

Late Triassic Vertebrates from Syren (Luxembourg)

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With 10 figures and 1 table

GODEFROIT, P., CUNY, G., DELSATE, D. & ROCHE, M. (1998): Late Triassic Vertebrates from Syren (Luxembourg). – N. Jb. Geol. Paläont. Abh., **210**: 305–343; Stuttgart.

Abstract: The palynological analysis of a new Triassic locality at Syren (Luxembourg) reveals the presence of all typical species of the *Rhaetipollis germanicus* Assemblage, ascribing a Rhaetian age to the level. The vertebrate fauna is dominated by a marine component with a typical Rhaetian facies association. The enameloid ultrastructure shows that “*Hybodus*” *minor* is a neoselachian and that teeth previously referred to this species may be attributed to *Nemacanthus monilifer*. The terrestrial component is very diversified, including Phytosauria, Pterosauria, ?Ornithischia, Cynodontia and Mammalia (Haramiyidae, Morganucodontidae and Kuehneotheriidae). In opposition to the marine component, the terrestrial fauna shows little variation throughout the Rhaetian transgression.

Résumé: Un nouveau gisement d'âge triasique supérieur a été découvert à Syren (G.-D. Luxembourg). Son analyse palynologique révèle la présence de toutes les espèces typiques de l'Assemblage à *Rhaetipollis germanicus*, permettant d'attribuer un âge Rhétien au niveau étudié. La faune de vertébrés est dominée par des formes marines typiques du faciès rhétien. L'étude de l'ultrastructure de l'émail montre qu' “*Hybodus*” *minor* est un Neoselachii et que les dents attribuées dans le passé à cette espèce pourraient en fait appartenir à *Nemacanthus monilifer*. La composante terrestre de la faune est très diversifiée, incluant des dents de Phytosauria, Pterosauria, ?Ornithischia, Cynodontia et Mammalia (Haramiyidae, Morganucodontidae et Kuehneotheriidae). Contrairement à la composante marine, la faune terrestre montre très peu de variations au cours de la transgression rhétienne.

Zusammenfassung: Eine neue Obertrias-Fundstelle (Syren, Luxemburg) kann aufgrund der palynologischen Analyse durch die typischen Arten der *Rhaetipollis germanicus*-Gesellschaft in das Rhät eingeordnet werden. Die Wirbeltierfauna ist

durch marine Vertreter typisch rhaetischen Charakters dominiert. Anhand der Ultrastruktur des Enameloids zeigt sich, daß „*Hybodus*“ *minor* ein Neoselachier ist und daß Zähne, die ihm zugeordnet wurden, zu *Nemacanthus monilifer* gehören. Die terrestrische Komponente ist sehr vielfältig und enthält Phytosaurier, Flugsaurier, fragliche Ornithischier sowie Cynodontia und Mammalia (Haramiyidae, Morganucodontidae und Kuehneotheriidae). Im Gegensatz zum marinen Faunenanteil zeigt der terrestrische wenig Veränderungen im Zuge der Rhät-Transgression.

Introduction

Since the beginning of the eighties, Late Triassic outcrops from the Lorraine-Luxembourg area have been intensively investigated by both amateur and professional palaeontologists, because some localities have yielded numerous vertebrate remains and particularly mammal teeth, amongst the oldest in the world: Saint-Nicolas-de-Port (Meurthe-et Moselle, France; see e. g. SIGOGNEAU-RUSSELL 1983), Varangéville (Meurthe-et-Moselle, France; GODEFROIT 1997), Habay-la-Vieille (Belgian Lorraine; see e. g. HAHN et al. 1987), Attert (Belgian Lorraine; DUFFIN & DELSATE 1993) and Medernach (Luxembourg; see e. g. CUNY et al. 1995). The northeastern margin of the Paris Basin is actually regarded by palaeontologists as one of the main areas in the world for the study of earliest mammals.

OPPEL (1856-58) described a Rhaetian bonebed at Dalheim (Luxembourg), a locality close to Syren, and identified fish teeth of the following taxa: *Sargodon tomicus*, “*Sphoerodus*” *minimus*, *Saurichthys acuminatus* and *Gyrolepis tenuistriatus*. HEUERTZ (1934) and MÜLLER (1964) describe an Upper Triassic exposure at Syren, close to the railway line Bettembourg-Oetrange. They describe conglomeratic layers, but do not point out the presence of vertebrate remains. In 1996, the construction of a new housing estate exposed a new section in the Upper Triassic of Syren. Washing and screening of a conglomeratic layer by a team of the Musée national d'Histoire naturelle de Luxembourg lead by one of us (D.D.) revealed the presence of vertebrate micro-remains. These fossils are described and discussed in the present paper.

Abbreviation: MNHNL: Musée national d'Histoire naturelle de Luxembourg.

Locality and Geological setting

The bonebed described in this paper was exposed at the place named „Auf dem Heftgen“ (Syren, city of Weyler-la-Tour), just at the northern wall of the cemetery (Fig. 1). The following succession was observed there, from bottom to top:

- 30 cm: Yellow/orange friable and clayey sandstone, with some pebbles.
- 30 cm: Green/black foliated clay.
- 7 to 10 cm: Lenticular bonebed: brown friable conglomerate, with siliceous pebbles reaching up to 8 cm in diameter.
- 70-80 cm: Gray/green sandy clay.
- ? cm: Base of the reddish Levallois Marls (Upper Rhaetian), visible on both sides of the cemetery portal.

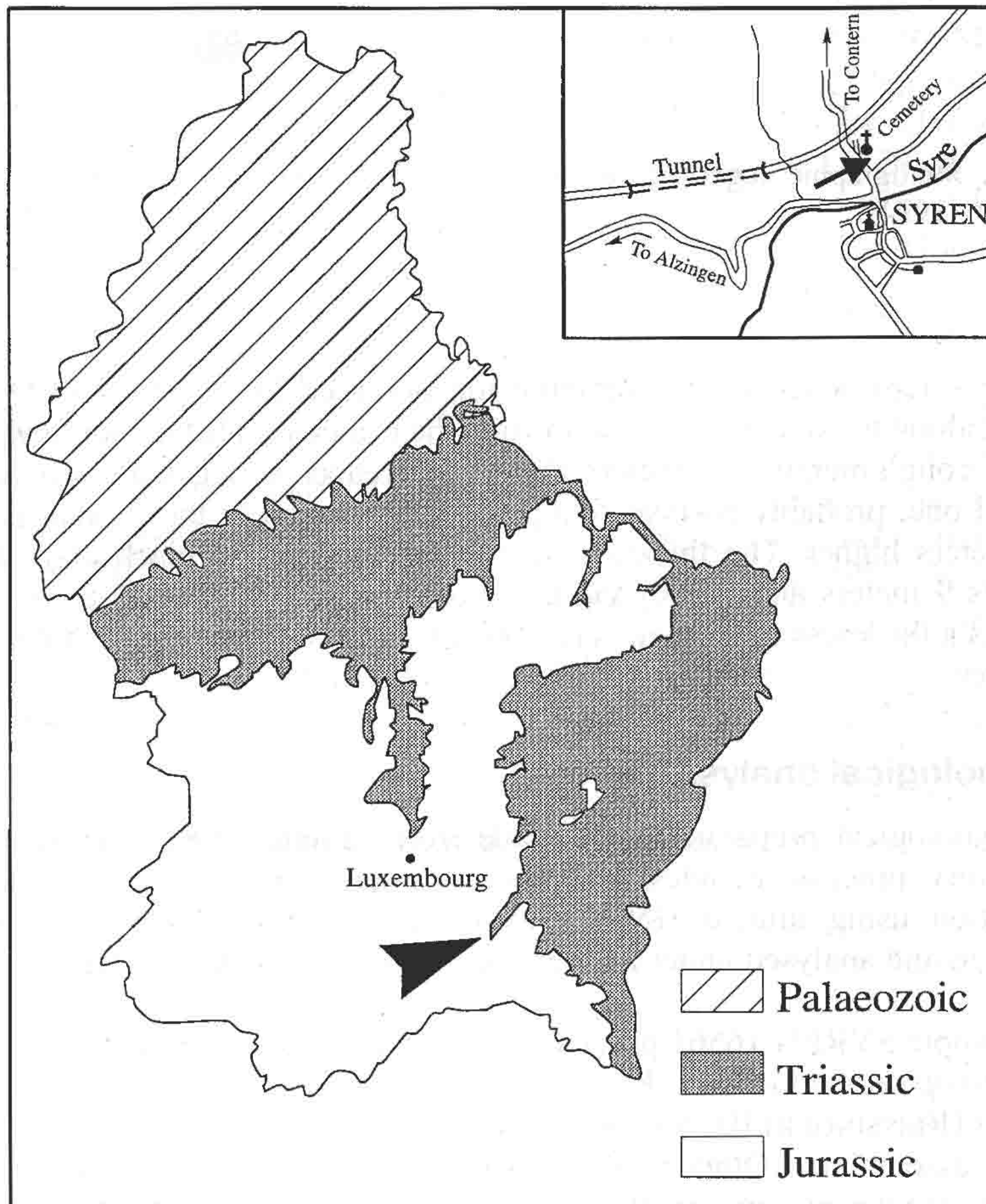


Fig. 1. Simplified geological sketch map of Luxembourg. Inset map shows the location of the fossil locality (indicated by an arrow) excavated at Syren.

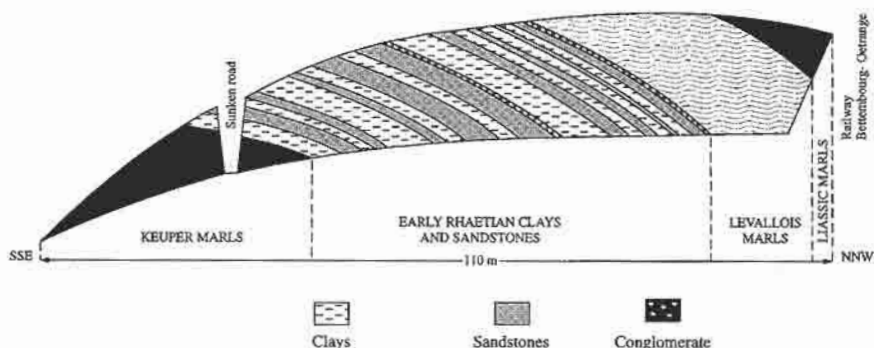


Fig. 2. Stratigraphic log observed at Syren, along the road to Contern (after HEUERTZ 1934).

Figure 2 represents the stratigraphic log observed by HEUERTZ (1934) at Syren, along the road to Contern down to the cemetery. This author observed a first conglomerate, 5.6 meters above the Keuper variegated marls and a second one, probably corresponding to that observed in the present paper, 3.2 meters higher. The thickness of the sandstones and black clays layer reaches 9 meters and that of the Levallois Marls, 4 m. The Rhaetian thus reaches a thickness of 13 meters (7.5 meters after MÜLLER 1964) in the area of Syren.

Palynological analysis

A palynological preparation was made from sample SYREN 16561. The laboratory process includes the following steps: HCl and HF, moderate oxydation using diluted HNO_3 and 12 μm filtration. Two slides were mounted and analysed under natural transmitted light with interference contrast.

The sample SYREN 16561 provides an association of miospores dominated by *Gliscopollis meyeriana* (KLAUS) VENKATACHALA 1966 and *Classopollis torosus* (REISSINGER) BALME 1957. These two species make up around 90 % of the assemblage. Other common species are: *Ovalipollis pseudoalatus* (THIERGART) SCHUURMAN 1976, *Rhaetipollis germanicus* SCHULZ 1967, *Ricciisporites tuberculatus* LUNDBLAND 1954 and *Granuloperculatipollis rudis* (VENKATACHALA & GÓCZÁN) MORBEY 1975. Rare specimens of *Quadraeculina anellaeformis* MALJAVKINA 1949, *Lunatisporites rhaeticus*

(SCHULZ) WARRINGTON 1974, *Alisporites* sp. and *Chasmatosporites magnolioides* (ERDTMAN) NILSSON 1958 complete the assemblage (Fig. 3).

All the typical species of the *Rhaetipollis germanicus* Assemblage *sensu* SCHUURMAN (1977 and 1979) are present in the observed association in Syren, which allows to assign by comparison a Rhaetian *sensu lato* Age to the studied level. Indeed, the *Rhaetipollis germanicus* Assemblage has been previously observed numerous times in uppermost Triassic sequences in Europe: in Great-Britain by ORBELL (1973), MORBEY (1975), WARRINGTON (1974, 1983 and 1984), WARRINGTON & WHITTAKER (1984), WARRINGTON et al. (1986) and LOTT & WARRINGTON (1988), in Germany by MÄDLER (1964), SCHULZ (1967), LUND (1977), SCHUURMAN (1979), ACHILLES (1981), BRENNER (1986) and WEISS (1989), in Poland by ORLOWSKA-ZWOLINSKA (1983), in the Netherlands by HERNGREEN & DE BOER (1974), in Austria by MORBEY (1975) and SCHEURING (in MOSTLER et al. 1978), in France by BIARD (1963), SCHUURMAN (1977), ADLOFF & DOUBINGER (1982), ROCHE (1994) and RAUSCHER et al. (1995), in Sweden by TRALAU (1975) and GUY-OHLSON (1981) and in Denmark by LUND (1977) and DYBKJAER (1988 and 1991).

Likewise, a sparse and badly preserved aquatic palynomorph association including dinoflagellate cysts and acritarchs is recorded. Circular to ovoidal specimens showing a marked broad paracingulum with a apical-intercalary archaeopyle (see Fig. 3, 12) could be reasonably assigned with a confer to the dinoflagellate cyst *Dapcodinium priscum* (EVITT) BELOW 1987. Acritarchs are only represented by long-spined acanthomorphs (*Micrhystridium* sp.). The nature and low diversity of this association is suggestive of a restricted coastal environment with a moderate marine influence (bay, lagoon).

Inventory of the vertebrate micro-remains

Class	Chondrichthyes
Subclass	Elasmobranchii
Cohort	Euselachii
Superfamily	Hybodontoidae
Family	Hybodontidae OWEN, 1846
Genus	<i>Hybodus</i> AGASSIZ, 1837
	<i>Hybodus cloacinus</i> AGASSIZ, 1837 (Fig. 4, 1)

Some fragmentary teeth discovered at Syren can tentatively be referred to *Hybodus cloacinus*. As usually observed elsewhere, these teeth are easily broken by transportation. The crown is very slender and elongated. The central cusp is not very high and rather slender. It bears vertical ridges on both

its lingual and labial sides. These ridges originate from the top of the crown shoulder and can reach the apex; they may bifurcate basally. A prominent labial node is developed at the base of the central cusp. There are several pairs of lateral cusplets of decreasing size: these are rather low and bulbous, ornamented on both sides by a few strong vertical ridges that can reach the apex and bifurcate basally. Labial nodes can be very prominent at the level of the crown shoulder. The edge connecting the cusps is sinuous and not very sharp. There is no lingual shelf. The root is rarely preserved in the material currently discovered at Syren.

The stratigraphic range of *Hybodus cloacinus* extends, according to DUFFIN & DELSATE (1993), from the Rhaetian to the ? Sinemurian.

Family	Polyacrodontidae, GLÜCKMAN, 1964
Genus	<i>Lissodus</i> BROUGH, 1935
	<i>Lissodus minimus</i> (AGASSIZ, 1839) (Fig. 4, 2)

The teeth of *Lissodus minimus* are frequent in the material discovered at Syren. The crown is elongated mesio-distally, very low and narrow. In occlusal view, the lateral ends of the crown may be lingually directed. The central

Fig. 3. Palynomorphs from the Upper Triassic of Syren (Luxembourg). All views are in natural transmitted light with interference contrast. The slides are housed in the MNHNL. The reference position stated after the slide number refers to the England Finder grid from Gromaticus LTD.

1: Cluster of *Gliscopollis meyeriana* (KLAUS) VENKATACHALA 1966; mean size = 26 µm; slide n° 45285; U32/2. 2: Dimorphic tetrad of *Classopollis torosus* (REISINGER) BALME 1957; maximum size = 32 µm; slide n° 45285; R31. 3: *Gliscopollis meyeriana* (KLAUS) VENKATACHALA 1966; size = 24 µm; slide n° 45285; 031. 4: *Lunatisporites rhaeticus* (SCHULZ) WARRINGTON 1974; size = 61 µm; slide n° 45285; N36. 5: *Ricciisporites tuberculatus* LUNDBLAD 1954; size = 90 µm; slide n° 45285; 033. 6 & 7: *Rhaetipollis germanicus* SCHULZ 1967; size of specimen 6 = 40 µm; size of specimen 7 = 38 µm; slide n° 45285; specimen 6: R29; specimen 7: L30/4. 8: *Quadraeculina anellaeformis* MALJAVKINA 1949; size = 49 µm; slide n° 45285; R42/3. 9: *Alisporites* sp.; size = 30 µm; slide n° 45285; D45. 10: *Granuloperculatipollis rudis* (VENKATACHALA & GÓCZÁN) MORBEY 1975; size = 35 µm; slide n° 45285; W41. 11: *Ovalipollis pseudoalatus* (THIERGART) SCHUURMAN 1976; size = 60 µm; slide n° 45285; V30. 12: cf. *Dapcodinium priscum* (EVITT) BELOW 1987; size = 31 µm; slide n° 45285; L52/3. 13: *Micrhystridium* sp.; size of central body = 18 µm; slide n° 45285; H37.

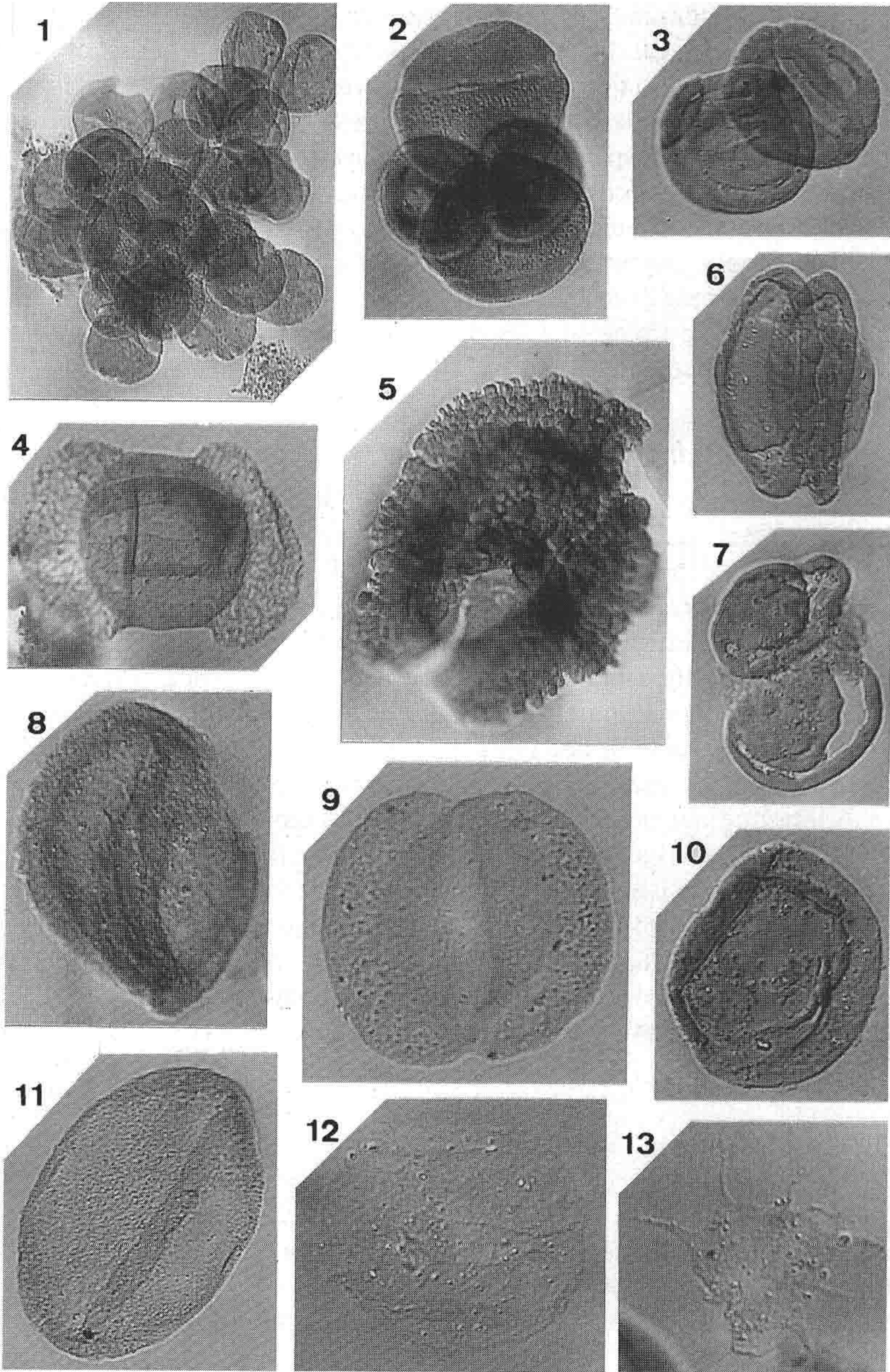


Fig. 3 (Legend see p. 310)

cuspid is always moderately developed and very obtuse; its base is diamond-shaped. At its base, the labial peg is well developed, but does not bear an accessory cusplet. A major vertical ridge forms a crest from the labial peg and ascends the main cusp. The occlusal crest is rather strong. Up to four pairs of tiny lateral cusplets may be developed. The crown may be ornamented by moderate vertical ridges, radiating from the apex of the cusps; they are progressively obliterated basally and can bifurcate. The crown/root junction is deeply incised around the whole crown. The root is never preserved in the material from Syren.

The stratigraphic range of *Lissodus minimus* appears to extend from the Ladinian to the Rhaetian (DUFFIN & DELSATE 1993).

Lissodus lepagei DUFFIN, 1993

Fossils referable to *Lissodus lepagei* are rare in the material discovered at Syren. Nevertheless, several teeth show a particular morphology, distinctly different from that observed in teeth identified as *Lissodus minimus*. *Lissodus lepagei* teeth are very small, less than 2 mm in length. A maximum of two pairs of lateral cusplets can be observed on the material from Syren. The enameloid is usually smooth, but fine and sparse vertical ridges can be observed on the upper part of the main cusp. The cutting edge is well-developed and crenulated. The labial peg is always well-developed and bears a distinct single cusplet, connected to the main cusp by a strong vertical ridge. A longitudinal ridge is present around the crown.

Lissodus lepagei has originally been described from the Steinmergelgruppe (middle Norian, Upper Triassic) of Medernach (Luxembourg). As noted by DUFFIN (1993a: 21), it can not be excluded that teeth of *Lissodus lepagei* represent in fact juvenile specimens of *Lissodus minimus*. Nevertheless, the absence of *Lissodus minimus* from the material discovered at Medernach makes this hypothesis very unlikely.

Fig. 4. Selachian teeth from the Upper Triassic of Syren (Luxembourg).

1: *Hybodus cloacinus* AGASSIZ, 1837 (MNHN ko177), X13. A: labial view; B: occlusal view. 2: *Lissodus minimus* (AGASSIZ, 1839) (MNHN ko178), X17. A: labial view; B: occlusal view. 3: "*Hybodus*" *minor* AGASSIZ, 1837 (MNHN ko179), X17. A: occlusal view; B: labial view. 4: *Pseudocetorhinus pickfordi* DUFFIN, 1998 (MNHN ko180), X16. A: labial view; B: occlusal view; C: mesial view.

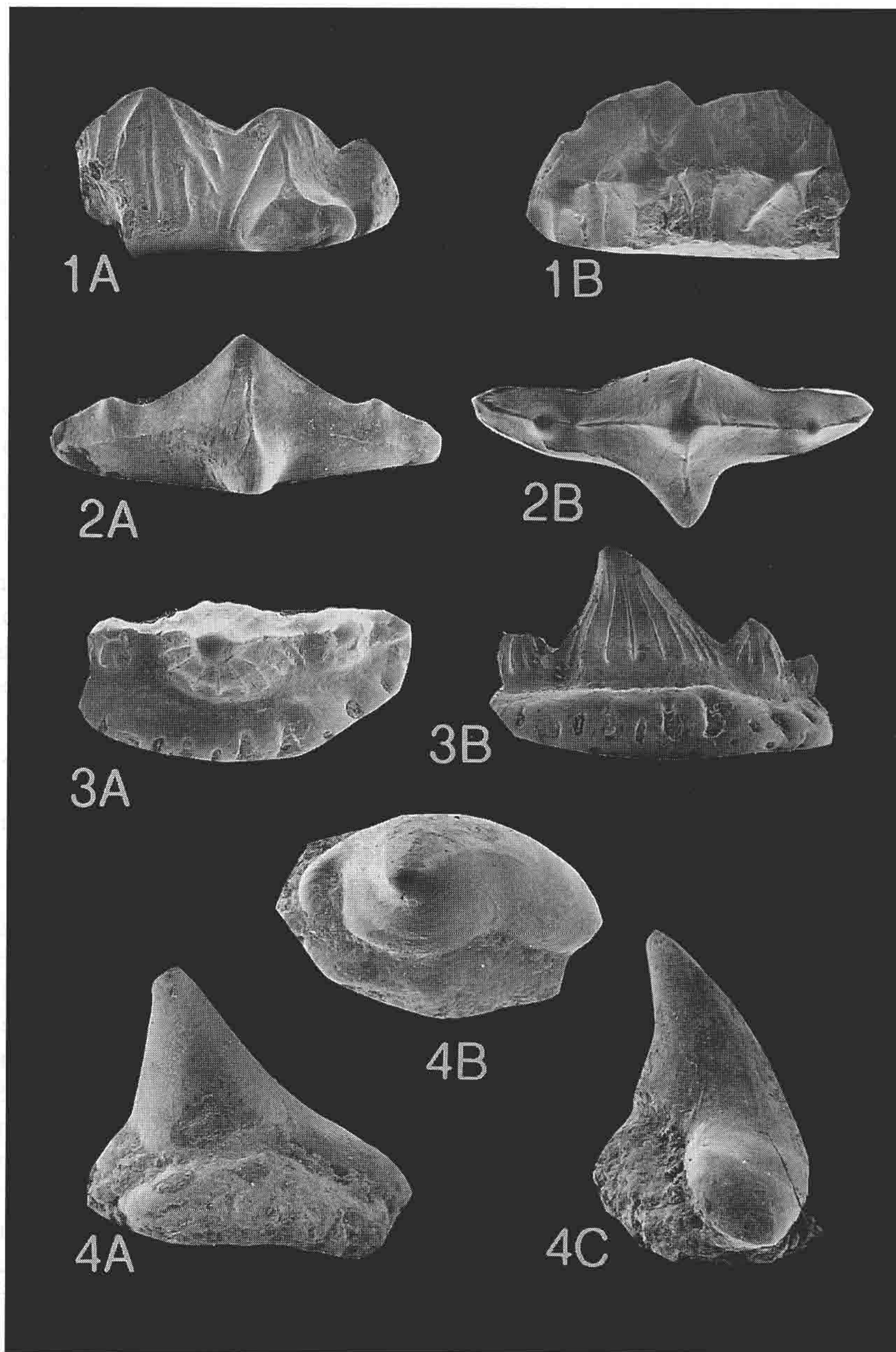


Fig. 4 (Legend see p. 312)

Subcohort Neoselachii
 Order, Superfamily and Family
 incertae sedis

"*Hybodus*" *minor* AGASSIZ, 1837 (Fig. 4, 3)

Teeth referable to "*Hybodus*" *minor* are frequent in the material discovered at Syren and their size varies much. The central cusp is high, upright and triangular in labial or lingual view. It is usually curved lingually and distally. One to three pairs of lateral cups of decreasing size can be observed. The first pair is about half the height of the main cusp. The height of the second pair varies from one quarter to one third of that of the central cusp. The occlusal crest forms a well-developed cutting edge along the mesio-distal length of the crown. The crown is ornamented by strong vertical ridges on both lingual and labial sides: they arise from a position close to the crown/root junction and ascend the central cusp and lateral cusplets, occasionally reaching the apices, but usually terminating just below them. The ridges do not bifurcate or anastomose. In occlusal view, the root has a semicircular shape, projecting lingually. The vascularization of the root is anaulacorhize. The labial side of the root is shallow and punctuated by several small vascular foramina on or above the basal border. The lingual side is very prominent in lateral view and penetrated by randomly distributed small foramina.

Three teeth were etched in 10 % HCl for 10 seconds up to 5 minutes in order to show enameloid ultrastructure. Photographs of the enameloid's surface were taken with a Cambridge Stereoscan 250 MK3 S.E.M. The enamel is mostly composed of parallel bundles of apatite fibres running in a basal-apical direction. The average diameter of the bundles is about 2.5 μm . This layer represents a parallel fibred enameloid (PFE, REIF, 1973; Fig. 5, 1), an apomorphy of neoselachian sharks (GAUDIN 1991). The cutting edges and the ridges ornamenting the crown show a thick shiny layered enameloid (SLE, Fig. 5, 3) covering the PFE. This SLE consists of randomly oriented single crystals of apatite about 1 μm long (Fig. 6, 6). At the level of the ridges, below the SLE, we notice a change in the orientation of the bundles of the PFE which become perpendicular to the ridge (Fig. 5, 4). A similar pattern is already known in *Hueneichthys costatus* from the Rhaetian of Germany (REIF 1977). At the apex of the teeth, the bundles of fibres seem to display a more random orientation (Fig. 5, 2), which could be interpreted as a clue to the presence of a tangled fibred enameloid (TFE). The enamel of "*Hybodus*" *minor* appears therefore to be triple-layered, as in modern Neoselachii.

These teeth perfectly correspond in general morphology to those of "*Hybodus*" *minor* AGASSIZ 1837 (see DUFFIN 1993a and b, for detailed

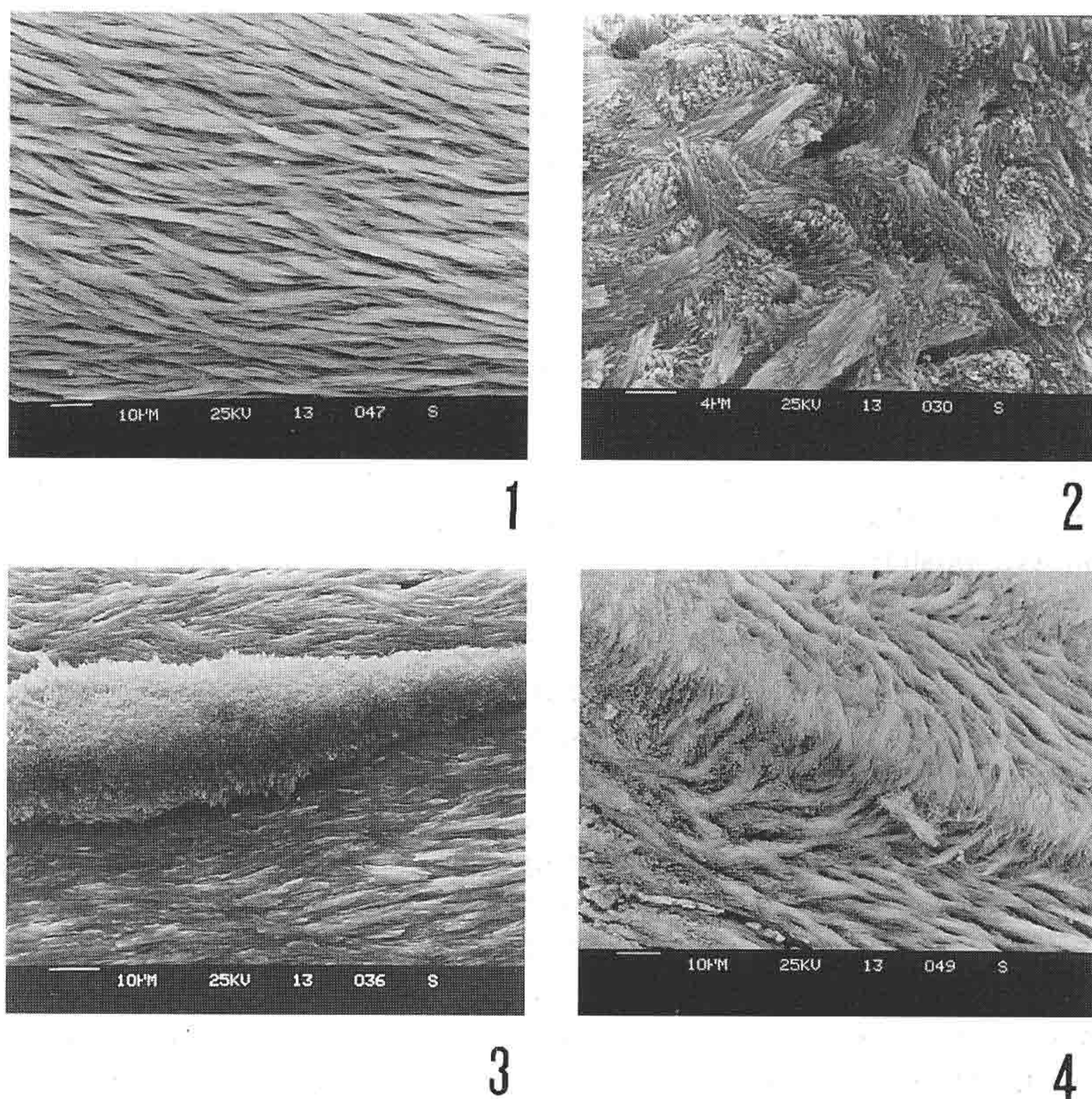


Fig. 5. Ultrastructure of the enameloid of the teeth of "*Hybodus*" minor from the Upper Triassic of Syren (Luxembourg).

1: Parallel fibred enameloid (PFE) near the apex of the crown, tooth etched 1 min. in 10 % HCl. **2:** Tangled fibred enameloid (TFE) underneath the PFE, tooth etched 6 min. in 10 % HCl. **3:** Ridge showing a thick shiny layered enameloid (SLE), while this layer has been removed on the other part of the crown, tooth etched 30 sec. in 10 % HCl. **4:** Structure of the ridge underneath the SLE, showing the change in the orientation of the PFE bundles, tooth etched 1 min. in 10 % HCl.

comparisons of the teeth within the genus *Hybodus*). A triple-layered enameloid was recognized in teeth of "*Hybodus*" *minor* from the Upper Triassic of Aust (U.K.), Medernach (Luxembourg), Habay-la-Vieille (Belgium), Saint-Germain-les-Arlay and Grozon (France) (CUNY 1997, and unpublished

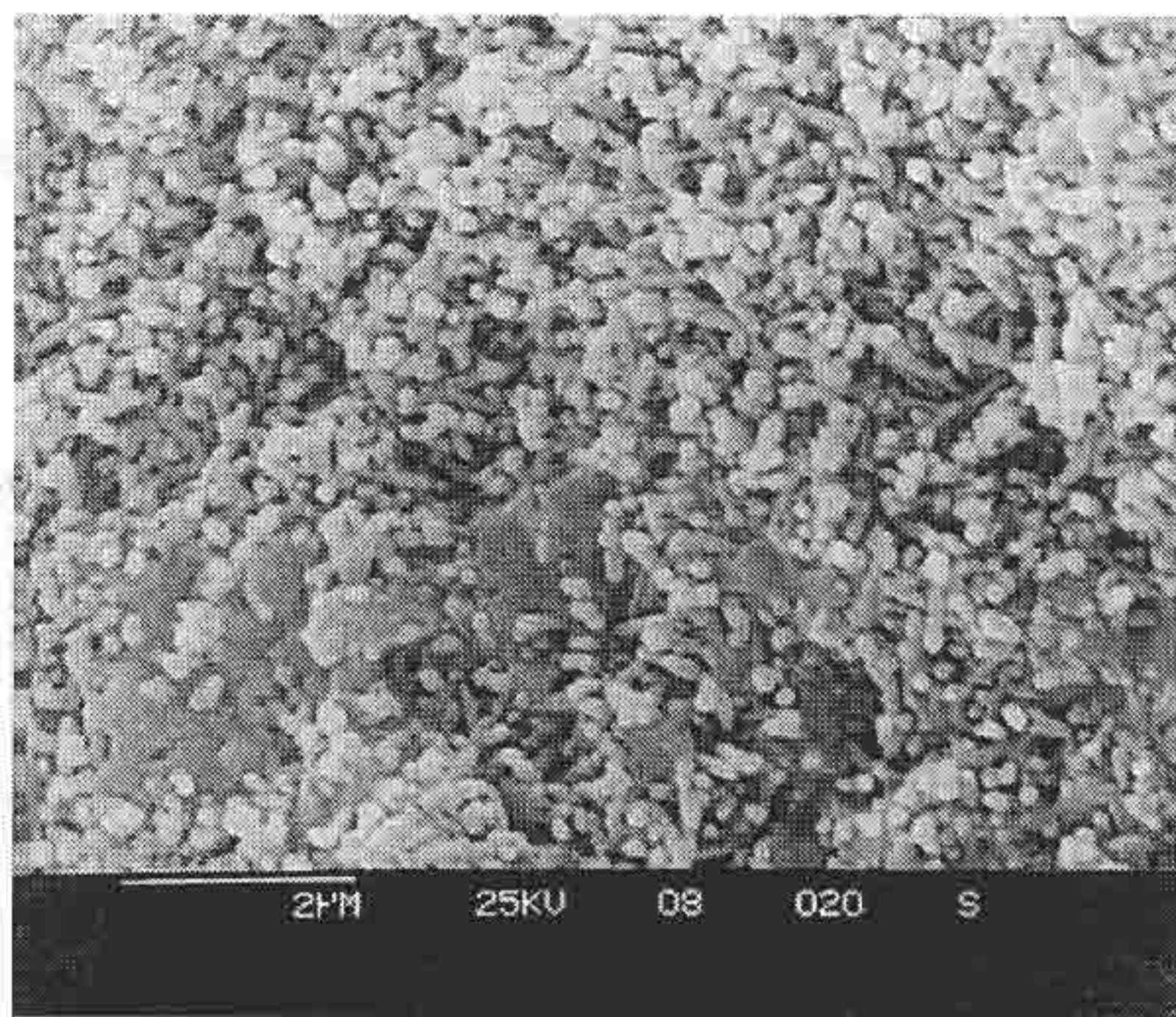
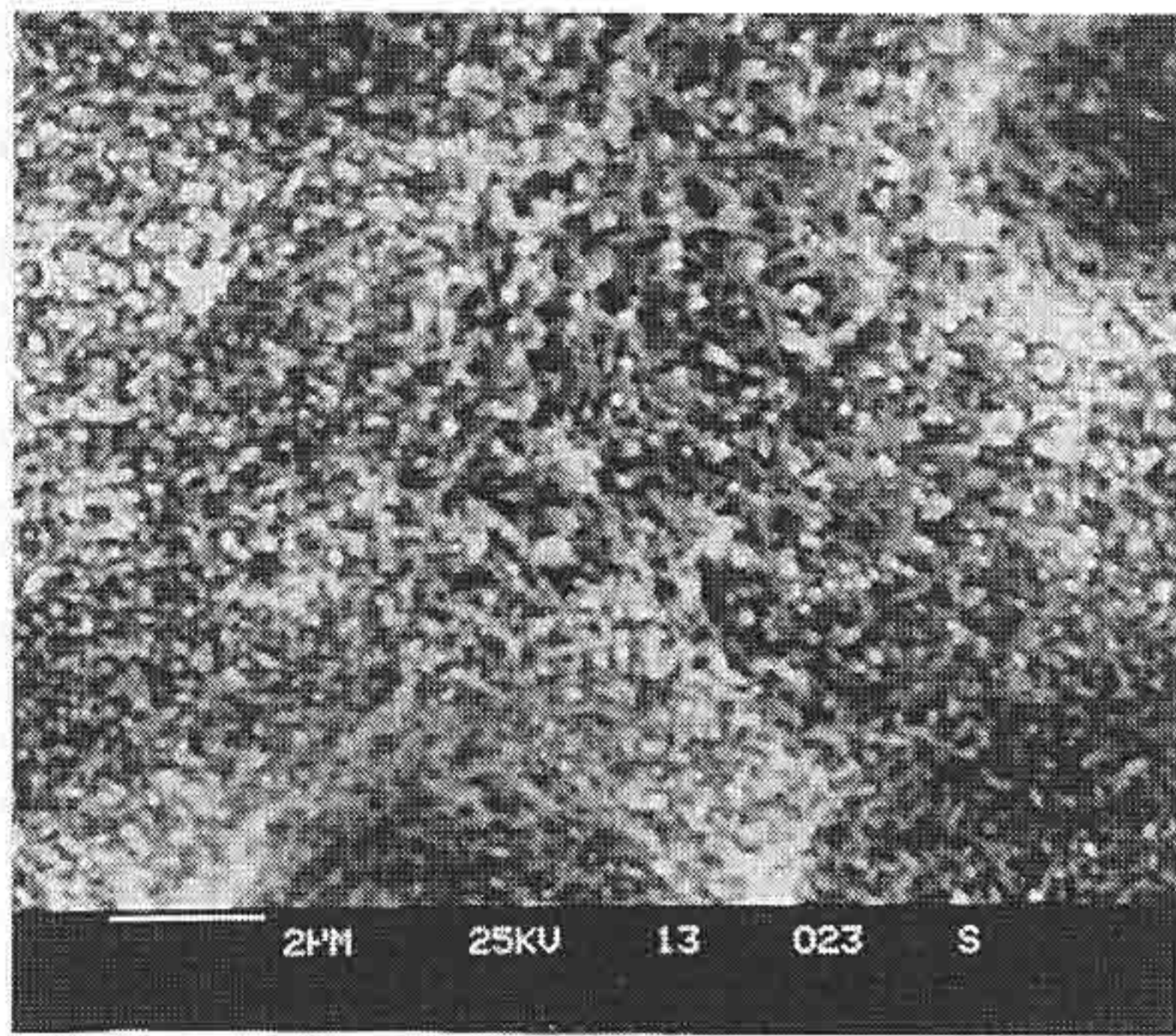
data; J. DAY pers. com.) and it is now clear that this genus belongs indeed to the neoselachian sharks. For DUFFIN & DELSATE (1993), "*Hybodus*" *minor* would extend stratigraphically from the Ladinian (although this requires verification) to the Rhaetian. A possible tooth of "*Hybodus*" *minor* was also mentioned in the Toarcian of Aubange (Belgium, see DELSATE & GODEFROIT 1995).

Genus *Nemacanthus* AGASSIZ, 1837
 Nemacanthus monilifer AGASSIZ, 1837

The fossil material discovered at Syren contains some fragments of fin spines. Some of these fragments appear triangular in cross-section, with a concave posterior wall. In cross-section, the central canal occupies a posterior position. The ornamentation is composed of small tubercles aligned longitudinally and an enameled carina is sometimes preserved on the anterior edge, which is a diagnostic character of the species. Unfortunately, hooks on the posterior wall are not preserved. The stratigraphic range of *Nemacanthus monilifer* extends from the Norian to the Rhaetian (CUNY 1995 b). As noted for a long time (SAUVAGE 1907, PRIEM 1908), fin spines of *Nemacanthus monilifer* are usually associated with teeth of *Hybodus minor*. The holotype of *Hybodus minor* is however a dorsal fin spine (AGASSIZ 1837, pl. 8 b, figs. 2, 3), held in the Bristol City Museum (BRSMG C 4583), which possesses all the characteristics of a hybodont fin spine: convex posterior wall and central canal situated in the middle of the spine. However, teeth referred to as *Hybodus minor* clearly belong to a neoselachian shark (see above) as it may be the case for the fin spine of *Nemacanthus monilifer* (CAPPETTA 1987, CUNY in press contra CUNY & RAMBOER 1991 and CUNY 1995 a). The only locality in the European Upper Triassic where fin spines of

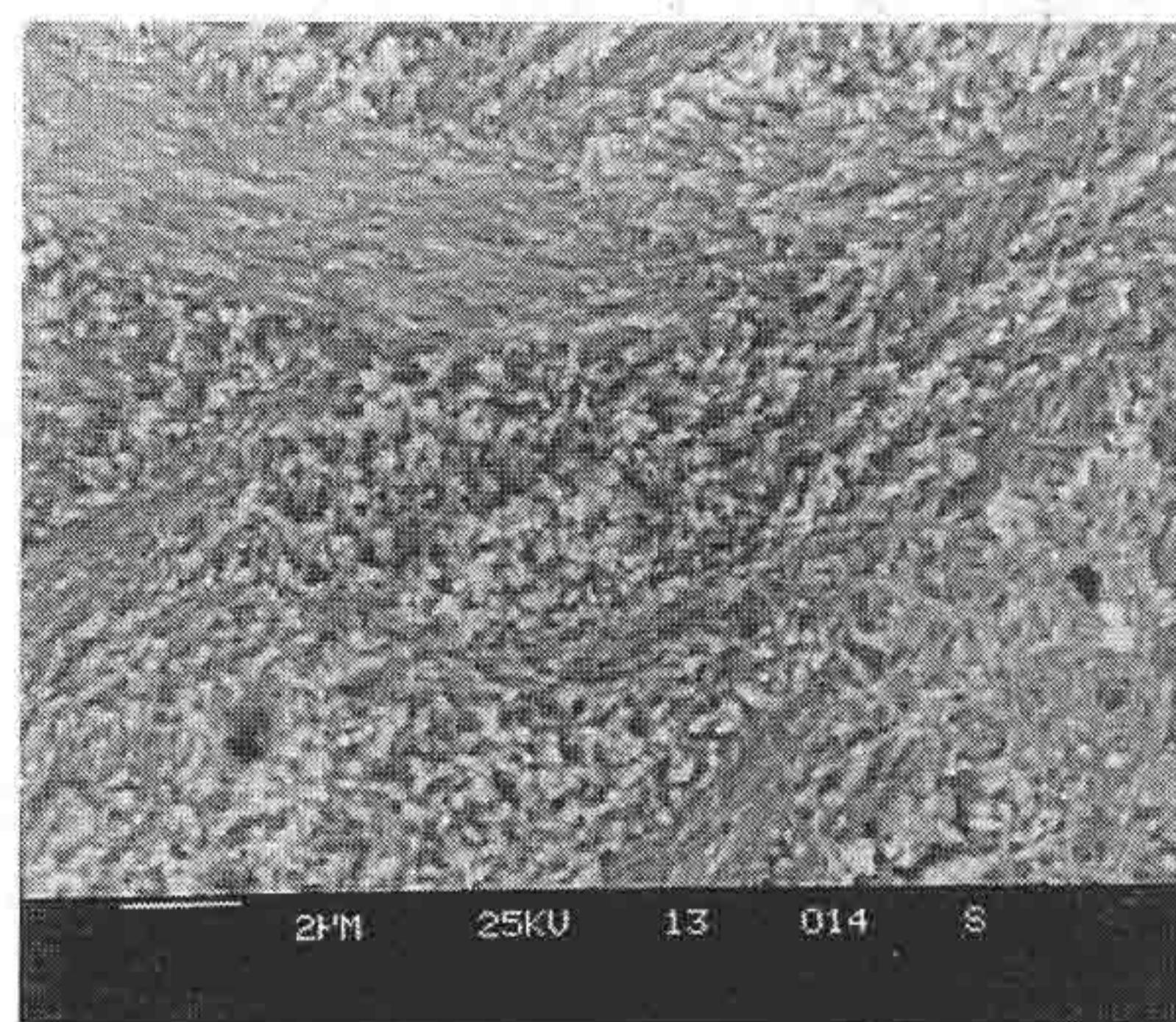
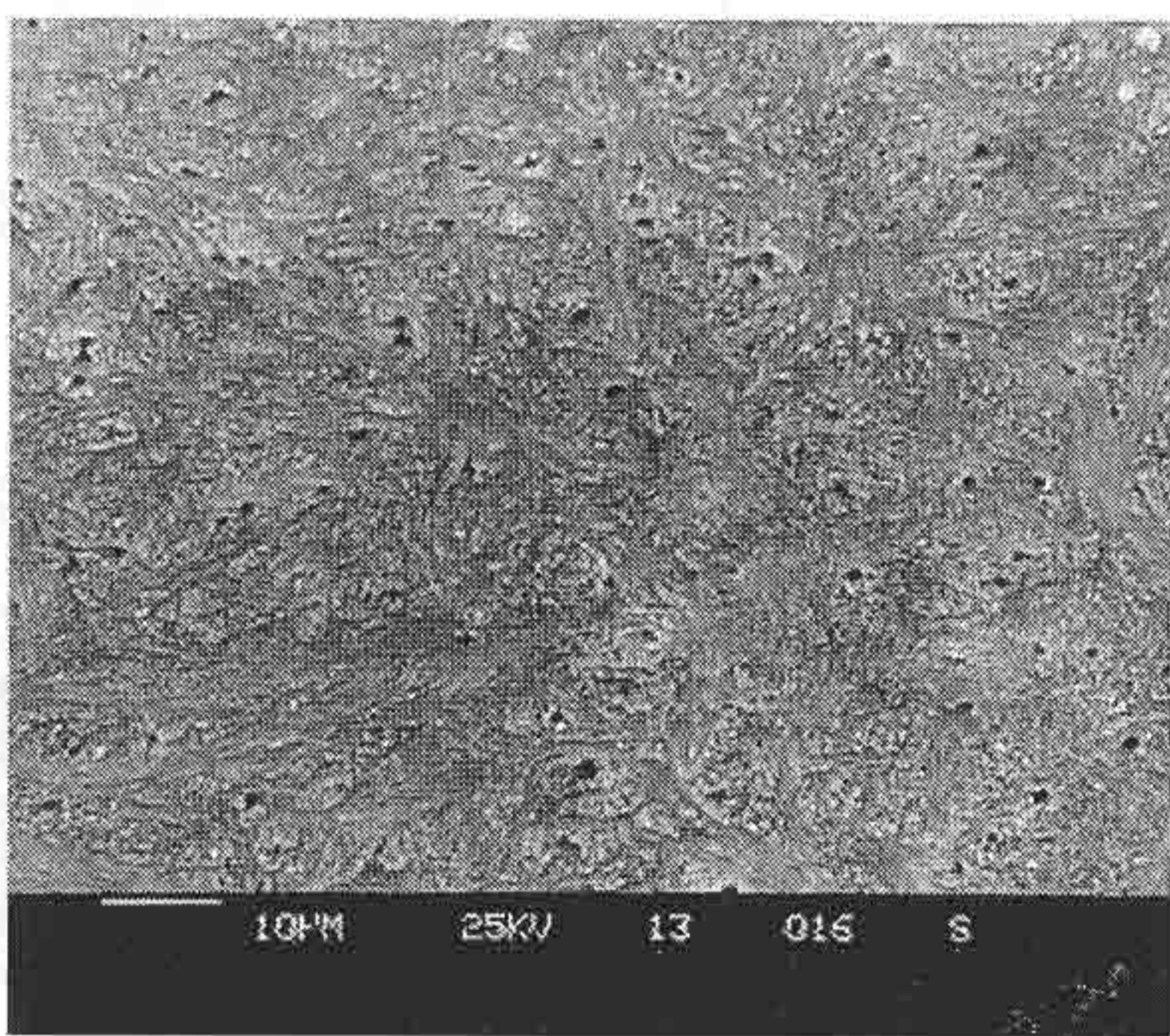
Fig. 6. Ultrastructure of the enameloid of the teeth of ?*Paralepidotus* or ?*Heterolepidotus* and "*Hybodus*" *minor* from the Upper Triassic of Syren (Luxemburg), and of *Paralepidotus ornatus* from the Norian of Lombardy (Italy).

1: ?*Paralepidotus* or ?*Heterolepidotus*, external layer of randomly oriented single crystals of apatite, tooth etched 2 min. in 10 % HCl. 2: *Paralepidotus ornatus* from Lombardy, tooth etched 30 sec. in 10 % HCl. 3 & 4: ?*Paralepidotus* or ?*Heterolepidotus*, internal layer with a criss-crossed structure, tooth etched 2.5 min in 5 % HCl. + 5 min. in 10 % HCl. 5: *Paralepidotus ornatus* from Lombardy, inner layer, tooth etched 9.5 min. in 10 % HCl. 6: "*Hybodus*" *minor*, shiny layered enameloid, tooth etched 10 sec. in 10 % HCl.



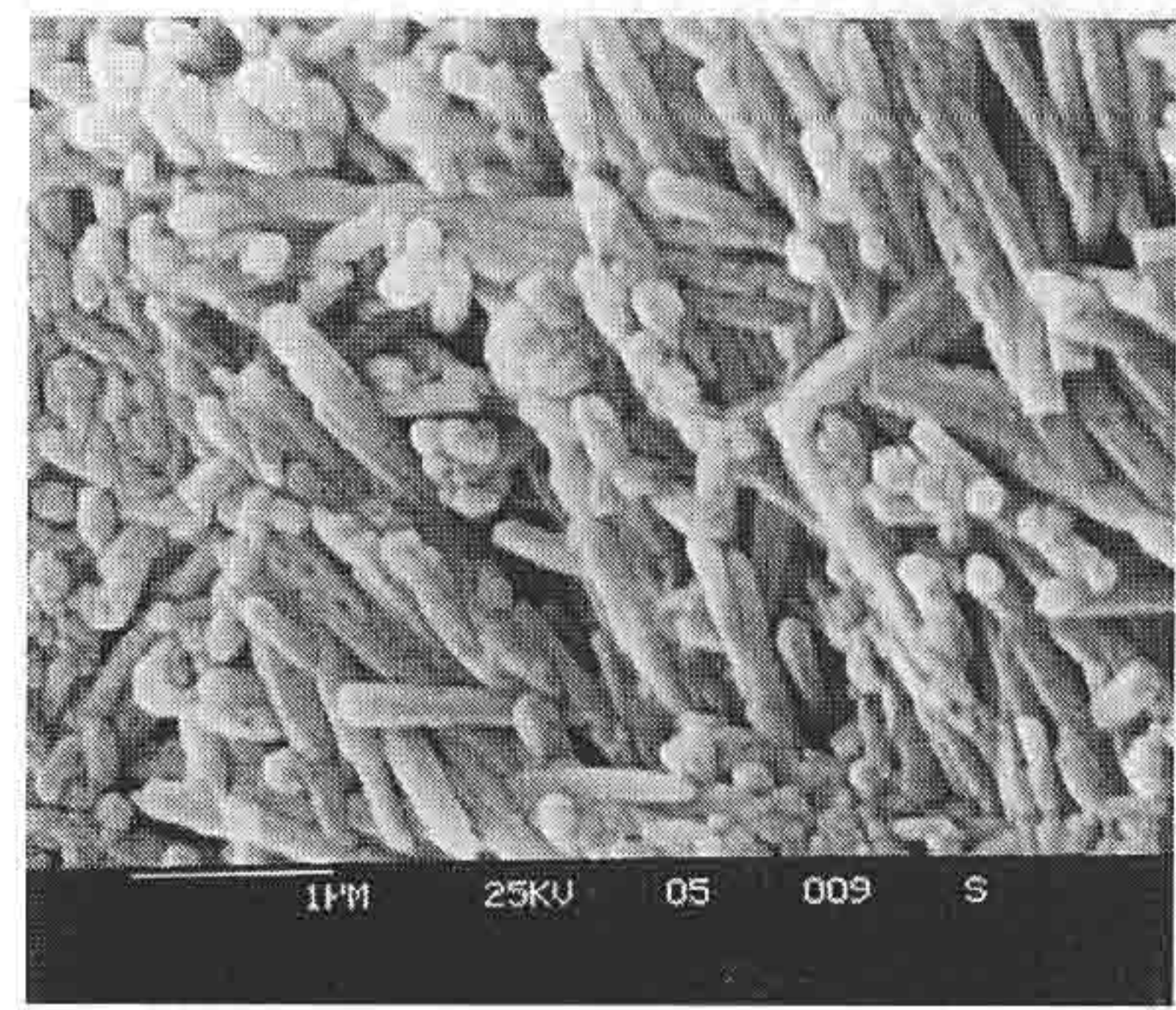
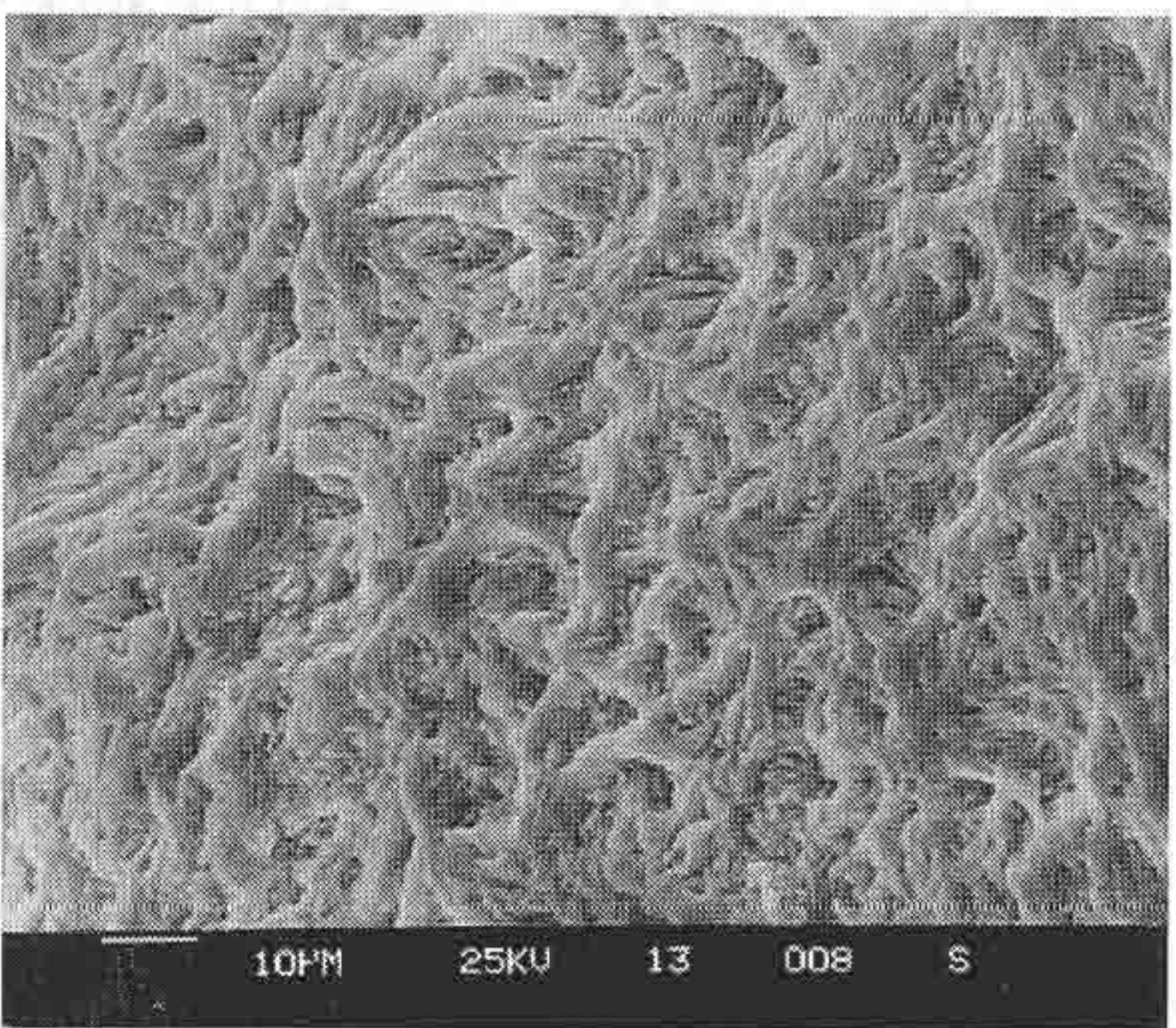
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2



3

4



5

6

Fig. 6 (Legend see p. 316)

Nemacanthus monilifer are not found in association with teeth of *Hybodus minor* is Saint-Nicolas-de-Port. They are found there in association with *Rhomphaiodon nicolensis*. However, teeth of *Rhomphaiodon nicolensis* show a morphology very similar to those of *Hybodus minor* but were recognized as a separate genus mainly on the basis of the enameloid ultrastructure (DUFFIN 1993b). It is now known that *Hybodus minor* also possesses a triple-layered enameloid (see above) and so the presence of *Hybodus minor* at Saint-Nicolas-de-Port is not impossible and has to be checked as soon as possible. Consequently, if the association of the teeth of *Hybodus minor* with the fin spines of *Nemacanthus monilifer* is confirmed on a systematic basis, all the material may be reported to *Nemacanthus monilifer*. *Hybodus minor* will therefore be considered as a *nomen dubium* as the holotype is a fin spine without any diagnostic characters.

Superorder Galeomorphii
 Order Lamniformes
 Family Cetorhinidae GILL, 1862
 Genus *Pseudocetorhinus* DUFFIN, 1998
Pseudocetorhinus pickfordi DUFFIN, 1998 (Fig. 4, 4)

Teeth attributable to *Pseudocetorhinus pickfordi* are very rare in the material discovered at Syren and the teeth are usually fragmentary. MNHNL ko180 is a nearly complete specimen although rather worn. Its crown is not perfectly symmetrical and formed by a single robust and thorn-like cusp. This cusp is curved lingually and inwards; it is not ornamented and does not bear cutting edges. Its labial base is slightly inflated. The lateral margins of the crown produce small lateral flanges, whose labial side is distinctly more convex than the lingual one. The crown/root junction is smooth. The labial side of

Fig. 7. Teeth of *Synechodus rhaeticus* DUFFIN, 1981 and of Actinopterygii from the Upper Triassic of Syren (Luxembourg).

1: *Synechodus rhaeticus* DUFFIN, 1981 (MNHNL ko181), X14. A: labial view; B: occlusal view. 2: "Birgeria" type of tooth (MNHNL ko182), X10. 3: "Gyrolepis" subtype 1 type of tooth (MNHNL ko183), X21. 4: "Gyrolepis" subtype 2 type of tooth (MNHNL ko184), X9. 5: ?*Paralepidotus* or ?*Heterolepidotus* (MNHNL ko185), X28. 6: ?*Dapedium* (MNHNL ko154), X80. 7: ?*Dapedium* (MNHNL ko155), X40. 8: *Sargodon tomicus* PLIENINGER, 1847 (MNHNL ko188), X9. Lingual view. 9: *Sargodon tomicus* PLIENINGER, 1847 (MNHNL ko188), X16.

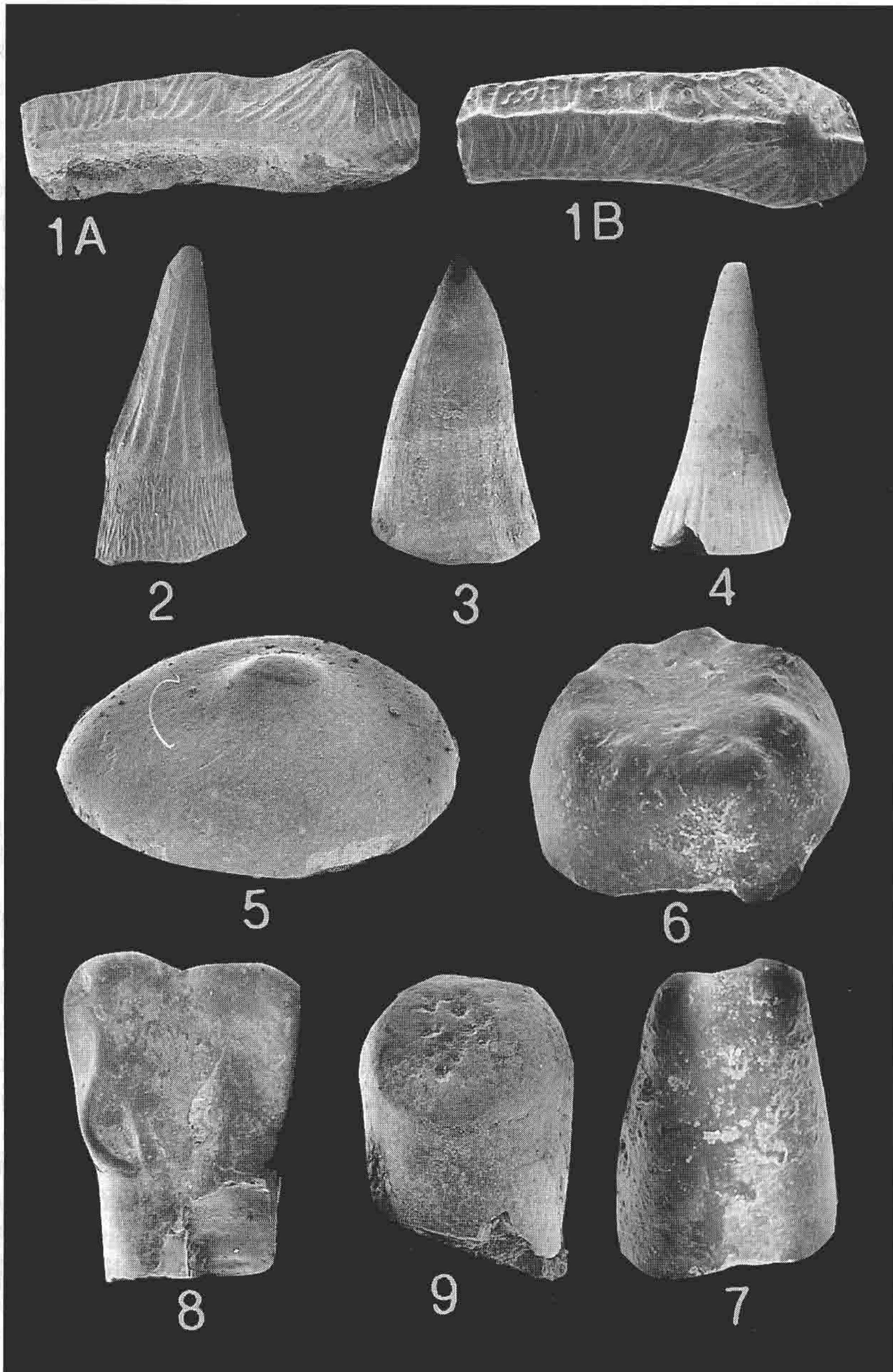


Fig. 7 (Legend see p. 318)

the root is punctuated by small lateral foramina; the root projects lingually from the crown's underside. The vascularization seems anaulacorhize. The slight asymmetry of the crown, curved cusp, lingual projection of the cusp and absence of ornamentation suggest that this specimen is a lateral tooth and not a posterior one. A recent study of the enameloid ultrastructure of some teeth from Habay-la-Vieille (Rhaetian, Belgium), carried out by one of us (G.C.), has revealed a triple-layered enameloid, which corroborates the neoselachian affinities of this species as discussed by DUFFIN (1998).

As far as we know, this taxon appears to be limited to the Rhaetian (DUFFIN, 1998).

Order	Synechodontiformes
Family	Palaeospinacidae REAGAN, 1906
Genus	<i>Synechodus</i> WOODWARD, 1888
	<i>Synechodus rhaeticus</i> DUFFIN, 1981 (Fig. 7, 1)

MNHNL ko 181 is a fragmentary dental crown which appears extremely elongated, low and narrow. The central cusp is relatively robust, but very low; its base is diamond-shaped. It is flanked on the preserved fragment by three mesial or distal faint lateral cusplets. A very strong median occlusal crest joins the apices of the cusps. Coarse vertical ridges ascend the cusps; they are coarser on the lingual side than on the labial one. They attain the cusp apices. The base of the crown is very worn on both sides; nevertheless, it seems that the labial ridges anastomose just above the crown shoulder to form a net of finer ridges. The lingual ridges unite labially to form a mesio-distal ridge, running along the full length of the preserved fragment of the crown.

Because of its elongated aspect and of its very low cusps, MNHNL ko 181 closely resembles the posterolateral teeth of "*Polyacrodus fissurae*" described by DUFFIN (1980: 86) in his unpublished Ph. D. thesis, from the Rhaetian of Holwell. DUFFIN (1981) subsequently described *Synechodus rhaeticus*, from fin spines discovered in Aust Cliff and Holwell. Based on correspondence with DUFFIN, DELSATE & LEPAGE (1991) refer teeth from Habay-la-Vieille to as *Synechodus rhaeticus*. These teeth correspond also to the posterior teeth of "*Polyacrodus fissurae*" as described in DUFFIN's thesis. Unfortunately, the situation remains unclear, as no formal description nor discussion of these teeth is currently available in published literature. Waiting for further evidence, it has been decided to refer temporarily MNHNL 181 to as *Synechodus rhaeticus* DUFFIN, 1981. In the current state of our knowledge, *Synechodus rhaeticus* (including "*Polyacrodus fissurae*" teeth) has only been found in Rhaetian localities (DUFFIN 1980, 1981, DELSATE & LEPAGE 1991).

Class	Osteichthyes
Subclass	Actinopterygii
Infraclass	Actinopteri

“*Birgeria*” type of teeth (Fig. 7, 2)

They are conical and upright teeth, measuring up to 8 mm in height. The enameloid apical cap is very high, extending up to two thirds of the height of the tooth, and is ornamented by rather prominent ridges which can attain the apex. A carina may be present. The shaft of the tooth is also coarsely ornamented by a net of small anastomosed ridges. The tooth is often slightly labio-lingually compressed and distolingually curved. Similar teeth are reported in Ladinian to Rhaetian rocks (DUFFIN & DELSATE 1993).

“*Gyrolepis*” types of teeth:

Subtype 1 (Fig. 7, 3):

These teeth are less numerous than the preceding ones in the fossil material discovered at Syren. These are upright conical teeth measuring up to 7 mm high. The acrodine apical cap is proportionally small and is never ornamented. The shaft of the tooth is often coarsely striated basally. The cross-section of the tooth is always nearly circular, but the tooth often shows a sigmoid curvature. Such teeth have been wrongly referred to as “*Saurichthys*” type of teeth by CUNY (1993, pl.6, fig. E) and CUNY et al. (1994, pl. 2, fig. G). They differ from typical “*Saurichthys*” type (see SYKES et al. 1970, pl. 16, fig. 2 & 3, DUFFIN & DELSATE 1993, pl. 4, fig. 3) by a weaker ornamentation of the shaft, which never attains the acrodine cap. These teeth are rather similar to typical “*Gyrolepis*” type of teeth, here denominated subtype 2, differing mainly by the presence of ridges at the base of the crown and by a larger average size. They probably belong to the same animal, reflecting some heterodonty in the dentition.

Subtype 2 (Fig. 7, 4):

These teeth are also upright, conical and circular in cross-section; they are covered by a small unornamented acrodine cap. They may be slightly curved lingually, but show no labio-lingual flattening. They differ from the teeth of subtype 1 in being distinctly bell-shaped basally. The pulp cavity is consequently much wider basally. The shaft ends at a greater distance from the acrodine cap. Similar teeth are known from the Anisian to the Rhaetian (DUFFIN & DELSATE 1993).

Superdivision Neopterygii

Division Halecostomi

Genera ?*Paralepidotus* and/or ?*Heterolepidotus* (Fig. 7, 5)

Some teeth are circular in outline and show a distinct "wart" in the middle of the occlusal surface. Only the acrodine cap, which is very low, is preserved in the material from Syren. A preliminary study of the enamelloid ultrastructure of some teeth reveals a homogeneous acrodine covering the whole tooth, and not a verruciform acrodine at the level of the "wart" only. This excludes that these teeth belong to a perleidiform. On the other hand, such a morphology is known among juvenile specimens of *Paralepidotus ornatus* (Semionotidae, TINTORI 1996) and in *Heterolepidotus dorsalis* (Caturidae, GORJANOVIC-KRAMBERGER 1905). The structure of the acrodine in juvenile *Paralepidotus ornatus* from Lombardy was studied by one of us (G.C.) for comparison purposes. It displays a very similar pattern to the one found in the teeth from Syren. Openings of canals are randomly distributed on the surface of the teeth and the external part of the acrodine is formed by a thin layer of randomly oriented single crystals of apatite (Fig. 6, 1-2). The average length of these crystals is 0.5 μm . The structure of this external acrodine is quite similar to the single crystallite enamelloid of the hybodont sharks. The inner part of the acrodine displays an irregular net of criss-cross bundles of fibres (Fig. 6, 3-5). This structure is similar to the irregular woven-textured acrodine as defined by ØRVIG (1978).

The bundles appear however better developed in the teeth from Lombardy, but the meaning of this difference is difficult to assess in our present state of knowledge. The irregular woven-textured acrodine is known in several genera (see ØRVIG 1978) and the external layer of randomly oriented crystals was also observed by one of us (G.C.) in *Sargodon tomicus* from the Rhaetic of Aust (England) and Saint-Germain-les-Arlay (France). Thus, the association of these two layers does not appear diagnostic of *Paralepidotus ornatus*. On the basis of the available data, both morphological and ultrastructural, it appears that there is no way to make the difference between isolated teeth of *Paralepidotus* and *Heterolepidotus*.

Paralepidotus is known from complete specimens in the middle and upper Norian of Austria and Lombardy, while *Heterolepidotus* is known from the Norian of Austria until the Upper Jurassic.

Family Semionotidae, WOODWARD, 1890

Genus *Sargodon* PLIENINGER, 1847*Sargodon tomicus* PLIENINGER, 1847 (Fig. 7, 8-9)

Teeth of *Sargodon tomicus* are abundant in the screened sediments from Syren. As usual, two types of teeth are present in the sample: incisiforms and

molariforms. The incisiform teeth measure up to 10 mm in height. They are formed by a long and straight shaft, with a narrow pulp cavity, and by a shovel-shaped enamelled crown. The labial side of the crown is inclined lingually, meeting the lingual side to form a strong occlusal crest; wear produces a deep V-shaped notch in the middle of the occlusal crest so that functional teeth appear bifid. The lingual side of the root often presents a deep wear surface, just below the crown/root junction. Some canals may be visible through the acrodine, so that the enameloid has a punctuated aspect. The crown of the molariform teeth is circular to oval in occlusal view. The occlusal surface is low, rounded and often worn at various points over its surface, forming in many cases flattened wear surfaces. The acrodine is characteristically punctuated by numerous small canals (ØRVIG 1978).

Teeth of *Sargodon tomicus* are very abundant in Rhaetian localities everywhere in Europe. Complete specimens have been described from the middle and upper Norian of the Italian Lombardy Alps (TINTORI 1983). Teeth have also been recorded in the upper Muschelkalk (Ladinian) and Lettenkohle (Carnian) of Germany (DEECKE 1926).

Family Dapediidae VOGT, 1852
Genus ?*Dapedium*
 ?*Dapedium* sp. (Fig. 7, 6-7)

Two teeth display a peculiar morphology. MNHNL ko154 is almost circular in outline, measuring nearly 0.7 mm in diameter, and shows a ring of ten tubercles on its border. Only the apex of this tooth is preserved and it is therefore difficult to say if the whole tooth was rather high or low. MNHNL ko155 is quite high and its apex shows two tubercles, thus displaying a bifid appearance. An indentate aspect, as observed in MNHNL ko155, is common among many families of Pycnodontiformes (MUDROCH & THIES 1996, SAINT-SEINE 1949, WOODWARD 1895, 1916-19), but Late Triassic pycnodonts recorded so far (*Brembodus ridens* and *Gibbodon cenensis* in Lombardy, and *Eomesodon hoeferi* in Lombardy and Austria) apparently possess only smooth crushing teeth (TINTORI 1981, WOODWARD 1916-19). The genus *Dapedium* has a rather variable dentition and a few species have bifid or mammiliform apex (JAIN 1973, WENZ 1967, PATTERSON 1975, THIES 1988), which appear quite similar to the teeth reported here. However, the only Triassic *Dapedium* reported so far, *D. noricum*, has only styliform teeth with a single apex (TINTORI 1983). Related genera such as *Dandya*, *Hemicalypterus*, *Tetragonolepis* and *Paradapedium* apparently possess styliform teeth with a single apex (JAIN 1973, SCHAEFFER 1967, TINTORI 1983), while the anterior teeth of *Gibbodon cenensis* are bifid (LAMBERS 1992). The small size of MNHNL ko154 speaks for its attribution to *Dapedium* rather than to

a pycnodont in which crushing teeth are enlarged. However, size is not a definitive argument and we cannot rule out the pycnodont hypothesis until more complete teeth are found.

A tooth very similar to MNHNL ko154 was discovered by one of us (G.C.) in the Rhaetic at Aust (basal bonebed of the Westbury Formation, England). It differs from the one described here above by a more circular outline and a ring of only 7 tubercles. It is however slightly smaller, measuring 0.5 mm in diameter. Both indentate and bifid teeth very similar to the ones described in Syren have also been found by one of us (D.D.) in the Toarcian of Lorraine.

Class	Diapsida
Subclass	Archosauromorpha
Infraclass	Archosauria
Subdivision	Crurotarsi
Order	Phytosauria
Family	Phytosauridae MEYER, 1861
	Phytosauridae, gen. et sp. indet. (Fig. 8, 1)

MNHNL ko156-157 are strong and recurved teeth with a nearly circular cross-section. Their mesial and distal edges form a non-serrated carina. Their enamel is definitely fluted, the fluting disappearing towards the apex.

MNHNL ko158 is a strong and slightly mediolaterally compressed tooth with a blade-like outline in lateral view. It is slightly labio-lingually compressed. The labial side is distinctly more convex than the lingual side. The enamel is perfectly smooth. The mesial and distal edges form serrated (6 serrations per mm) carinae.

MNHNL ko159 is a very small, triangular and blade-like crown. Its base is nearly circular in cross-section and it progressively flattens towards the apex. The labial side is distinctly more convex than the lingual side, both mesio-distally and vertically. It bears well-developed mesial and distal carinae, which are symmetrically serrated. The serrations are dense (about 14 serrations per mm), small, regular and perpendicular to the carinae. The enamel is ornamented by smooth longitudinal ridges on both sides of the crown.

MNHNL ko160 differs from MNHNL ko159 in being distinctly recurved backwards.

MNHNL ko158-160 are reminiscent of the posterior teeth of heterodont Phytosauridae: the crown is blade-like and asymmetrical in lateral view, serrations are small and perpendicular to the carina. MNHNL ko156-157 perfectly fit with the description of the intermediate teeth of such a hetero-

dent phytosaur. Similar teeth have been abundantly discovered in the Upper Triassic of Saint-Nicolas-de-Port. BUFFETAUT & WOUTERS (1986) and CUNY & RAMBOER (1991) refer these teeth to the species *Rutiodon ruetimeyeri*. The attribution of the species *ruetimeyeri* to the genus *Rutiodon* is however incorrect (GODEFROIT & CUNY 1997) and the original generic name "*Angistorhinopsis*" has to be retained. Nevertheless, other species of Phytosauridae present a similar heterodonty, with the same tooth types differentiated along the dental series (see LONG & MURRY 1995, GODEFROIT & CUNY 1997). Waiting for further evidence on the dental morphology in heterodont phytosaurs, it has been decided to refer the specimens discovered in Syren, as well as those from Saint-Nicolas-de-Port, to as Phytosauridae, gen. et sp. indet.

Subdivision Ornithodira
Order Pterosauria
Family Eudimorphodontidae WELLNHOFER, 1978
Genus aff. *Eudimorphodon* (Fig. 8, 2)

In MNHNL ko 161, the base and the apex of the crown are broken. It is formed by a very high, triangular, straight and mediolaterally flattened main cusp. Its labial (?) side is convex, while its lingual (?) side is nearly flat. The enamel forms some irregular longitudinal ridges on both sides. Its anterior and posterior edges bear carinae. The main cusp bears three prominent triangular denticles, asymmetrically set on its edges.

This tooth closely resembles the enlarged maxillary teeth of the Late Triassic pterosaur *Eudimorphodon ranzii*: the most striking features are the asymmetrical distribution of the denticles along the edges of the main cusp and the enamel ornamented on both sides.

Superorder Dinosauria
Order Ornithischia
?Ornithischia, fam., gen. et sp. indet. (Fig. 8, 3)

Despite its incomplete dental crown, MNHNL ko 162 appears low, triangular in shape and not recurved. It is labio-lingually compressed and not perfectly symmetrical in occlusal view: one of the side is slightly more convex than the other. The mesial and distal cutting edges bear several prominent denticles: these are not perpendicular to the edge, but they are set at about 45°. The enamel appears perfectly smooth.

This tooth shows several of the dental apomorphic characters which distinguish, according to SERENO (1986) and HUNT & LUCAS (1994), the maxillary/dentary teeth of the primitive ornithischians: the crown is low, triangular in lateral view and asymmetrical, and it bears prominent denticles arranged at 45° to the edges of the crown. However, this specimen is too incomplete to allow a more precise identification. In most prosauropods, the crown is usually higher, the sides are symmetrical and the denticles are less prominent. Nevertheless, according to GAUFFRE (1993), teeth of prosauropods can sometimes be mistaken with those of primitive ornithischians. The posterior teeth of heterodont phytosaurs differ in their much smaller denticles, perpendicular to the edges.

Archosauria, fam., gen. et sp. indet. (Fig. 9, 1)

The crown of MNHNL ko 163 is caniniform, compressed laterally, slightly curved lingually and very compressed labio-lingually. Its labial side is convex mesio-distally, whereas its lingual side is nearly flat. The enamel is perfectly smooth on its labial side; on the lingual side, it forms a dense net of thin longitudinal ridges. The root is higher than the crown, elliptical in cross-section and slightly compressed labio-lingually. Its diameter slightly decreases towards its tip. It is not separated from the crown by a distinct neck.

This tooth is reminiscent of the anterior teeth of the early pterosaur *Eudimorphodon ranzii* (see WILD 1978, fig. 8). Nevertheless the crown is ornamented on both sides in the latter. The enamel appears, on the other hand, perfectly smooth in *Eudimorphodon rosenfeldi* (see DALLA VECCHIA 1995). Archosaurian teeth similar to MNHNL ko 163 are relatively frequent in the Lorraine-Luxembourg area: they have been previously described at Medernach (CUNY et al. 1995, fig. 8 h-j), Varangéville (GODEFROIT 1997, pl. 1, fig. 5) and Saint-Nicolas-de-Port (GODEFROIT & CUNY 1997, pl. 3e-f).

Fig. 8. Archosaurian teeth from the Upper Triassic of Syren (Luxembourg).

1: Phytosauridae, gen. et sp. indet. (MNHNL ko 159), X22. A: mesial or distal view; B: lingual view. 2: aff. *Eudimorphodon* (MNHNL ko 161), X25. A: lingual view; B: mesial or distal view. 3: ?Ornithischia, fam., gen. et sp. indet. (MNHNL ko 162), X38. A: occlusal view; B: lingual view.

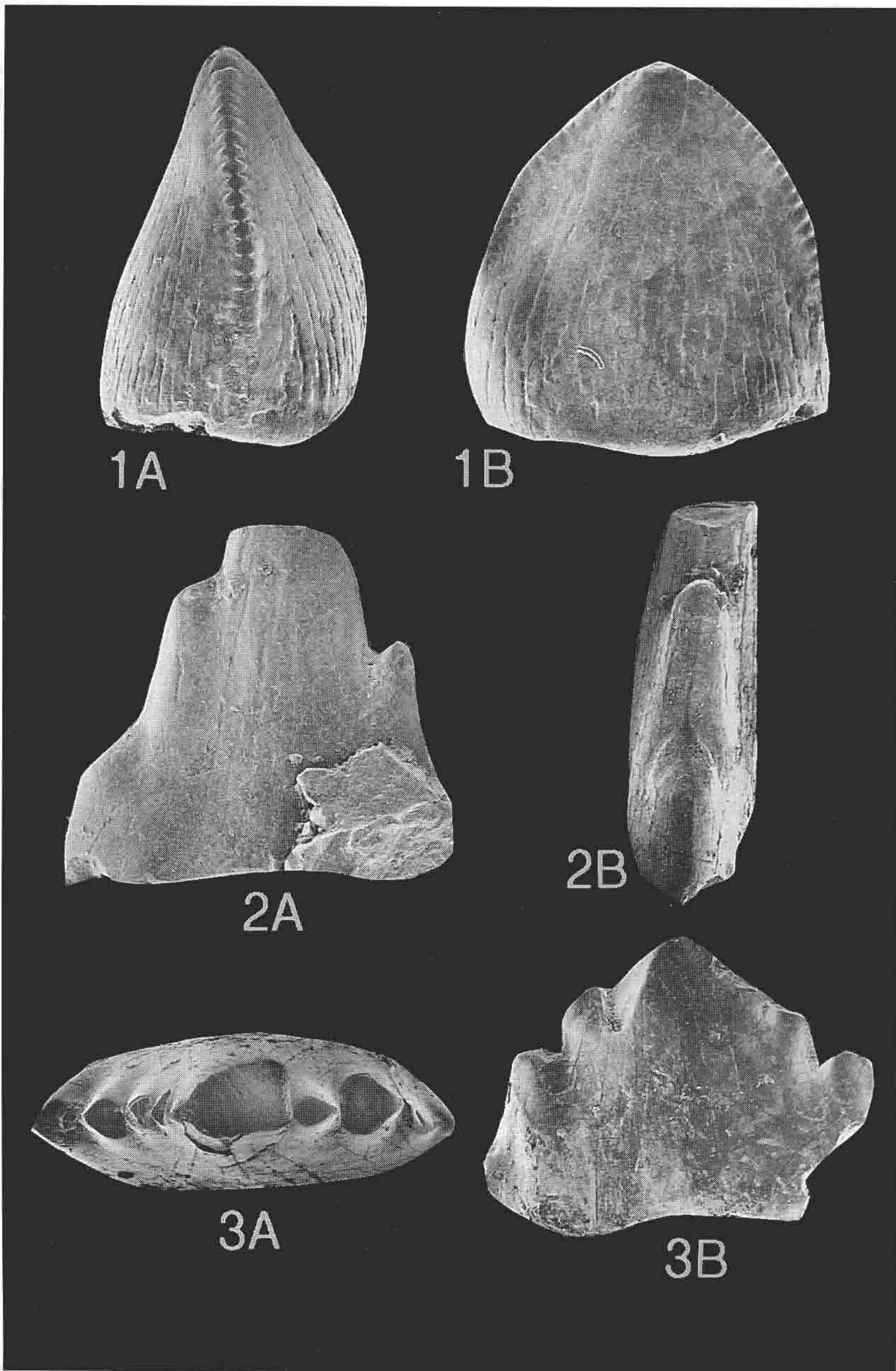


Fig. 8 (Legend see p. 326)

?Diapsida fam., gen. et sp. indet.

MNHNL ko189 is a high caniniform tooth. Its section is regularly elliptical: the two sides are labiolingually compressed and symmetrically slightly convex. The anterior edge is rounded, whereas the posterior one is sharper; both are not crenulated. The enamel is regularly fluted on both sides.

Class	Synapsida
Order	Therapsida
Infraorder	Cynodontia
Family	Dromatheriidae GILL, 1872
Genus	<i>Tricuspes</i> E. v. HUENE, 1933
	<i>Tricuspes sigoneauae</i> HAHN, HAHN & GODEFROIT, 1994 (Fig. 9, 2)

The crown of MNHNL ko164 (length = 1.42 mm; width = 0.8 mm; height = 1.1 mm) appears relatively stout in occlusal view. As to the orientation proposed by HAHN et al. (1994), its labial side is more convex than its lingual side. The crown is formed by three main cusps: these are not perfectly aligned mesio-distally, but rather arranged in a V-like manner: the mesial cusp B and the distal cusp C are more lingual in position than central cusp A. The cutting edge connecting these cusps is not very developed. The central cusp A is by far the highest and triangular in lateral view; cusps B and C are very bulbous, but C is distinctly better developed than B. The posterior wall of the crown bears a tiny bulbous cusp D at the base of the distolingual side of C. This accessory cusp is not incorporated into the cutting edge of the crown. A large triangular wear facet affects the labial side of the crown, extending from the posterior half of A to the anterior half of D and from the apex of A to the base of the crown. This indicates that this is a left lower molar, if the proposed orientation is correct. The roots are not preserved in this specimen.

This tooth closely resembles the molariform teeth of *Tricuspes sigoneauae*, from the Late Triassic of Saint-Nicolas-de-Port. In *Tricuspes tuebingensis*, an accessory cusp M is present on the distolingual side of the crown and cusp D is incorporated into the cutting edge. The crown of *Tricuspes tapeinodon* is distinctly lower and the accessory cusp D is also incorporated into the cutting edge.

Tricuspes tapeinodon GODEFROIT & BATTAIL, 1997 (Fig. 9, 3)

The crown of MNHNL ko165 (length = 2.5 mm; width = 0.4 mm; height > 1.4 mm) is very eroded, so that the apex of the cusps is not completely preserved. This tooth is tricuspid. In occlusal view, it is proportionally long

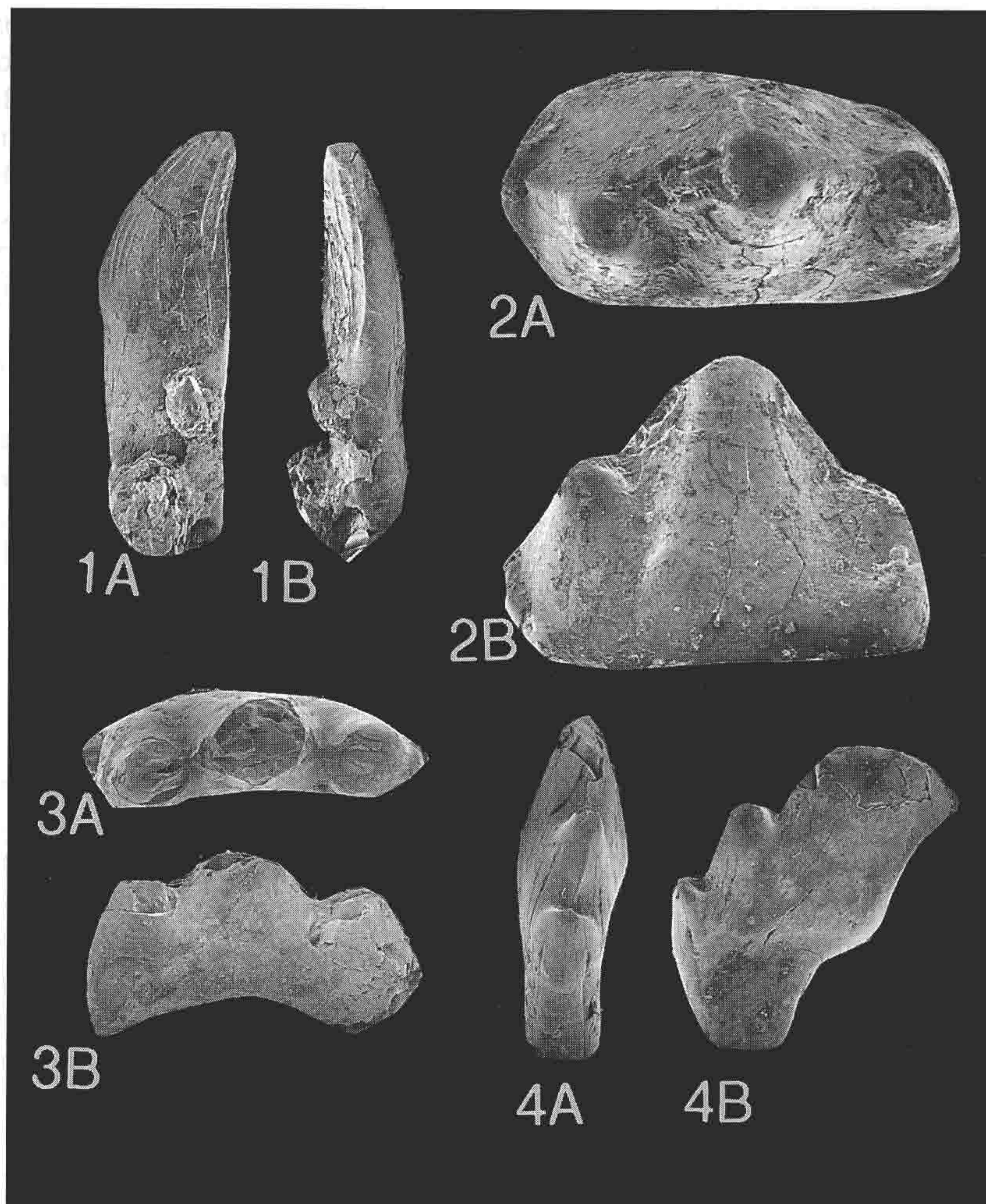


Fig. 9. Archosaurian and therapsid teeth from the Upper Triassic of Syren (Luxembourg).

1: Archosauria, fam., gen. et sp. indet. (MNHNL ko163), X22. **A:** lingual view; **B:** distal view. **2:** *Tricuspes sigogneauae* HAHN, HAHN & GODEFROIT, 1994 (MNHNL ko164), X34. **A:** occlusal view; **B:** lingual view. **3:** *Tricuspes tapeinodon* GODEFROIT & BATTAIL, 1997 (MNHNL ko165), X15. **A:** occlusal view; **B:** lingual view. **4:** aff. *Pseudotriconodon* (MNHNL ko166), X18. **A:** mesial or distal view; **B:** lingual or labial view.

and narrow. It has an arched aspect: the side regarded as labial is convex, while the opposite side is concave. The cusps are not perfectly aligned mesio-distally, but arranged in a V-like manner. The cutting edge joining the apex of the cusps is not very developed. In lingual view, the crown is very low: the central cusp is not much higher than the mesial and distal ones. The cusps are slightly inclined distally and they are well-separated from each other by deep notches. A tiny accessory cusp is present on the posterior end of the crown, being incorporated into the cutting edge. Wear facets cannot be discerned, because of the poor state of preservation of this specimen. So, it cannot be stated whether it belongs to the upper or lower tooth row. The root is not preserved.

Although badly preserved, this tooth closely resembles the molariforms of *Tricuspes tapeinodon* GODEFROIT & BATAIL, 1997: the crown is long, low and curved in occlusal view; the main central cusp is very low, not much higher than cusps B and C; there is no distolingual accessory cusp and the posterior accessory cusp is incorporated into the cutting edge.

Genus aff. *Pseudotriconodon* (Fig. 9, 4)

MNHNL ko166-171 are fragmentary teeth which, although incomplete, are reminiscent of the molariforms of the dromatheriid *Pseudotriconodon*. The crown is strictly sectorial, formed by a high central cusp, triangular in lateral view and flanked by one or two anterior and posterior cusps. The cusps are perfectly aligned antero-posteriorly and are distinctly separated from each other by deep notches. The crown is very compressed labio-lingually, with nearly parallel labial and lingual sides. The enamel is perfectly smooth, like in *Pseudotriconodon wildi* HAHN, LEPAGE & WOUTERS, 1984, but contrary to *Pseudotriconodon chatterjeei* LUCAS & OAKES, 1988, there is no trace of ornamentation. The root is not separated from the crown by an indentation. In MNHNL ko166 and ko167, which possess partially preserved roots, these look regularly semielliptical in outline, very compressed laterally and not very high.

Class	Mammalia
Order	Haramiyida
Family	Haramiyidae SIMPSON, 1947
Genus	<i>Thomasia</i> POCHE, 1908
	<i>Thomasia antiqua</i> (PLIENINGER, 1847) (Fig. 10, 1-2)

The fossil material discovered at Syren contains several haramiyid teeth. The orientation of molariform teeth proposed by SIGOGNEAU-RUSSELL (1989)

and BUTLER & MACINTYRE (1994) is followed in the present paper. This orientation, based on isolated teeth, has been recently confirmed by the discovery of more complete material from Greenland (JENKINS et al. 1997). Lower teeth ("*Thomasia*" ssp.) have a more or less mesially open basin, the row with the highest mesial cusp (row A) is lingual. In upper teeth ("*Haramiya*" ssp.), the enclosed end of the central basin is mesial and the row of three cusps (row A) is labial.

MNHNL ko172 (length = 2.2 mm; width = 1.3 mm) is a left lower molar ("*Thomasia* I" of SIGOGNEAU-RUSSELL 1989). In occlusal view, the crown is ovoid and mesio-distally elongated. The lingual row is formed by two cusps. The mesial cusp A1 is the largest and the highest; it is slightly inclined rearwards. Its lingual side is regularly convex mesio-distally, while its labial side is nearly flat. Its apex is very rounded. Its mesial side is well-rounded, whereas its distal side bears a low crest. Cusp A2 is half the height of A1. It is mesio-distally elongated and rather labio-lingually compressed. Its height regularly decreases distally. Its mesial and distal edges are rather acute. This cusp extends distally in a low and rounded crest, meeting cusp B4 and closing the distal end of the crown. The labial row is formed by four low and bulbous cusps. The height of these cusps regularly decreases distally. They are separated from each other by short furrows forming a small dimple at their labial end. Their labial side is slightly convex mesio-distally and nearly vertical; their lingual side is more angulous and more inclined inwards. B4 is lingually curved, meeting the distal lingual crest on the median axis of the crown. The median basin is narrow and mesio-distally elongated; it progressively deepens towards the distal end of the crown. It is bordered mesially by the inner side of A1 and B1 meeting in the midline and distally by the crest between A2 and B4. The mesio-internal sides of A1 and B1 delimit a small anterior basin closed by a very low mesial wall. A tiny cusp b is developed on the labial half of this wall. There is no trace of cingular element. The roots are completely broken. Attrition and abrasion are very slight on this molar, which appears very fresh.

MNHNL ko173 (length = 1.78 mm; width = 1.18 mm) is also a left lower molariform ("*Thomasia* I"). Although complete, the crown is very eroded. It is smaller and proportionally less elongated than MNHNL ko172. Row A is also composed by two cusps, A1 being the largest of the crown, and row B by four cusps of decreasing size. The central basin is extensively enlarged by the confluent attrition facets on the inner side of the cusps. Unfortunately, the bad state of preservation of the tooth prevents an accurate description of the occlusion pattern. Attrition facets are well-developed on the labial side of the apex of the B row cusps.

MNHNL ko174 fits with the description of the ?lower incisiforms in the Haramiyids from Saint-Nicolas-de-Port (see SIGOGNEAU-RUSSELL 1989, figs. 65-66). The crown is slender, lanceolate and curved inwards. The labial side is very convex, nearly angulous; the lingual side is formed by a median longitudinal ridge symmetrically bordered by lateral furrows. The mesial and distal edges, separating the labial and lingual borders, are not perfectly symmetrical: one is slightly convex, whereas the other is concave. Both edges join each other at the base of the lingual side, but do not form a basal denticle.

From a morphometrical point of view, MNHNL ko172 and ko173 are comparable to the molariforms referred to as "*Thomasia* I" from Saint-Nicolas-de-Port. They can therefore be referred to as *Thomasia antiqua* (PLIENINGER 1847) sensu BUTLER & MACINTYRE 1994.

Subclass	Eotheria
Family	Morganucodontidae KÖHNE, 1958
	Morganucodontidae, gen. et sp. indet. (Fig. 10, 3)

MNHNL ko175 is the distal portion of a right upper molariform tooth as attested by the presence of both labial and lingual cingula. Unfortunately, the crown is very eroded, so that very few characters can be observed. It shows the typical pattern of a Morganucodontidae: the cusps seem nearly perfectly antero-posteriorly aligned, with cusp A being the largest. The crown is antero-posteriorly elongated and very low. The enamel is smooth. Cusp A appears rather bulbous and triangular in lateral view; its labial side is more convex than its lingual side; both its anterior and posterior edges are rather acute. Cusp C is separated from A by a deeply incised valley. Cusp D was probably prominent on the posterior corner of the crown. The lingual cingulum, although very faint and eroded, is continuous from the posterior corner of the crown to the anterior end of the preserved fragment. At the other end, the labial cingulum seems interrupted at the level of cusp A.

Fig. 10. Mammal teeth from the Upper Triassic of Syren (Luxembourg).

1: Haramiyid ?lower incisiform (MNHNL ko174), X35. **A:** lingual view; **B:** mesial or distal view. **2:** *Thomasia antiqua* (PLIENINGER, 1847), left lower molariform (MNHNL ko172), X18. **A:** occlusal view, **B:** labial view; **C:** lingual view. **3:** Morganucodontidae, gen. et sp. indet., right upper molariform (MNHNL ko175), X28. **A:** occlusal view; **B:** lingual view; **C:** labial view. **4:** *Kuehneotherium* sp. nov., left lower molariform (MNHNL ko176), X36. **A:** occlusal view; **B:** lingual view.

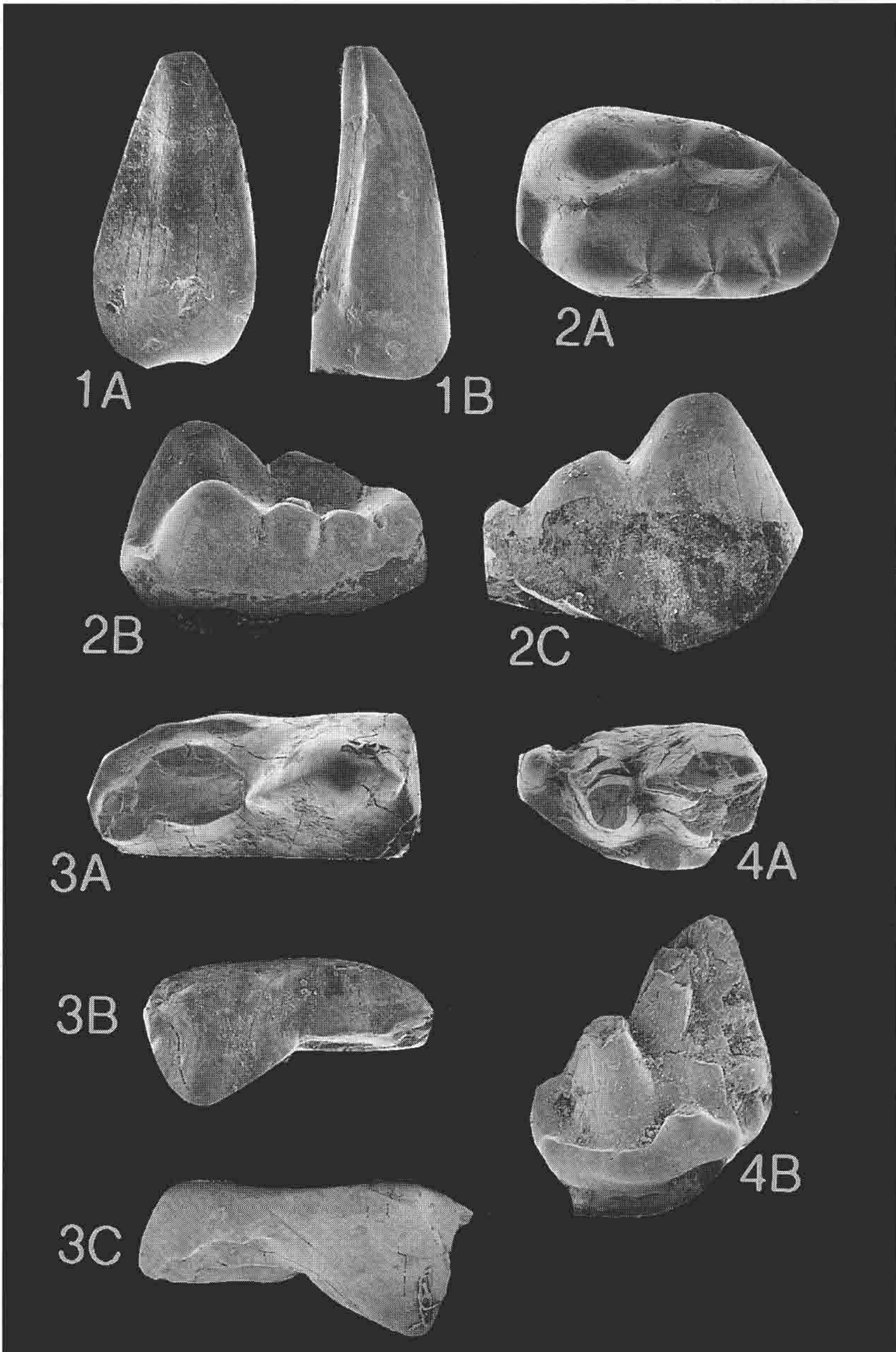


Fig. 10 (Legend see p. 332)

This specimen is too fragmentary and too eroded to allow a more precise identification at the generic level. Nevertheless, it significantly differs from the upper molariforms of *Brachyzostrodon* in its perfectly smooth enamel and in its well-developed cusp D.

Subclass	Theria
Order	Symmetrodonta
Family	Kuehneotheriidae KERMACK, KERMACK & MUSSETT, 1968
Genus	<i>Kuehneotherium</i> KERMACK, KERMACK & MUSSETT, 1968 <i>Kuehneotherium</i> sp. nov. (Fig. 10, 4)

MNHNL ko176 is the distal part of a left lower molariform tooth. The apex and the lingual side of the protoconid are broken. Nevertheless, this cusp appears relatively broad and high, dominating the crown. The metaconid is conical in shape and set in a more lingual position than the protoconid. The protocristid is sharp, but not angulous. The talonid is restricted to a small hypoconulid. The labial side of the crown is regularly antero-posteriorly convex. The posterior part of the lingual cingulum is prominent; it bears, at the base of the protoconid, a salient "kuehneocone". The roots are broken, but appear to be separated along their full height.

This specimen closely resembles the lower molars of *Kuehneotherium*, originally described from the Lower Lias of Wales (KERMACK et al. 1968, MILLS 1971): the crown is elevated and relatively slender, the metaconid is set slightly lingually to the protoconid, the protocristid is not angulous and is restricted to a small hypoconulid, and the lingual cingulid is rather prominent. Nevertheless, the lingual cingulum never develops a median "kuehneocone" in *Kuehneotherium praecursoris* KERMACK, KERMACK & MUSSETT, 1968, from Pontalun, as also in the numerous specimens from Pant. On the other hand, numerous *Kuehneotherium* lower molariform teeth discovered in the Upper Triassic of Saint-Nicolas-de-Port bear a prominent "kuehneocone" (GODEFROIT et al. in preparation): this character is not constant, but indicates that these teeth probably belong to a different species than the Welsh specimens.

Discussion

This fauna is dominated by a marine component, with a typical Rhaetian facies association (*Hybodus cloacinus* + *Lissodus minimus* + ("Hybodus" *minor* + *Nemacanthus monilifer*) + *Pseudocetorhinus pickfordi* + *Synechodus rhaeticus* + *Sargodon tomicus*). The species *Lissodus lepagei*, thought to be restricted to the Norian, is recorded in the Rhaetian for the first time. The

study of the enameloid ultrastructure of some shark teeth demonstrates the importance of the neoselachian component of this assemblage ((*Hybodus* minor + *Nemacanthus monilifer*) + *Pseudocetorhinus pickfordi* + *Synechodus rhaeticus*), but the most common species of sharks remains the hybodont *Lissodus minimus*. Among the Osteichthyes, the teeth of "*Birgeria*" and "*Gyrolepis*" types are abundant, but the exact relationships of these fishes cannot be ascertained on the basis of isolated teeth. Likewise, crushing teeth with a central "wart" are difficult to ascribe to a precise taxon (?*Paralepidotus* or ?*Heterolepidotus*) and the presence of *Dapedium*, although probable, cannot be ascertained. The only Osteichthyes which is recognized with an acceptable degree of certainty is the Semionotidae *Sargodon tomicus*. The composition of the bony fishes assemblage remains therefore badly known. Table 1 shows that this marine-related assemblage is very similar to the one found in other "Rhaetian" sites from the Lorraine area or the British Rhaetian (STORRS 1994). The reptile fauna is quite diverse with a phytosaur, a pterosaur, a possible ornithischian dinosaur and a small carnivorous archosaur, but represented by a few teeth. Cynodonts (*Tricuspes sigogneauae*, *T. tapeinodon* and aff. *Pseudotriciconodon*) and mammals (*Thomasia antiqua*, Morganucodontidae indet. and *Kuehneotherium* sp. nov.) are well-represented and diversified as usual in the Lorraine area (GODEFROIT & SIGOGNEAU-RUSSELL 1995, DELSATE 1995, GODEFROIT 1997) and this new site highlights the importance of the whole area for the understanding of mammalian early radiation. All the terrestrial components of this fauna are represented within the site of Saint-Nicolas-de-Port (see CUNY 1995c, GODEFROIT & CUNY 1997) and most of them, except the ornithischian dinosaur, *Thomasia* and *Kuehneotherium*, are also present, at least at a generic level, in the older site of Medernach (see CUNY et al. 1995). This indicates that these faunas, contrary to the more marine ones, show little variation throughout the Rhaetian transgression. Indeed, these remains all belong to small animals, not exceeding one meter in overall length, which probably did not suffer from the Rhaetian transgression-induced diminution of the surface of the emerged land. Moreover, the separation of several populations between different islands may have facilitated the radiation of the mammalian faunas which occurred at the end of the Triassic in Europe.

Acknowledgements

The authors thank the authorities of Weyler-la-Tour who provided facilities for excavations at Syren. A. TINTORI (University of Milano) kindly provided teeth of *Paralepidotus ornatus* for comparison with the teeth from Syren. Works of P. G. are funded by a FRFC grant, those of G. C., by a MARIE CURIE Fellowship

ERBFMBICT950059 and NERC grant GR3/11124, and those of D.D., by a Luxembourg Ministry of Culture Grant. SEM photographs by J. CILLIS (IRSNB) and S. POWELL (University of Bristol). C. HERZÉ (IRSNB) kindly improved the linguistic aspect of the manuscript.

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Received April 23, 1998.

Accepted by the Tübingen editors June 2, 1998.

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