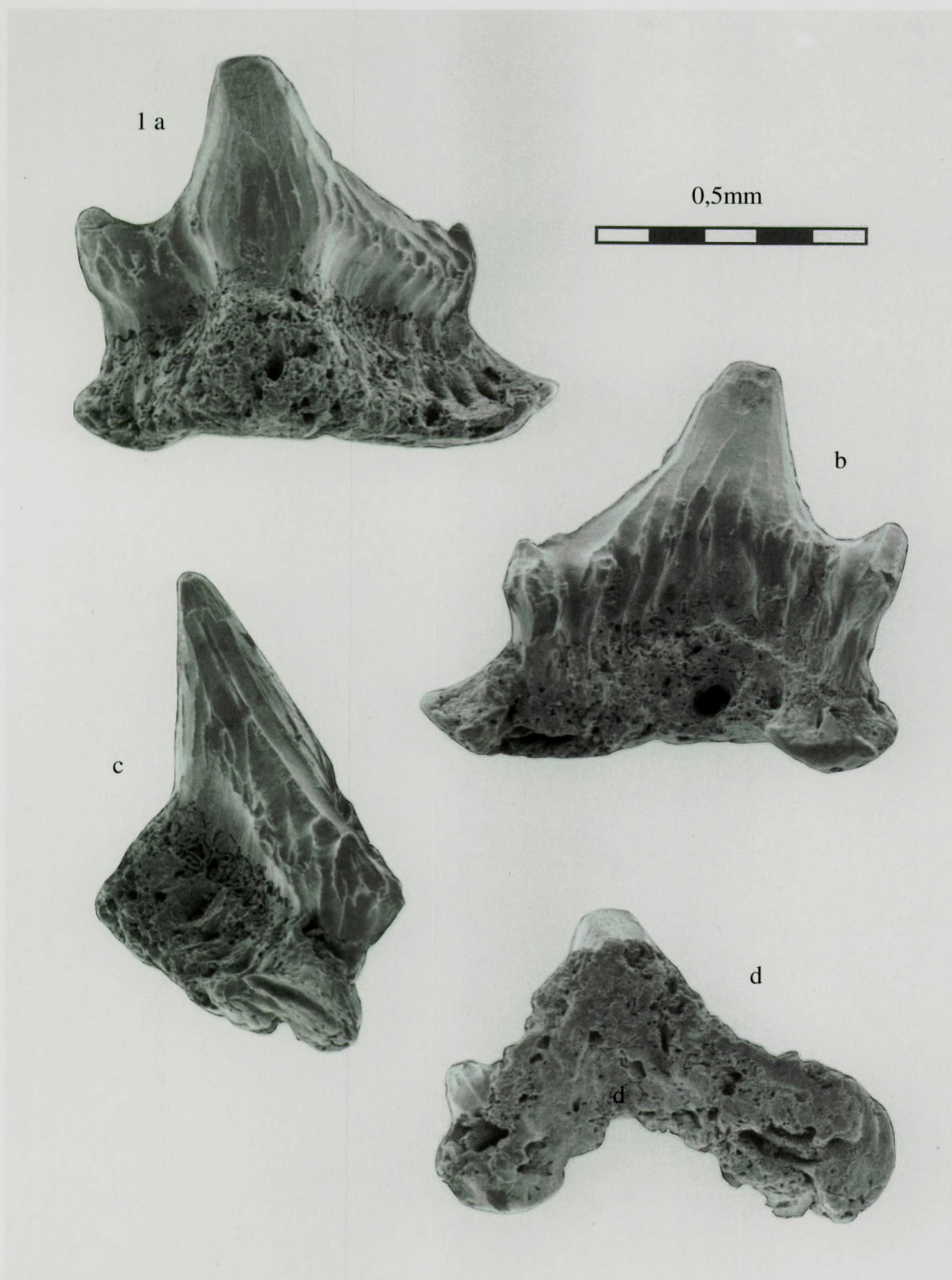


**Plate 10.** *Scyliorhinus luybaertsi* sp. nov.: 1. Paratype 1: I.R.S.N.B. P. 6351 (Locality 2): **a**: lingual view, **b**: labial view. 2. Paratype 2: I.R.S.N.B. P. 6352 (Locality 2): **a**: lingual view, **b**: labial view. 3. Paratype 3: I.R.S.N.B. P. 6353 (Locality 2): **a**: lingual view, **b**: labial view.





**Plate 11.** *Scyliorhinus luybaerti* sp. nov.: 1. Paratype 4: I.R.S.N.B. P. 6354 (Locality 2): **a**: lingual view, **b**: labial view, **c**: mesial lateral view, **d**: basal view. 2. Paratype 5: I.R.S.N.B. P. 6355 (Locality 2): **a**: lingual view, **b**: labial view.



**Plate 12.** *Scyliorhinus luybaerti* sp. nov.: 1. Paratype 6: I.R.S.N.B. P. 6356 (Locality 2): **a**: lingual view, **b**: labial view, **c**: mesial lateral view, **d**: basal view.

