

A new neoselachian shark from the Upper Triassic of Grozon (Jura, France)

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Abstract – Two successive assemblages of vertebrate microremains have been found at Grozon (Jura, northeastern France). Palynological analysis confirms a Norian age for the first one and a Rhaetian age for the second. A new species of neoselachian shark, *Grozonodon candaui*, is erected from isolated teeth of Norian age, based on their enameloid ultrastructure. Distinctive parallel-fibred enameloid is recognized among teeth previously assigned to *Hybodus minor*, which therefore represents another early neoselachian shark. These structural characteristics confirm the close relationship of hybodont and neoselachian sharks.

1. Introduction

The site of Grozon is located 3.5 km north of the town of Poligny (Jura, Fig. 1) and was visited briefly by two of us (GC and JMM) in 1992 and 1994. It is a small disused quarry, belonging to the society Platrières de Grozon. This locality was cited more than a century ago by Henry (1876, p. 381), who described from it bones belonging to a possible prosauropod dinosaur. Nowadays, only a thin bed of green sandy marl (GR3) in the Marnes de Châlins Formation (Norian) and a bed of foliated black marl (GR4) from the Rhaetian yield vertebrate remains. However, Henry (1876) gave no precise position of his locality, and it is unclear if the quarry described here is the same as Henry's.

Abbreviations used in the text are as follows: BRSUG – University of Bristol, Department of Geology. SMNS – Staatliches Museum für Naturkunde, Stuttgart. GSC – Geological Survey of Canada, Ottawa.

2. Geological setting

On the east side of the quarry, there is a good section of the Marnes de Châlins Formation. It is characterized by typical facies of variegated, purple, green and grey marls, which dip at 15° N. The marls are of uppermost Norian ages and have no equivalent in the Rhaetian (Kerrien, 1982). The horizon has previously yielded remains of the prosauropod dinosaur *Plateosaurus*, mainly near Poligny and at Lons-le-Saunier (Cuny & Mazin, 1993) (Fig. 1). In 1992, three

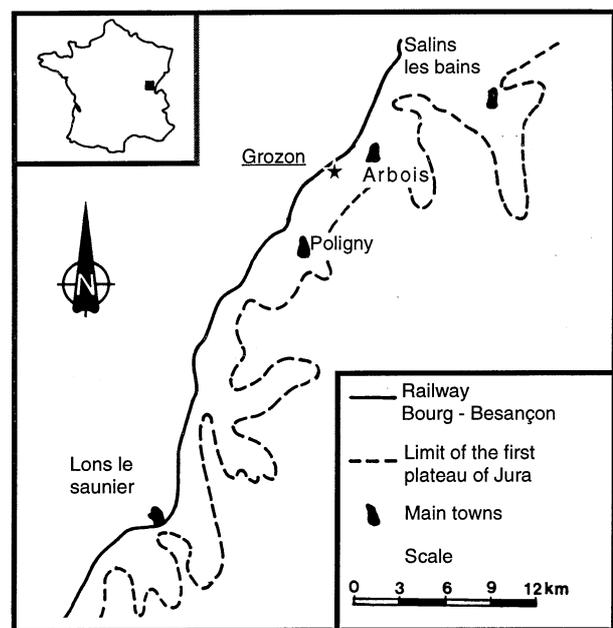
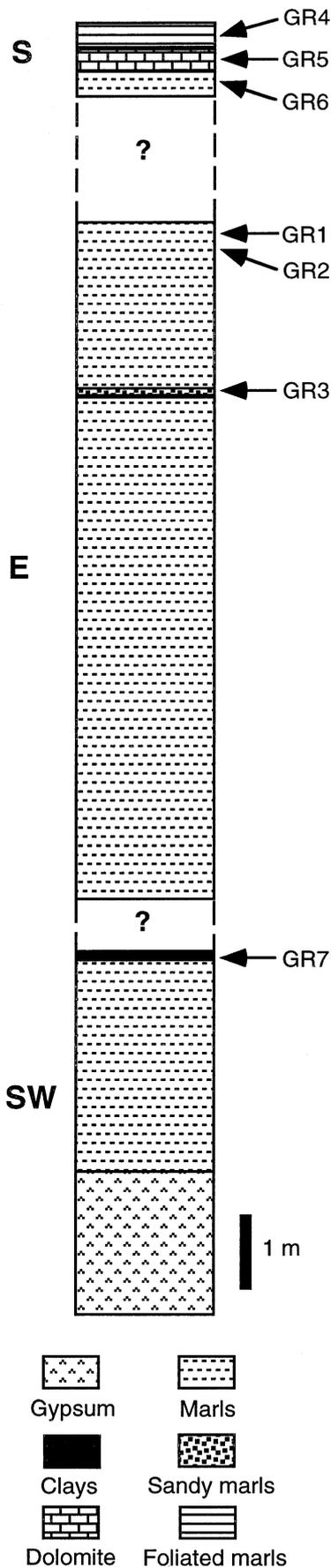


Figure 1. Location map of the site of Grozon.

samples were taken from the upper part of this exposure: GR1, GR2 and GR3 (Fig. 2). GR3 was sampled from an irregular 0.1-m-thick bed of green sandy marls which yielded some bone remains (maximum size 0.1 m), among them a tooth of a lungfish and some vertebrate microremains.

The Marnes de Châlins Formation also crops out on the southwest side of the quarry. At the top of the outcrop, there is a 0.1-m-thick bed of green clay from

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which sample GR7 was taken (Fig. 2). Beneath the Marnes de Châlines, there is a two-metre-thick gypsum bed.

On the south side of the quarry, there is a small Rhaetian outcrop from which samples were collected (Fig. 2). GR4, a bed of black foliated marls at the top, yielded some vertebrate microremains. GR5 was sampled from a 0.3-m-thick beige dolomite, containing thin clay inter-layers. Sample GR6 was collected from a layer of black marls.

The vegetation and the presence of occasional faults make correlation between the three sides of the quarry unclear.

3. Materials and methods

Palynological samples were processed in the Department of Palynology of the Geological Institute of Strasbourg (see Rauscher, Merzeraud & Schuler, 1992, for details). The sediment was disaggregated using hydrogen peroxide and vertebrate microremains were picked up under a binocular microscope from the fraction > 500 µm. In order to study the ultrastructure of the enameloid, some teeth were etched for between 30 and 90 seconds in 5% HCl. Photographs of the surface of the enameloid were taken between each treatment with a Cambridge Stereoscan 250 MK3 S.E.M., using an acceleration voltage of 25 kV to study the different layers. Although this method is destructive, it allows the study of the whole surface of the different layers of the enameloid.

4. Palynological analysis

Palynological analysis of the samples from Grozon was conducted by one of us (RR). Except for sample GR3, all of the samples yielded a palynoflora, although the assemblages are not diverse. The GR4 level is by far the richest of the studied levels and is the only one with a sufficiently high abundance to generate a meaningful count. The results are as follows:

- Spores: 0%
- Circumpolles: 59.34%
- Rhaetipollis*: 1.62%
- Bisaccate pollens: 0.81%
- Ovalipollis*: 4.10%
- Marine elements (dinocysts, acritarchs and tintinnids): 34.13%

Figure 2. Stratigraphic log of the Quarry of Grozon. Lower part of the log from the south west side of the quarry, middle part from the east side, and upper part from the south side. Question marks indicate faults and vegetation which do not allow precise correlation between the three sides of the quarry. Arrows indicate where the seven samples analysed in this paper come from.

The other palynofloras contain a low diversity, low abundance spore flora (including *Ricciisporites*), some marine algae (dinocysts and acritarchs) and elements in common with GR4, including *Circumpolles*, *Rhaetipollis* and *Ovalipollis*. Additionally, GR5 and GR6 yielded some foraminiferan test linings.

4.a. Discussion

This study fits well with similar studies conducted in Lorraine (east of the Parisian Basin, Rauscher *et al.* 1995). According to these authors, there are five succeeding palynological assemblages at the Triassic–Jurassic boundary. Their episode 1, the oldest, includes very poor assemblages with rare *Rhaetipollis germanicus* (Schulz 1967) Schuurman 1977 and *Ricciisporites tuberculatus* Lundblad 1954 and more common *Granuloperculatipollis rudis* Venkatachala & Goczan 1964 and *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976. This episode is characteristic of the boundary between the Marnes Irisées Supérieure (uppermost Keuper) and the Grès et Schistes à *Avicula contorta* (referred to here as GSAC, the ‘lower Rhaetian’ of most authors). Samples GR1, GR2 and GR7 belong to this episode. Episode 2 includes assemblages poor in spores and dominated by *Circumpolles* and marine palynomorphs. This is characteristic of the GSAC. Samples GR4, GR5 and GR6 belong to this episode. The only difference between typical assemblages from episode 2 in Lorraine and sample GR4 from Grozon is the complete absence of *Ricciisporites* from the latter. However, the presence of tintinnids in GR4 suggests a close correlation with level R36 of Lons-le-Saunier (located about 30 km south of Grozon, Fig. 1) and therefore falls within the upper half of the GSAC of the Jura area (Cuny, 1995a). Stages 3 to 5 are not recorded here. It can be concluded that the Marnes de Châlins is equivalent to the Marnes Irisées Supérieures of Lorraine and that the ‘lower Rhaetian’ of the Jura area is a southern extension of the GSAC of Lorraine. These correlations are further supported on sedimentological grounds.

Moreover, this confirms that palynomorphs usually considered as typical of the Rhaetian are present, although much less abundant, in the late Norian (Rauscher *et al.* 1995). However, since there is a very gradual transition between the Norian and Rhaetian palynofloras (Adloff & Doubinger, 1982, 1983; Rauscher *et al.* 1995), we should be cautious with the palynological definition of the Rhaetian, and its lower boundary remains difficult to define (Rauscher *et al.* 1995).

5. Systematic palaeontology

5.a. Vertebrates from the GR3 level

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Cohort EUSELACHII Hay, 1902

Superfamily HYBODONTIDAE Zangerl, 1981
Family POLYACRODONTIDAE Glückman, 1964
Genus *Lissodus* Brough, 1935
Lissodus lepagei Duffin, 1993a

Four teeth (BRSUG 26348), with no preserved root, were recovered from the fine fraction of the sediment. The main cusp of these teeth is low, diamond-shaped at its base, with a well-developed labial peg possessing a strong accessory cusplet. An occlusal crest runs the length of the crown through the apices of all cusps. A major vertical ridge forms a crest to the labial peg and ascends the main cusp. A similar ridge, but fainter, is present on the lingual side of the main cusp. Apart from these ridges, the enameloid of the crown appears smooth (Fig. 5b). The best preserved tooth from Grozon shows a pair of well-developed lateral cusplets, so the occlusal crest appears crenulated in labial view (Fig. 5a). Such characters distinguished these teeth from *Lissodus minimus*, a common species in the Rhaetian of this area (Cuny, 1995a; Cuny, Mazin & Rauscher, 1994) and fit well with the teeth of *Lissodus lepagei* from Medernach figured by Duffin (1993a).

The GR3 level also yielded three hybodontid dermal denticles with a rounded and knob-shaped crown (BRSUG 26347), ornamented by strong radial ridges, usually bifurcating once (Fig. 5c). There is no distinct neck separating the crown from the base, but one specimen shows a shallow constriction all around the base of the crown. The base is shallow, wider than the crown and almost circular in outline in basal view. The basal surface is flat, with some small randomly distributed foramina in one specimen. These dermal denticles belong to morphotype 1 of Thies (1995) or to type B as defined by Sykes, Cargill & Fryer (1970). According to Thies (1995), such a morphotype can be attributed either to *Hybodus* or to *Lissodus* but, in the absence of reports of *Hybodus* at Grozon, we refer these dermal denticles to *Lissodus lepagei*. It should be noted, however, that Hampe (1996) does not figure similar dermal denticles in his description of the dermal skeleton of *Lissodus* from the early Permian of Germany. Hence, our attribution is tentative, pending further study of the variation in shape of the dermal denticles of *Lissodus*.

Subcohort NEOSELACHII Compagno, 1977
Order, Superfamily and Family *incertae sedis*
Genus *Grozonodon* gen. nov.

Derivatio nominis. From Grozon, the type locality and odous (Greek), tooth.

Type species. *Grozonodon candau* sp. nov.

Diagnosis. Labiolingually compressed cusps with well-developed cutting edges and no (or very reduced) lateral cusplets. Crowns ornamented by ridges that do not reach the apex of the cusps. Triple layered enameloid, with a surface of shiny enameloid, a middle parallel

fibred enameloid and a basal tangled fibre enameloid which is less randomly oriented at the base of the crown than near the apex. In the parallel fibred enameloid, the fibres are perpendicular to the ridges ornamenting the crown in the lower part of the tooth. Root semi-circular in basal view and projecting lingually, perpendicular to the crown. Shallow labial root wall. Root vascularization anaulacorhize.

Grozonodon candaui sp. nov.

Holotype. BRSUG 26316 (one anterior tooth with one lateral cusplet preserved).

Paratypes. BRSUG 26317 (78 more or less complete teeth, among which BRSUG 26317-2 has been etched with 10% hydrochloric acid and not completely destroyed).

Derivatio nominis. In honour of Ms. Marianne Candau who participated voluntarily and enthusiastically for the five years of our palaeontological work in the Jura area.

Locus typicus. Quarry of 'Frétilles', 1500 m southeast of the village of Grozon (Jura, France), lat. 5°42'47"N, long. 46°52'44"E.

Stratum typicum. Upper part of the Marnes de Châlins, Norian, Upper Triassic.

Diagnosis. As for the genus *Grozonodon* gen. nov. (monospecific genus).

Description. These teeth (BRSUG 26316, 26317) show a labio-lingually compressed main cusp with two well-developed cutting edges, one mesial and one distal. Some cusps have a sigmoid curve in mesial and distal views while others just show a lingual recurvature (Fig. 3b, g). They are ornamented by ridges, well marked at the base of the crown but which generally do not reach the apex. The ridges are often more developed on the labial face than on the lingual one. In labial view, the crown is triangular, often with a wide base and overhangs the crown/root junction (Fig. 3a, f). The highest tooth of the sample (BRSUG 26316), 6 mm high, possesses one pair of very reduced lateral cusplets, less than one sixth the height of the main cusp (Fig. 3a, c). Unfortunately, there is just one cusplet preserved in this specimen. Most other teeth of the sample (BRSUG 26317) show no preserved lateral cusplets (Fig. 3f, g, h) and often are lingually inclined. They probably represent more posterior teeth. The root is semicircular in occlusal view, projecting lingually from the crown base (Fig. 3d). In mesial or distal view, it appears slightly concave, with a marked mesio-distal hollow in the labial part. In lingual view the root is generally penetrated by randomly distributed vascular foramina of varying size. In labial view, the root is shallow compared to the height of the crown.

Enameloid ultrastructure of the teeth. Three teeth were studied, of which only one has not been completely

destroyed. There are some thin apatite crystallites randomly oriented at the surface of the teeth, which could be evidence of a shiny enameloid (SLE). This shiny enameloid is best preserved on the cutting-edges of the teeth (Fig. 4d). Just below this there is a layer containing surface-parallel apatite fibre bundles running in a basal-apical direction (Fig. 4a). In the lower part of this layer, radial fibres exploit the interstices between the surface parallel fibres (Fig. 4b). The pattern of this parallel fibred enameloid (PFE) is very similar to that of '*Orthacodus*' (Reif, 1973, a junior synonym of *Sphenodus*, Cappetta, 1987; Duffin & Ward, 1993), *Hueneichthys costatus* (Reif, 1977) and *Rhomphaiodon nicolensis* (Duffin, 1993b). However, in *R. nicolensis*, the average diameter of the bundles is 7.5 µm compared to 2 µm in the above mentioned taxa, and in the teeth from Grozon. At the level of each ridge ornamenting the crown, the apatite fibre bundles change orientation, becoming perpendicular to the ridge (Fig. 4c). This is similar to the pattern illustrated in the cutting edges of *Paragaleus* by Reif (1973). This pattern could also be very similar to the one described in *Hueneichthys costatus* (Reif, 1977), although in the figure given (Reif, 1977, fig. 4) this is unclear because of the high percentage of radial fibres. Deeper in the enameloid, the fibres become more randomly oriented and correspond to a tangled fibred enameloid (TFE, Fig. 4e). At the base of the tooth (Fig. 4f), however, the pattern appears less chaotic than in that illustrated by Reif (1973, fig. 3). This pattern appears to be linked more particularly to the ridges ornamenting the crown. At the apex of the tooth, the tangled fibred enameloid has the same appearance as that illustrated by Reif (1973, fig. 3).

The enameloid of the teeth from Grozon therefore appears triple layered as is typical in neoselachian sharks (Reif, 1973, 1977; Duffin, 1980, 1993b; Thies, 1982).

'Hybodus' minor Agassiz, 1837

These teeth (BRSUG 26318) appear quite small, less than 3 mm high, and are often poorly preserved. Their main cusps are almost circular at the base, have blunt cutting edges and are flanked by one or two pairs of well-developed lateral cusplets (Fig. 3i, k). The crowns are ornamented by strong ridges, which are well marked at the base of the cusps but which generally do not reach the apex. In labial view, the crowns are triangular, often with a wide base. The roots are semicircular in occlusal view, projecting lingually from the crown base (Fig. 3j). In mesial or distal view, their bases appear slightly concave. In lingual view the roots are generally penetrated by randomly distributed vascular foramina of varying size. In labial view, the roots are shallow compared to the height of the crowns. These fit well with the teeth described as *Hybodus minor* by Duffin (1993a). However, one of us (GC) observed a typical PFE layer (Fig. 4g) as well as a shiny layered enameloid (Fig. 4h) in these specimens

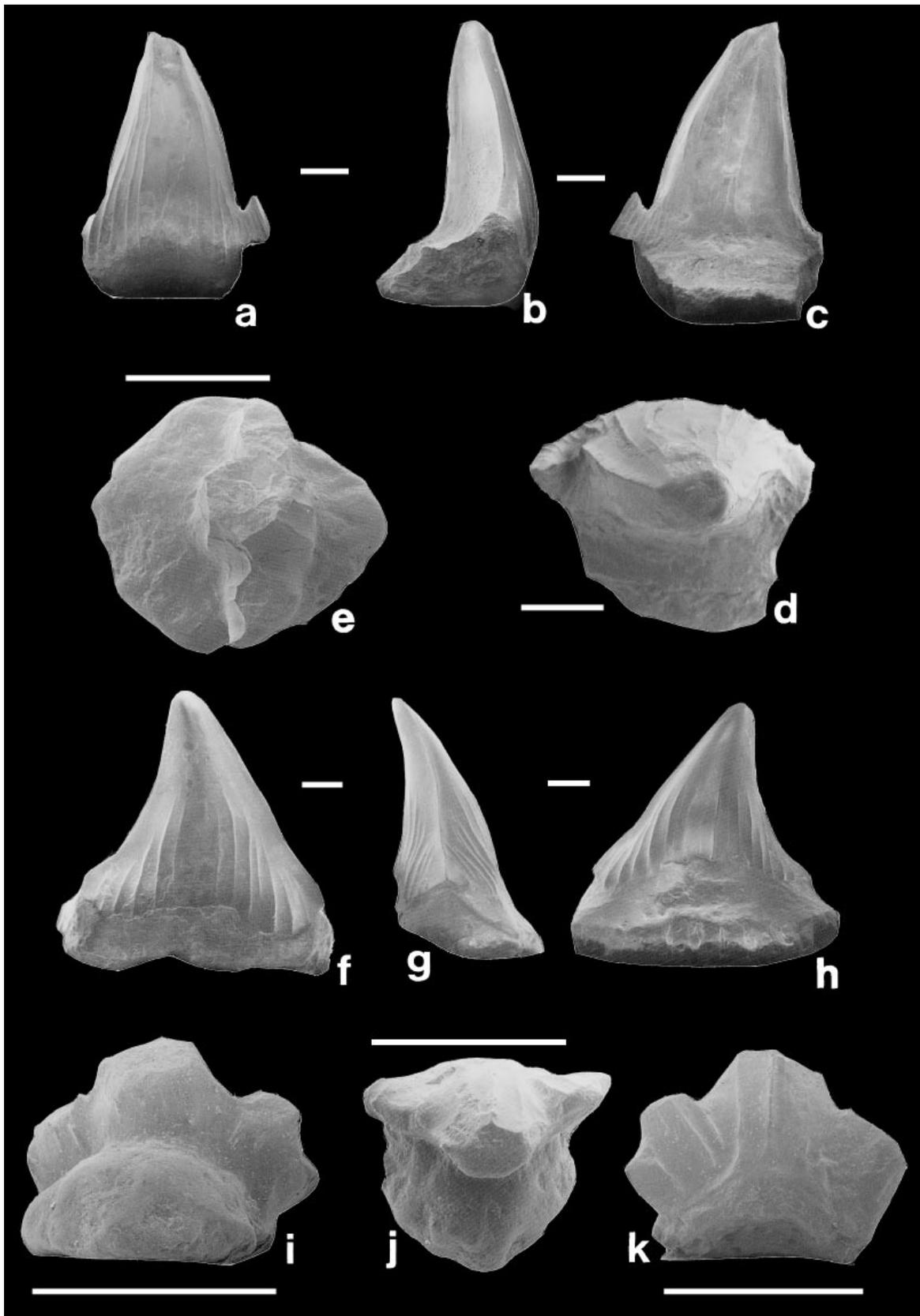


Figure 3. (a–d) Holotype (BRSUG 26316) of *Grozonodon candaui* (GR3 level) in labial (a), lateral (b), lingual (c) and apical (d) views. (e) Pathological tooth (?) or scale (?) of '*Hybodus*' *minor* (BRSUG 26319, GR3 level) in apical view. (f–h) More posterior tooth of *G. candaui* (BRSUG 26317-1) in labial (f), lateral (g) and lingual (h) views. (i–k) Posterior tooth of '*Hybodus*' *minor* (GR3 level, BRSUG 26318-1) in lingual (i), apical (j) and labial (k) views. Scale bars: 1 mm.

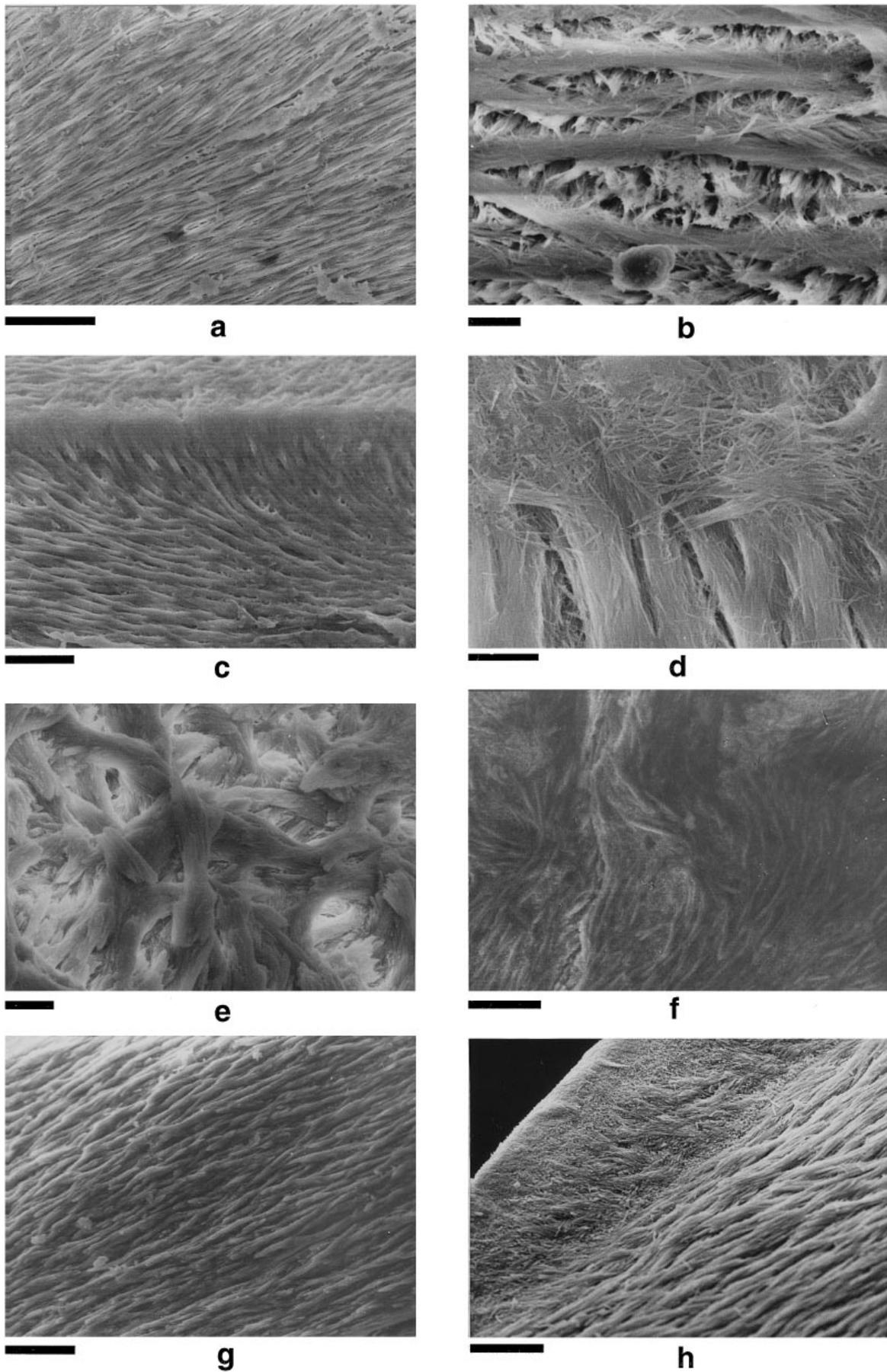


Figure 4. For legend see facing page.

and in teeth of '*Hybodus*' *minor* from the ? middle Norian of Medernach (Luxemburg) as well as in teeth attributed to the same species from the Rhaetian at Aust Quarry (the quarry at Manor Farm, close to the motorway services at Aust, Gloucestershire, England) and Habay-la-Vieille (Belgium). It seems that most of the teeth previously attributed to '*Hybodus*' *minor* belong in fact to a neoselachian, a hypothesis first proposed by Maisey (1977) (J. Day, pers. comm., has independently reached a similar conclusion). The species *Hybodus minor* was originally defined from a fin-spine found in the Upper Triassic of Purton Passage (Gloucestershire, England: Agassiz, 1833–43) which, although undoubtedly belonging to a hybodont shark, is not diagnostic at species level. Shortly after naming this species, Agassiz (1833–43, p. 183, tab. 23, figs 21–24) ascribed to it isolated teeth from other Upper Triassic sites from southwestern England. These teeth, deposited in the Natural History Museum (London), have to be examined before we can remove all the teeth previously ascribed to *H. minor* from this species and erect a new genus and species (*H. minor* would therefore be restricted to undiagnostic fin-spines and so considered as *nomen dubium*). However, considering the historical importance of these specimens, this is not really possible as the method used to study the enameloid ultrastructure is destructive. This problem thus needs further study before it can be resolved. Meanwhile, these neoselachian teeth will be referred to as '*Hybodus*' *minor*.

One specimen (BRSUG 26319) appears unusual. The crown is very similar to those known among teeth of '*Hybodus*' *minor* but three of the four cusps are broken. Originally, there was one main cusp flanked by one lateral cusplet on one side and two lateral cusplets on the other. Only the smallest lateral cusplet is preserved. The root is enlarged posteriorly as well as anteriorly and so appears almost circular in apical view (Fig. 3e). Its basal face is almost flat. A groove cuts across the base from the posterior to anterior side. This groove is not centrally situated but laterally displaced, and disappears just before reaching the anterior edge of the base. This fossil could be interpreted as a pathological posterior tooth of '*Hybodus*' *minor* on which the root extends both lingually and labially. However, Maisey (1987) noticed the presence of placoid scales with an almost tooth-like appearance on the fringe of the mouth in the living shark *Chlamidoselachus*. In the

absence of further evidence, this specimen could be considered either a pathological tooth or a fringing scale from the mouth. Since this specimen is unique, its enameloid ultrastructure was not examined.

The faunas also include:

teeth of undetermined Actinopteri (BRSUG 26349, 26350 and 26351, Fig. 5e, f, h);

Ptychoceratodus rectangularis (Linck, 1936) (BRSUG 26352, Fig. 5j);

teeth of undetermined Archosauriformes (BRSUG 26353-1 and 26353-2, Fig. 5i);

undetermined bone fragment.

5.b. Vertebrate from the GR4 level

As the exposure was reduced and difficult to access, only one sample was taken, and yielded the following vertebrate microremains:

Lissodus minimus (Agassiz, 1839) (BRSUG 26354, Fig. 5g);

undetermined Actinopteri (Fig. 5d);

? *Gyrolepis* sp. (BRSUG 26355).

6. Early radiation of neoselachian sharks

The existence of *Grozonodon candau*, and the recognition that most teeth attributed to '*Hybodus*' *minor* belong to neoselachian sharks, are both further indications that this group underwent some diversification before the end of Triassic time. Neoselachian species from the Norian now include *Reifia minuta* (Duffin, 1980) from Germany, *Rhomphaiodon nicolensis* from France and Germany (?) (Duffin, 1993b), *Synechodus incrementum* from Canada (Johns, Barnes & Orchard, 1997), *Nemacanthus monilifer* from France and Luxemburg (Cuny & Ramboer, 1991; Delsate, 1995), '*Hybodus*' *minor* from Grozon and Medernach (this paper) and *Grozonodon candau* (this paper). '*Hybodus*' *minor* is represented only by teeth in the middle Norian while *Nemacanthus monilifer* is known only from fin-spines, and it is possible that both taxa belong to the same species (Maisey, 1977; Storrs, 1994; Cuny 1995b).

The pre-Norian neoselachian fossil record based on isolated teeth possibly includes *Mcmurdodus whitei* from the early–middle Devonian of Western Queensland (Australia) and *Mcmurdodus featherensis* from the mid-

Figure 4. (a–c) Parallel fibred enameloid of an anterior tooth of *G. candau*, (b) shows the radial fibres which exploit the interstices between the surface parallel fibres while (c) shows the change of orientation of these fibres at the level of the ridges ornamenting the surface of the crown. (d) Shiny Layered Enameloid above the Parallel Fibred Enameloid at the level of the cutting-edge of a tooth of *G. candau*; (e) Tangled Fibred Enameloid near the apex of a tooth of *G. candau*; (f) Primitive Tangled Fibred Enameloid near the base of a tooth of *G. candau*; (g) Parallel Fibred Enameloid of a tooth of '*Hybodus*' *minor* from Aust Quarry (base of the Westbury Beds, Rhaetic, England); (h) Parallel Fibred Enameloid, on the right side of the photograph, and Shiny Layered Enameloid at the level of the cutting-edge on the left side of the photograph of a tooth of '*Hybodus*' *minor* from Manor Farm Quarry at Aust (base of the Westbury Formation, Rhaetian, England). Scale bars: (a, c, f, g): 40 mm; (b, d): 4 mm; (e, h): 10 mm.

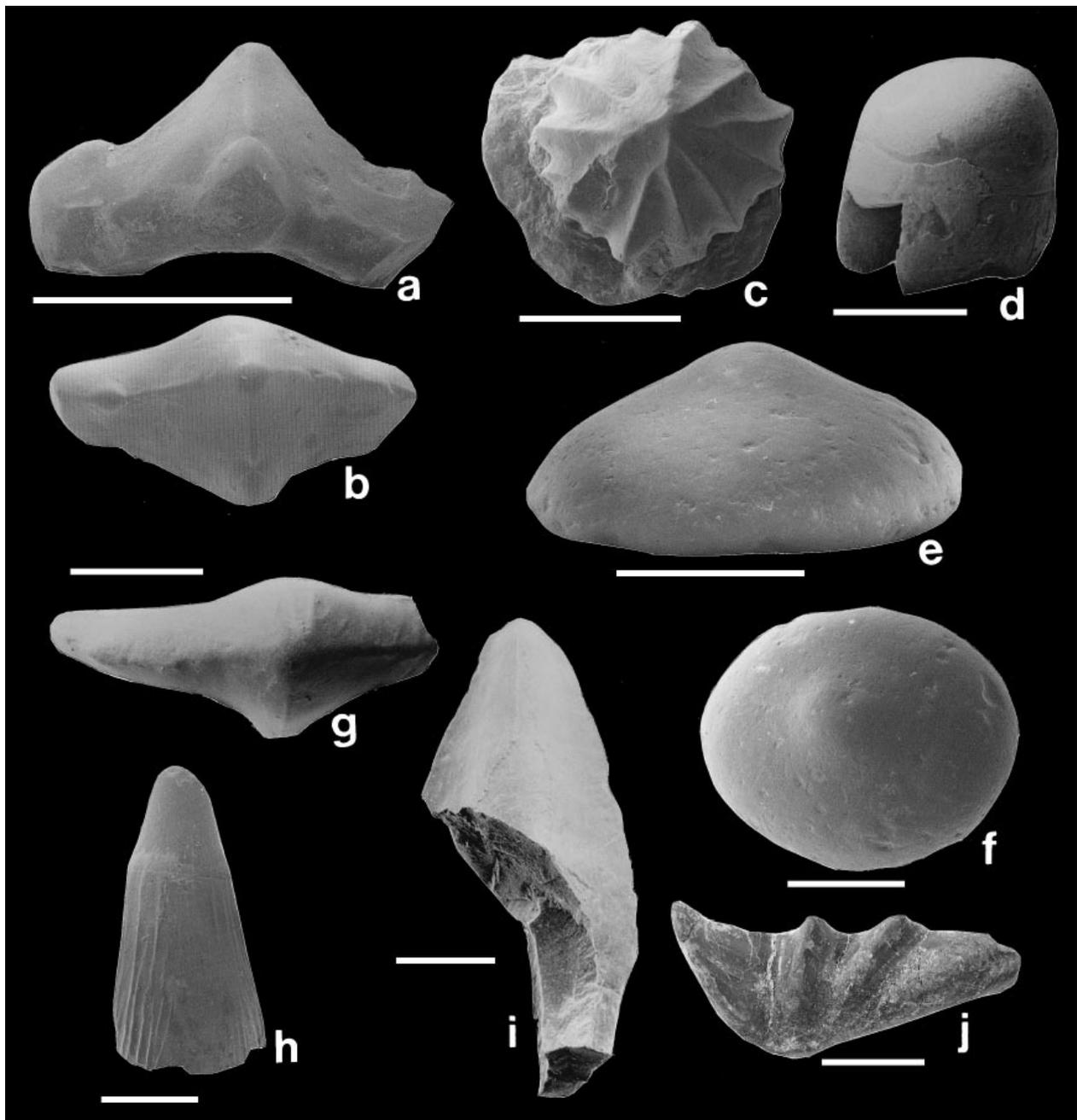


Figure 5. (a, b) Tooth of *Lissodus lepagei* (GR3 level, BRSUG 26348-1) in labial (a) and apical (b) views. (c) Hybodontid scale (GR3 level) in apical view. (d) Tooth of an undetermined crushing Actinopteri (GR4 level, lost specimen) in lateral view. (e, f) Tooth of Perleidiformes or young specimen of *Paralepidotus* (GR3 level, BRSUG 26351-1) in apical (f) and lateral (e) views. (g) Tooth of *Lissodus minimus* (GR4 level, BRSUG 26354) in apical view. (h) 'Saurichthys' type of teeth (GR3 level, BRSUG 26349-1) in lateral view. (i) Tooth of an undetermined Archosauriformes (GR3 level) in labial (?) or lingual (?) view. (j) Tooth of *Ptychoceratodus rectangulus* (GR3 level, BRSUG 26352) in apical view. Scale bars: (a, b, d, g, h, i): 1 mm; (c, e, f): 0.5 mm; (j): 10 mm.

dle-late Devonian of Antarctica (Turner & Young, 1987), as well as *Cooleyella peculiaris* from the late Carboniferous of North America (Gunnell, 1933), *C. amazonensis* from the late Carboniferous of Brazil (Duffin, Richter & Neis, 1996) and *C. fordi* from the early Carboniferous of Great-Britain and the Permian of North America (Duffin & Ward, 1983). The teeth of *McMurdodus* are strikingly similar to those of the

Hexanchidae, although the first record of this family does not occur until early Jurassic time (Cappetta, 1987). Therefore, the similarity may simply be a result of convergence in tooth morphology (Cappetta, Duffin & Zidek, 1993). The teeth of *Cooleyella* lack an enameloid cover (Duffin & Ward, 1983), which is quite a problematic feature. Recent phylogenetic hypotheses accept the Hybodontoidea as the sister-group of the Neoselachii

(Maisey, 1984; Gaudin, 1991) and the structure of the enameloid in some late Triassic Neoselachii may suggest that it is derived from a more primitive single crystallite enameloid (Cuny, unpub. data). There is therefore little support for Duffin & Ward's (1983) hypothesis concerning the presence of unenamelled teeth in primitive neoselachians. A secondary loss of the enameloid cover seems unlikely as there is no other example of such a loss across the whole lineage, and it is difficult to justify this in mechanical terms. Although the hemiaulacorhize vascularization of the teeth of *Cooleyella* is unknown outside the Neoselachii, convergence cannot be ruled out. Indeed, there is no unequivocal evidence that either *Mcmurdodus* or *Cooleyella* belong to neoselachian sharks.

Unfortunately, the phylogenetic relationships of more complete fossils are just as difficult to define. *Hopleacanthus richelsdorfensis* from the Permian of Germany (Schaumberg, 1982) displays a mixture of hybodontid, ctenacanthid and palaeospinacid features (Schaumberg, 1982). Maisey (1984) considered it as the sister-taxon of *Palaeospinax* + modern elasmobranchs on the basis of three synapomorphies: (1) notochordal sheath segment calcified anteriorly; (2) fin-spines with a mantle of shiny enameloid and lacking posterior tubercles; and (3) dermal denticles with a simple pulp cavity and a single basal canal. Gaudin (1991) questioned Maisey's first and third synapomorphies and pointed out that the structure of the pectoral fins is primitive (*contra* Maisey, 1984). Schaumberg's reference to "Placoidschuppe des *Hybodus*-types" appears quite unclear. The drawing of the vertical section of a placoid dermal denticle (Schaumberg, 1982, fig. 2) was made according to a single abraded scale (Schaumberg, pers. comm.), and a new study of the dermal skeleton of this genus would be welcome. The second character is also recognizable in *Amelacanthus* from the British Carboniferous (Maisey, 1982), *Eunemacanthus*, from the Carboniferous of Europe, North America and Russia (Maisey, 1982), *Nemacanthus* from the early Triassic of Spitzbergen (Stensiö, 1921), East Greenland (Stensiö, 1932), North America (Evans, 1904) and the late Triassic of Western Europe (Cuny, 1995b; Cuny & Ramboer, 1991; Delsate, 1995) and *Acronemus*, from the middle Triassic of Switzerland (Rieppel, 1982). *Amelacanthus*, *Eunemacanthus* and *Nemacanthus* are known from isolated fin-spines only (however, see above concerning the possible association of '*Hybodus*' *minor* and *Nemacanthus monilifer*), and their exact relationships are therefore difficult to assess. On the other hand, *Acronemus* displays associated teeth and dermal denticles (Rieppel, 1982). Despite this, the teeth possess a single crystallite enameloid (SCE) only, which would exclude this genus from the Neoselachii. *Acronemus*, *Hopleacanthus*, *Amelacanthus* and *Eunemacanthus* may represent a paraphyletic sister-group of the Neoselachii, as suggested by Maisey (1984). This would imply that the character 2 is a primitive character for Neoselachii.

The earliest unequivocal neoselachian tooth is known from Lower Triassic strata of Turkey (Thies, 1982) and was attributed to the genus *Palaeospinax* Egerton, 1872. This tooth displays a SLE and a PFE, but as there is only one known tooth, it was impossible to look further to check the presence of a TFE. The association of a SLE and a PFE is unknown outside the neoselachian sharks (Reif, 1977) and there is no doubt that this tooth belongs to a true neoselachian. To a large extent, the diagnosis of the *Synechodontiformes*, including the *Palaeospinacidae*, is based on the structure of the root, with a peculiar vascularization termed pseudopolyaulacorhize (Cappetta, 1987, 1992; Thies, 1993; Duffin & Ward, 1993), while the overall morphology of the crown appears quite primitive inside the *Palaeospinacidae*. As the root is not preserved in the Turkish specimen, it is difficult to assess whether this tooth does indeed belong to *Palaeospinax*. Moreover, *Palaeospinax* is a *nomen dubium* (Duffin & Ward, 1993; Thies 1993), and if this tooth does belong to a palaeospinacid, it should be attributed to the genus *Synechodus*. Similar teeth have recently been reported from the middle Triassic strata of Nevada (USA) and identified as *Palaeospinax* sp. by Rieppel, Kindlimann & Bucher (1996). The roots of these teeth are poorly preserved and the vascularization system cannot be determined. It is therefore impossible, for the same reasons as those given above, to assess whether these teeth belong to a true palaeospinacid. Furthermore, the lateral cusplets appear to be well separated from the main cusp, which Cappetta (1992) and Duffin & Ward (1993) suggested as being a characteristic of *Paraorthacodus* rather than of *Synechodus* (the latter including teeth formerly described as *Palaeospinax*). The oldest teeth unequivocally attributable to the genus *Synechodus* (*S. volaticus* and *S. sp. 1*) were recently described from the Ladinian of Canada, in addition to three other species from the Carnian and Norian (*S. incrementum*, *S. multinodosus*, and *S. sp. 2*: Johns, Barnes & Orchard, 1997). *S. volaticus* displays an SLE and a PFE, but no TFE, while all three layers are present in *S. multinodosus*. The enameloid ultrastructure of *S. incrementum* on the other hand appears unusual. The structure of GSC 105113 (Johns, Barnes & Orchard, 1997, pl. 7, figs 1–4) is indistinct due to recrystallization, but the other teeth figured (pl. 7, figs 6–9) show bundles of poorly separated fibres, oriented more or less perpendicular to the surface of the teeth. A similar pattern was observed by one of us (GC) in teeth attributed to *Synechodus rhaeticus* from the Rhaetian of Lons-le-Saunier (France) and Habay-la-Vieille (Belgium) but is unknown in other neoselachian teeth studied so far. Johns, Barnes & Orchard (1997) noted many similarities between the majority of *S. incrementum* teeth and those of *Lissodus minimus*. However, the latter typically possess a single crystallite enameloid totally lacking fibre bundles. Current knowledge suggests that the enameloid of the

teeth of *Synechodus incrementum* and some teeth of *Synechodus rhaeticus* is unique, making the exact relationships of these species problematic.

The neoselachian fossil record from the Devonian up to the middle Triassic thus remains sparse, at low diversity, and with most of the fossils having uncertain phylogenetic positions. In comparison, the middle Norian fauna from Western Europe appears much more diverse. It is, striking, however, to note the convergence in the shape of the teeth between most Triassic neoselachians displaying a triple-layered enameloid (*Palaeospinax*, *Synechodus*, '*Hybodus*' *minor*, *Rhomphaiodon*, *Grozonodon*) and the Hybodontidae. *Grozonodon candau*, '*Hybodus*' *minor* and *Rhomphaiodon nicolensis* are certainly closely related and would appear to be evolutionary intermediates between hybodonts and *Synechodontiformes*. Indeed they differ from *Synechodontiformes* only by the lack of open canals in the basal face of the root. It is also striking that in these Triassic teeth possessing a triple-layered enameloid the root is enlarged lingually, and projected at nearly a right angle from the axis of the crown (the lingual torus of Maisey, 1975). This character is known among Ctenacanthoidea (Maisey, 1975) and to a lesser extent among Hybodontoidea, although in the latter, this lingual torus is never as well developed as in primitive neoselachians (see, for example, *Egertonodus basanus*, Patterson, 1966; Maisey, 1983; Maisey, 1987). It is highly probable that the reduced lingual torus of the Hybodontoidea is a derived character, and that the primitive Neoselachii have retained the primitive condition. When it is not possible to check the enameloid ultrastructure, the presence of a lingual torus may therefore be useful in distinguishing between teeth of Hybodontoidea and those of primitive Neoselachii.

So far, *Grozonodon candau* appears to be the only one with a quite peculiar, primitive tangled-fibred enameloid at the level of the ridges ornamenting the base of the tooth, but this remains difficult to explain in the present state of our knowledge.

7. Conclusions

The site of Grozon appears interesting as it is the only site in the Jura that has yielded vertebrate microremains both from the Norian and the Rhaetian. Palynological analysis allows the recognition of episodes 1 and 2 of Rauscher *et al.* (1995) which correspond respectively to the Norian (Marnes Irisées Supérieures) and to the lower part of the Rhaetian (Grès et Schistes à *Avicula contorta*, GSAC). The microremains from the Norian appear quite different from those recovered in the GSAC, and from other localities in the Jura (Cuny, 1995a; Cuny, Mazin & Rauscher, 1994). Moreover, a new species of neoselachian shark of doubtful affinity, *Grozonodon candau*, and the recognition of teeth of '*Hybodus*'

minor as belonging to a neoselachian shark indicate that the neoselachians were already well diversified by Norian times and probably closely related to hybodonts.

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