Teeth of enigmatic neoselachian sharks and an ornithischian dinosaur from the uppermost Triassic of Lons-le-Saunier (Jura, France)

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With 9 figures

Kurzfassung: Von einer neuen rhätischen Fundstelle bei Lons-le-Saunier (Jura, Frankreich) werden Zähne von Haien und einem Dinosaurier der Ordnung Ornithischia beschrieben. Die stratigraphische Einordnung der Fundstelle basiert auf palynologischen Daten. Die Struktur des Enameloides von *Synechodus rhaeticus* wird beschrieben; sie unterscheidet sich deutlich von jener der Neoselachier, wodurch die systematische Zuordnung dieser Art erschwert wird. '*Hybodus*' *minor* wird zu den Synechodontiformes gestellt. Ornithischier sind aus der neuen Fundstelle durch einen Zahn nachgewiesen. Die Befunde von Lons-le-Saunier deuten auf einen Faunenwechsel im marinen Bereich während der Rhät-Transgression hin, wobei besonders die Neoselachier sowie die durophagen Actinopterygier, letztere überwiegend mit der Art *Sargodon tomicus*, deutlich häufiger werden.

Abstract: Shark teeth and an ornithischian dinosaur tooth are described from a new palynologically dated Rhaetian locality at Lons-le-Saunier (Jura, France). The structure of the enameloid of the teeth of *Synechodus rhaeticus* has been studied, but this appears quite different from the usual pattern seen in neoselachian sharks, making the precise relationships of this species difficult to determine. On the other hand, '*Hybodus*' *minor*, which has long be thought to be a hybodont shark, is included among the Synechodontiformes. The find of the tooth of an ornithischian dinosaur is also reported. Study of the Lons-le-Saunier site seems to indicate a change in the marine faunas during the Rhaetian transgression, preferentially affecting the neoselachian sharks, which increase in abundance, and the durophagous bony fishes, which become dominated by *Sargodon tomicus*.

Introduction

In 1982, two teenagers who were passionately fond of palaeontology found some dark fossil bones in a roadside bank of the town of Lons-le-Saunier (Jura, France; Fig. 1). The bones remained unstudied until 1990 when G.C. & J.M.M. heard about the discovery and organised an excavation, which lasted from 1990 to 1994. Hundreds
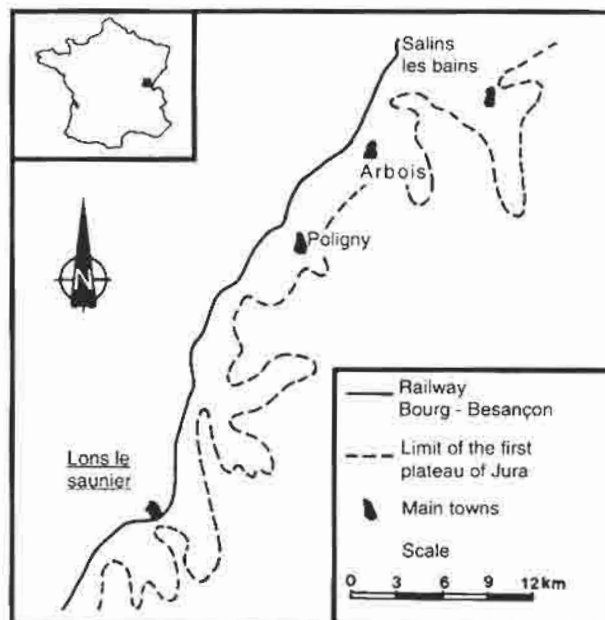

Fig. 1. Location map of the site of Lons-le-Saunier.

of bones belonging to *Plateosaurus* sp. were extracted from the 'Marnes de Châlins', a formation which lies at the top of the Keuper (Upper Triassic) in this area (CUNY & MAZIN 1993; MAZIN & CUNY 1992). These bones are currently under study. The Rhaetian formations overlying the 'Marnes de Châlins' yielded the vertebrate microremains which are the subject of this paper.

Abbreviations used in the text: MALS: Musée d'Archéologie de Lons-le-Saunier; PFE: Parallel-Fibred Enameloid; SCE: Single Crystallite Enameloid; SLE: Shiny-Layered Enameloid; TFE: Tangled-Fibred Enameloid (see REIF 1973, for details).

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Geology

In this area, the Rhaetian transgression began with deposition of the 'Grès de Boisset' (Bed R1 of Fig. 2), a unit consisting of a very hard yellowish or whitish sandstone with occasional small pockets of green marl reworked from the 'Marnes de Châlins'. The unit thickness varies between 15 and 30 cm. These sandstones contain isolated fossil teeth and scales ranging from 1 to 10 mm in size. However, the hardness of the matrix prevents manual extraction of specimens, and chemical processing with acids and/or hydrogen peroxide has been unsuccessful, making precise identification of these fossils problematic.

A sequence of marls and sandstones overlies the 'Grès de Boisset', and it was possible to measure a stratigraphic section of these Rhaetian beds in the bank along the road, despite vegetation cover (Fig. 2). The 23 m-thick sequence exhibits lateral changes in facies with beds dipping at an angle of 30° and orientated 124° SE. Three beds in the lower part of the section yielded vertebrate microremains (R11, R20 and R22), although it was only possible to sample some tens of kilogrammes of sediment. Bed R11 consists of 1.30 m of blackish sandy clay in which occasional lenses of lighter and more sandy marls reach a maximum thickness of 10 cm. One of these lenses yielded the richest vertebrate fauna of the section, in addition to a small (2 mm) internal mould of a gastropod. Bed R20 consists of 2 m thick blackish shales which lack lenticular accumulations of fossils and, in general, yield a less diverse fauna than R11. Numerous internal moulds of bivalves and gastropods are present, as well as fragmentary shells belonging to *Chlamys*? sp. Echinoderms are represented by long, smooth, filiform spines and a fragment of a sea urchin test. This invertebrate fauna seems to indicate more marine influence than in bed R11. Bed R22 consists of blackish shales, 1.20 m thick, that are very similar to those of R20. It yielded some fragments of bivalve (*Chlamys*?) shells.

At the top of the Rhaetian section, there is a bed of rust-coloured clay (R62), 1 m thick, which yielded neither palynomorphs nor vertebrate microremains. The facies within this clay is very reminiscent of the 'Argiles de Levallois', a formation marking the end of the Rhaetian in eastern France. In the Jura area, this formation never exceeds a thickness of 3 m (DE LUCA 1975; KERRIEN 1982), its thinness being attributed to a trend towards regional uplift and a regression at the end of the Rhaetian (LAUGIER 1971; AL KHATIB 1976). It is unclear if the measured section represents the entire thickness of this Formation, for a fault separates bed R62 from the overhanging Sinemurian. The section therefore lacks the Hettangian, represented in this area by a blue limestone (CONTINI pers. comm.) which may be part of the 'Argiles de Levallois'. The Sinemurian is characterized by a limestone known as the 'Calcaire à Gryphées' which contains numerous fossils of *Liogrypha*. The shells of *Liogrypha* show a well developed lateral sulcus, indicating that they
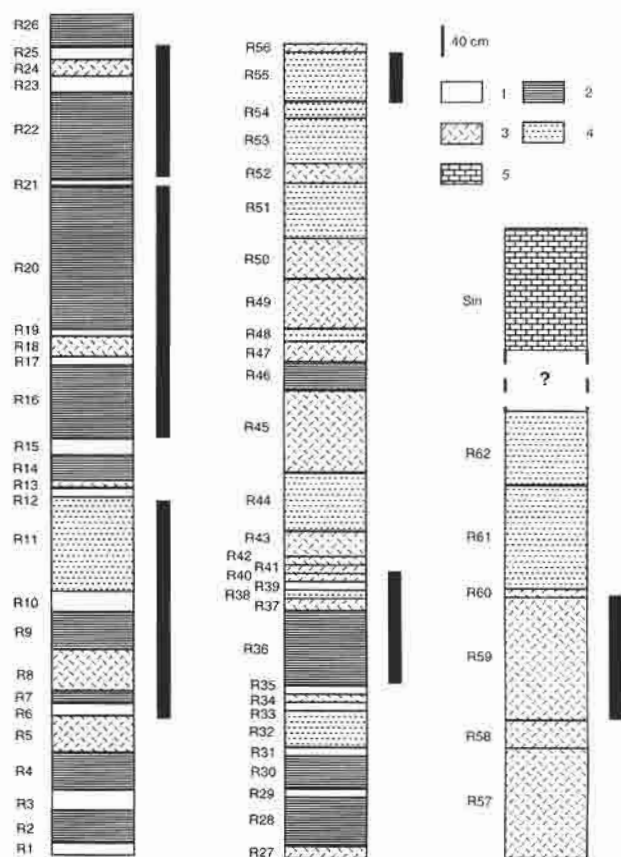

Fig. 2. Stratigraphic log of the site of Lons-le-Saunier. – R1 to R62: Rhaetian beds, Sin: Sinemurian. 1: sandstone, 2: shales, 3: marls, 4: clay, 5: limestone. The black strips indicate the beds in which palynomorphs have been found. – Scale bar = 40 cm.

belong to the species *L. arcuata* (MICHIELS 1993). Bands of yellow marl several cm thick sometimes occur in the lower part of the limestone.

Palynological study

Samples were taken from each bed for palynological analysis, which was carried out by R. R. Palynomorphs are absent from the 'Marnes de Châlins' samples, which yielded *Plateosaurus* bones, but several other beds of the Rhaetian section were sufficiently rich in palynomorphs to allow detailed analysis (Fig. 2). The assemblages found in each of these beds are very similar. The spores, apart from *Riccisporites*, are always rare, with Circumpolles being the most abundant and most typical elements. *Rhaetipollis* and *Ovalipollis* are well represented, while the bisaccate pollens are rare. Marine elements (acritarchs, dinocysts, rare Foraminifera and tasmanitids) are always largely dominated by the sporomorphs, although these are more common at the base of the section (R1 - R40), which is generally more fossiliferous than the top. The presence of *Rhaetipollis germanicus*, *Granuloperculatipollis rudis* and *Rhaetogonyaulax rhaetica* in all of the fossiliferous beds allows the section to be dated to the Rhaetian with great confidence, and the scar-

city of these spores is characteristic of the lower part of this stage (episode 2 of RAUSCHER et al. 1995). The composition of these assemblages allows the reconstruction of the palaeoenvironment as "a coastal environment, protected against open sea influences and bordered with a littoral fringe of Cheirolepidiacae, producing the considerable amount of Circumpolles, and with an inland cover of conifers" (RAUSCHER 1992a, b).

Inventory of the vertebrate microremains

Beds R11, R20 and R22 yielded a typical Rhaetian fish assemblage comprising chondrichthyan dermal denticles (Fig. 3A-H), *Gyrolepis* scales, teeth of *Lissodus minimus*, *Pseudocetorhinus pickfordi*, '*Hybodus*' minor, *Sargodon tomicus*, and '*Birgeria*', '*Saurichthys*' and '*Gyrolepis*' type teeth. Some taxa are restricted to bed R11 (*Hybodus cloacinus*, *Pseudodalatias barnstonensis*) or to bed R20 and R 22 (*Synechodus rhaeticus*). Moreover, bed R11 has also yielded a terrestrial component, with a ?rhynchocephalian jaw fragment (Fig. 6H) and a dinosaur tooth. Most of the components of these faunas are well known from other European sites and have been described extensively elsewhere (see SYKES et al. 1970; STORRS 1994 and CUNY 1995a for references). We shall therefore focus on the most unusual taxa, i.e. the neoselachian sharks and the dinosaur.

Class Chondrichthyes HUXLEY 1880
Subclass Elasmobranchii BONAPARTE 1838
Cohort Euselachii HAY 1902
Subcohort Neoselachii COMPAGNO 1977
Superorder ?Galea SHIRAI 1996
Order ?Lamniformes BERG 1958
Family ?Cetorhinidae GILL 1862

Genus *Pseudocetorhinus* DUFFIN 1998

Pseudocetorhinus pickfordi DUFFIN 1998
Figs. 3K-M, 5A-C

Materials: 1 tooth from bed R11 (MALS 1998.2.12) and 1 tooth from bed R22 (MALS 1998.2.13).

Description: The tooth from bed R11 is strongly asymmetric with a smooth crown (Fig. 3K, M). It possesses a single cuspid, broken at its apex, nearly circular at its base and lacking cutting edges (Fig. 3L). The distal margin of the crown produces a flange with a convex labial face and a concave lingual face. The crown-root junction is smooth with the root projecting lingually from the crown underside. The poor preservation of the root means that nothing can be said about its vascularization. The tooth from bed R22 is more symmetric and its lateral flanges are not so well developed, but they are more labially oriented, giving the labial base of the crown a concave appearance. The root is badly preserved.

Discussion: The asymmetry of MALS 1998.2.12 suggests that it is a posterolateral tooth (DUFFIN 1998a),

while the more symmetrical MALS 1998.2.13 is probably an anterior tooth. *Pseudocetorhinus pickfordi* was recently described as a neoselachian shark on the basis of its morphology only (DUFFIN 1998a). However, REIF (1973) demonstrated that the teeth of neoselachian sharks possess a triple-layered enameloid made of an internal tangled-fibred enameloid (TFE), a central parallel-fibred enameloid (PFE) and an external shiny-layered enameloid (SLE, equivalent to the terminal membrane enameloid, LUND 1989) while hybodont and ctenacanth sharks possess a single-layered enameloid made of single crystallite (SCE, Fig. 4). Among these layers, the PFE is considered an autapomorphy of the Neoselachii (REIF 1977; THIES 1982; MAISEY 1984a, b, 1985; THIES & REIF 1985; GAUDIN 1991), although this character is secondarily lost in *Heterodontus* and in batoids (THIES 1982; MAISEY 1985) as a mechanical adaptation toward a durophagous diet (PREUSCHOFT et al. 1974). As the method used to study the ultrastructure of the enameloid requires the etching of the teeth with HCl, and is therefore destructive, it was not possible to conduct such a study on the teeth from Lons-le-Saunier, which are rare. However, teeth of *Pseudocetorhinus pickfordi* from another Rhaetian site, Habay-la-Vieille in Belgium, have been studied (Fig. 5A-C and CUNY 1998). They possess a triple-layered enameloid, which confirms the neoselachian affinities of this species suspected by DUFFIN (1998a). However, the outer layer may be unusually thick in some teeth, looking more like a SCE than the SLE typical of neoselachians. This probably explains why DUFFIN (1998a) did not recognize a triple layered enameloid in teeth from the Holwell Quarry, although the function of this unusually thick SLE remains enigmatic in these supposedly vestigial teeth.

The attribution of *Pseudocetorhinus* to the Cetorhinidae by DUFFIN (1998a), although tentative, is not without problem. This family is not known with certainty before the Oligocene, maybe the Eocene (CAPPETTA et al. 1993), which represents an important gap with the report of *Pseudocetorhinus* in the Late Triassic. Morever, no lamniform shark is known before the Cretaceous (CAPPETTA et al. 1993; SHIRAI 1996). The teeth collected in the Rhaetian of Habay-la-Vieille might help to make the precise phylogenetic relationships of this genus clear, and pending their description, its attribution to the Lamniformes and to the Cetorhinidae is questionable.

Superorder *incertae sedis*
Order Synechodontiformes
DUFFIN & WARD 1993
Family Palaeospinacidae REAGAN 1906

Genus *Synechodus* WOODWARD 1888

Synechodus rhaeticus DUFFIN 1982
Figs. 5D-E, 6D-G

Materials: 11 teeth from bed R20 (MALS 1998.2.14) and 14 from bed R22 (MALS 1998.2.15).
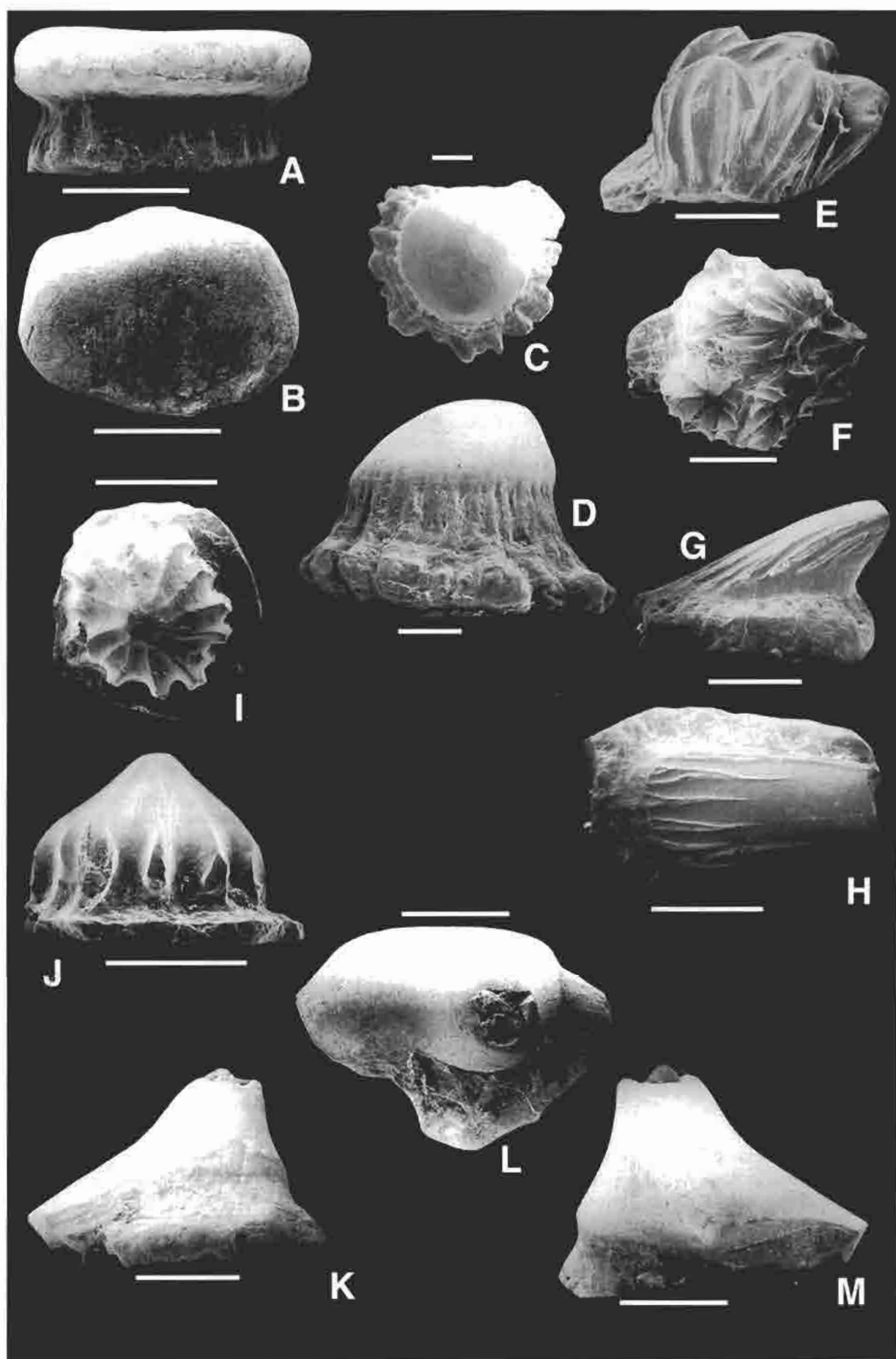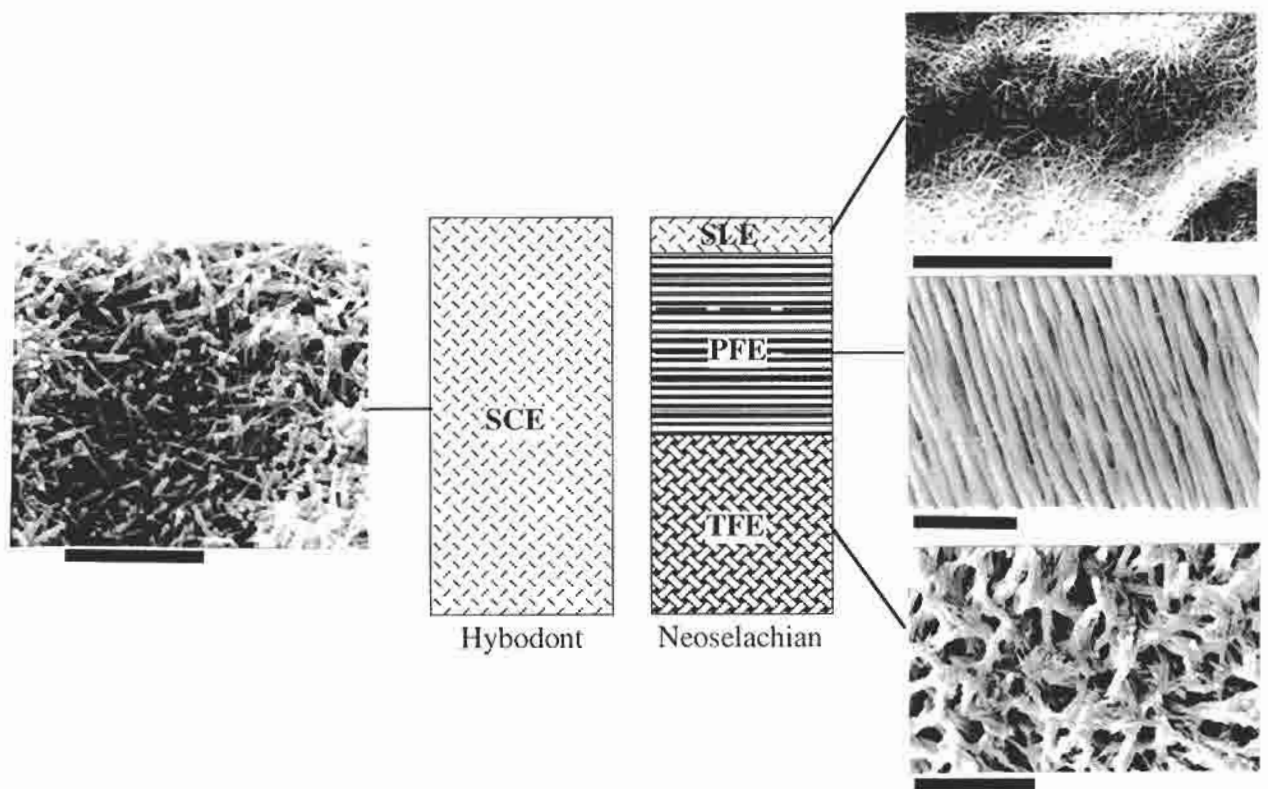
Fig. 4. Comparison of the ultrastructure of the enameloid of the teeth of a hybodont (left) and a neoselachian (right) shark. Photographs show the aspect of each kind of tissue in surface view after various time of etching. – Abbreviations: PFE = parallel-fibred enameloid; SCE = single-crystallite enameloid; SLE = shiny-layered enameloid; TFE = tangled-fibred enameloid. Scale bars represent 2 µm for the hybodont, and 35 µm for the neoselachian.
SCE from *Hybodus cloacinus*, Rhaetic of Habay-la-Vieille (Belgium); SLE and PFE from *Striatolamia* sp., Lower Eocene of Chambray (France); TFE from *Carcharinus* sp., Madagascar, Recent.

Description: The best preserved specimen, from bed R20, comprises half of a crown of a postero-lateral tooth (Fig. 6D-G). The main cusp is bulky and not very high. Four well developed lateral cusplets are present, their heights diminishing regularly to the ?mesial or ?distal end of the tooth. There is no well defined valley separating the cusps from each other. A strong occlusal crest runs the length of the crown, through the apices of all cusps.

The labial face of the tooth is ornamented by ridges, which appear to be less developed and more densely arranged than those in the primitive neoselachian (long thought to be an hybodont, see CUNY 1998; GODEFROIT et al. 1998) '*Hybodus*' *minor* (Fig. 6A). These are anastomosed at the base of the cusps, so that the ornamentation

appears almost reticulated. This ornamentation dies out just above the crown-root margin. All the ridges attain the apex of the cusps or the occlusal crest, giving the occlusal crest a denticulate appearance. On the lingual face, the ridges show a less dense distribution, and some of them only reach the apex of the cusps. At the base of the crown, the ornamentation always appears almost reticulated and does not reach the crown-root junction, which is incised. The labial base of the crown moderately overhangs the crown-root junction.

The root projects moderately (less than in '*Hybodus*' *minor*) lingually and its upper part is ornamented by a series of laminae and grooves, which may correspond to the opening of a series of unroofed canals. The base of the labial face also shows a series of laminae and grooves, with canal openings at their extremity, which correspond to the pseudo-polyaulacorhize vascularization stage (CAPPETTA 1987). In basal view, the labial part of the root is concave while the lingual part is flat, so that the labial part is thinner than the lingual. This morphology disappears in more posterior teeth which have a flat basal root face.

Enameloid ultrastructure: Three posterior teeth, two from bed R22 and one from bed R20, and one anterior tooth from bed R22, were etched for between 5s and

Fig. 3. – **A, B:** cf. *Complanicorona* (MALS 1998.2.1) in A: lateral, and B: apical view. **C, D:** Undeterminate dermal denticle (MALS 1998.2.3) in C: lateral, and D: apical view. **E, F:** Hybodont dermal denticle (MALS 1998.2.42) in E: lateral, and F: apical view. **G, H:** ?Hybodont dermal denticle (MALS 1998.2.45) in G: lateral, and H: apical view. **I, J:** Hybodont dermal denticle (MALS 1998.2.4) in I: apical, and J: lateral view. **K-M:** Tooth of *Pseudocetorhinus pickfordi* (MALS 1998.2.12) in K: lingual, L: apical, and M: labial view. – All scale bars = 0.5 mm.
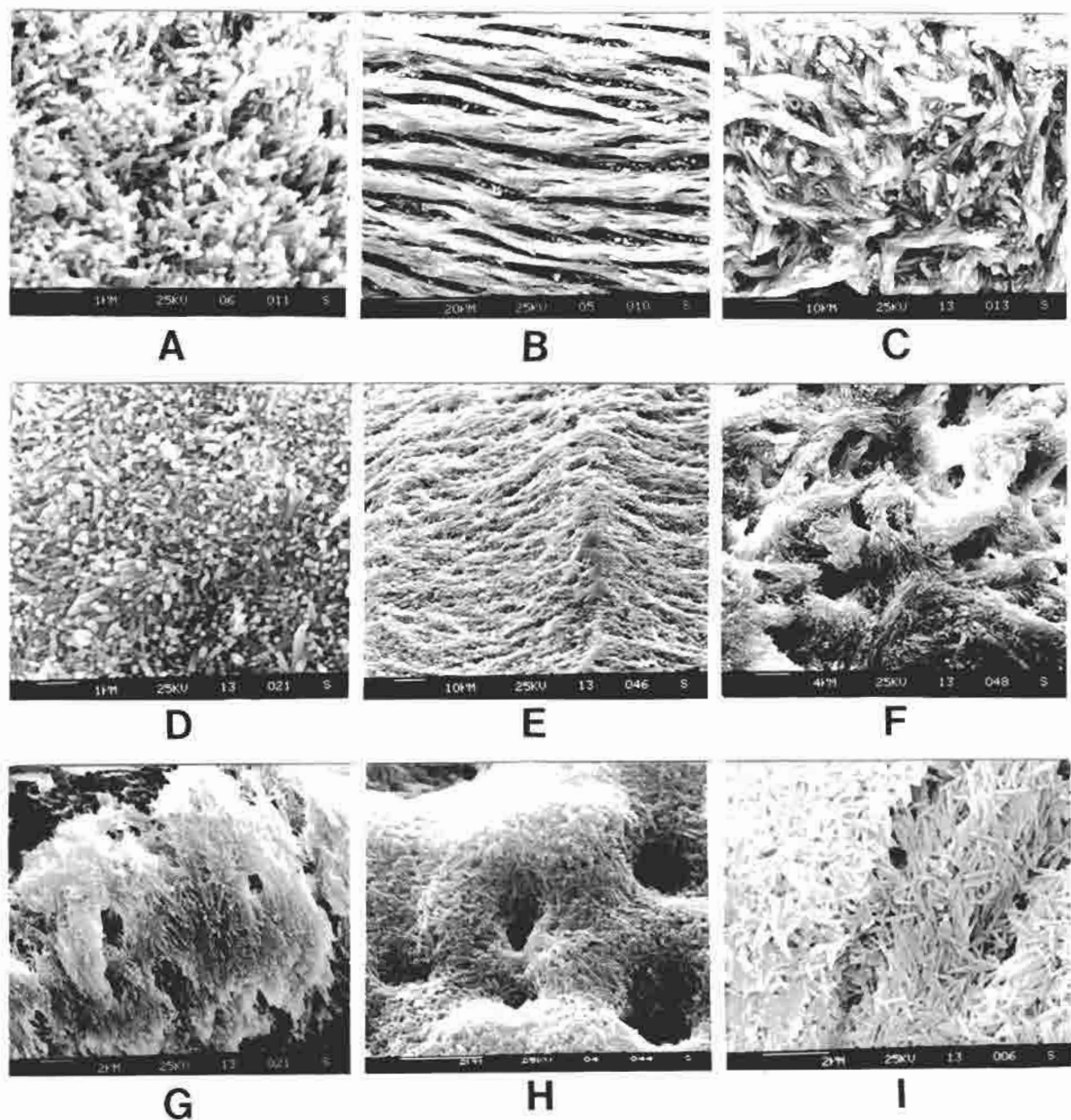
Fig. 5. – A-C: Enameloid of a tooth of *Pseudocetorhinus pickfordi* from Habay-la-Vieille (Belgium, Rhaetian). A: Surface of the tooth etched 20s in 10% HCl, showing the SLE, ×7000. B: Surface of the tooth etched 40s in 10% HCl, showing the PFE, ×550. C: Surface of the tooth etched 340s in 10% HCl showing the TFE, ×600. **D-G:** Enameloid of the teeth of *Synechodus rhaeticus* from Lons-le-Saunier. D: Surface of a postero-lateral tooth etched 65s in 10% HCl, showing the SLE, ×6000. E: Surface of a postero-lateral tooth etched 120s in 10% HCl, showing indistinct bundles of fibres perpendicular to the axis of the tooth, ×500. F: Surface of a postero-lateral tooth etched 185s in 10% HCl, showing randomly orientated bundles of fibres, ×1250. G: Transverse section of the enameloid of an anterior tooth etched 10s in 10% HCl, showing poorly defined bundles of crystallites perpendicular to the surface, ×2500. **H:** Surface of a tooth of *Lissodus minimus* from bed R22 etched 90s in 5% HCl, ×6000. **I:** Transverse section of the enameloid of a tooth of *Lissodus minimus* from Aust Quarry (Westbury beds, Gloucestershire, England) etched 5s in 10% HCl, ×5000.

3min 30s in 5% or 10% HCl. Photographs of the surface of the enameloid were taken between each treatment with a Cambridge Stereoscan 250 MK3 SEM using an acceleration voltage of 25 kV, to study the different layers. Although this method is destructive, it allows study of the whole surface of the different enameloid layers. A longi-

tudinal section of the anterior tooth was also studied. Superficially, the enameloid is formed of small (less than 1 µm in maximum length), thin crystallites of apatite (Fig. 5D), which are preferentially oriented perpendicularly to the surface. Underneath, in the apical part of the crown of posterior teeth, more or less parallel bundles of

fibres are oriented parallel to the surface and perpendicu-
lar to the ridges (Fig. 5E). These bundles of fibres have
an average diameter of about 4 μm. In between them,
there are smaller radial fibres. Near the contact of the
enameloid with the dentine, these bundles appear to be
more randomly oriented (Fig. 5F). The enameloid is
therefore triple-layered, made of a SCE, a PFE (in which
the bundles of fibres parallel to the surface show an unu-
sual orientation), and a basal TFE. In the anterior tooth,
and in the basal part of the crown of posterior teeth, the
enameloid comprises only poorly defined bundles of
crystallites perpendicular to the surface (Fig. 5G), and is
therefore single-layered.

Discussion: These teeth are very similar to those de-
scribed by DUFFIN (1998b) from the Rhaetian fissure fill-
ings of Holwell (England), and by DELSATE & LEPAGE
(1991) from the Rhaetian of Habay-la-Vieille (Belgium),
although the ornamentation appears denser, giving the
occlusal crest a denticulate appearance. This, however,
does not justify the erection of a new species and is here
attributed to some intraspecific variation. The teeth from
Lons-le-Saunier are therefore attributed to *Synechodus
rhaeticus*.

On the basis of tooth morphology, it has recently been
claimed that Synechodontiformes are squalean sharks
(JOHNS et al. 1997; DUFFIN 1998b), close to the Hex-
anchiformes (DUFFIN & WARD 1993). However, cranial
characters seem to favour classification of the Syn-
echodontiformes as galean sharks (MAISEY 1985). A re-
assessment of the taxonomic position of this order, tak-
ing all characters into account, is therefore desirable but
beyond the scope of this paper.

The enameloid ultrastructure of the teeth of *S. rhae-
ticus* is rather unusual for a neoselachian shark. When
present, the bundles of fibres are not very distinct, when
compared, for example, with the PFE of the contempo-
rary '*Hybodus*' minor or *Pseudocetorhinus pickfordi*
(CUNY 1998), and the orientation of these fibres, parallel
to the surface but perpendicular to the axis of the tooth, is
unusual. In primitive neoselachians, like '*Hybodus*' mi-
nor and *Grozonodon candaui*, the bundles of fibres in the
PFE change their orientation to become perpendicular to
the ridges, but this phenomenom is restricted to the vi-
cinity of the ridges (CUNY 1998; CUNY et al. 1998;
GODEFROIT et al. 1998), and there is no complete layer of
fibres perpendicular to the axis of the tooth. The bundles
of fibres are also smaller than those observed in the PFE
of the teeth of *Pseudocetorhinus pickfordi*, which aver-
age 6 μm in diameter compared with about 4 μm for *S.
rhaeticus*. The presence of radial fibres in between the
bundles of fibres parallel to the surface is, however, a
typical feature of the PFE (REIF 1973).

The presence of bundles of crystals perpendicular to
the surface in the anterior teeth, and in the basal part of
the crown of the posterior teeth of *S. rhaeticus*, is remi-
niscent of the radial-bundled enameloid described by
LUND (1989) in teeth of Petalodontiformes, but in the lat-

ter, this layer is never directly above the dentine. This
arrangement of the enameloid is also reminiscent of the
SCE of some hybodonts, in which the crystallites of apa-
tite show mainly a radial orientation (REIF 1973: fig. 2C;
RIEPPEL 1981: fig. 11E). Like the posterior teeth of *S.
rhaeticus*, teeth of *Lissodus minimus* show a low profile
indicative of adaptation to a durophagous diet so, for
comparison, one tooth of *L. minimus* from bed R22 was
etched for 1min 30s in 5% HCl. The ultrastructure of the
enameloid appears different from that of *S. rhaeticus*. The
enameloid comprises single crystallite enameloid in
which the crystallites of apatite are randomly oriented,
with an average length of 0.5 μm and diameter of 0.05
μm (Fig. 5H). The crystallites therefore appear shorter
than those described by DUFFIN (1985) in this species, but
this could be related to the overall size of the tooth stud-
ied. The surface of the enameloid shows numerous 'ca-
nals', with diameters ranging from 0.5 to 1 μm. DUFFIN
(1985) noted that in teeth of *L. minimus*, the crystallites
tend to be organized into radially arranged bundles, a fea-
ture that G.C. has also found in sections of *L. minimus*
tooth enameloid from Aust Quarry (Fig. 5I). Again, this
arrangement is reminiscent of LUND's radial-bundled
enameloid (LUND 1989). The 'canals' on the surface of
the tooth from Lons-le-Saunier are probably set in be-
tween adjacent bundles. The enameloid ultrastructure is
therefore very different when comparing *S. rhaeticus* and
L. minimus.

Family *incertae sedis*

'*Hybodus*' minor AGASSIZ 1837
Fig. 6A-C

Materials: 51 varyingly preserved teeth from bed R11
(MALS 1998.2.16), 8 from bed R20 (MALS 1998.2.17), and 5
from bed R22 (MALS 1998.2.18).

Description: These teeth are often badly preserved.
They show a moderately labio-lingually compressed
main cusp, sometimes almost circular at its base. This
cusp has blunt cutting edges and is flanked by one or two
pairs of well developed lateral cusplets (Fig. 6A, B). In
some teeth, the second pair of cusplets originate from the
base of the first pair and are not in contact with the root,
giving the extremities of the crown a hooked appearance
in labial or lingual view. The crown is ornamented by
strong ridges, which are well marked at the base of the
cusps but which generally do not reach the apex. In la-
bial view, the crown is triangular in shape, often with a
wide base. The crown/root junction is not incised, and
the crown never overhangs this junction. The root is
semicircular in occlusal view, projecting lingually from
the crown base. In mesial or distal view, its base appears
slightly concave, with some open vascular canals in the
central depression of some teeth (Fig. 6C), which are ori-
ented labio-lingually and are parallel to each other. These
appear to be roofed in the labial and lingual extremities
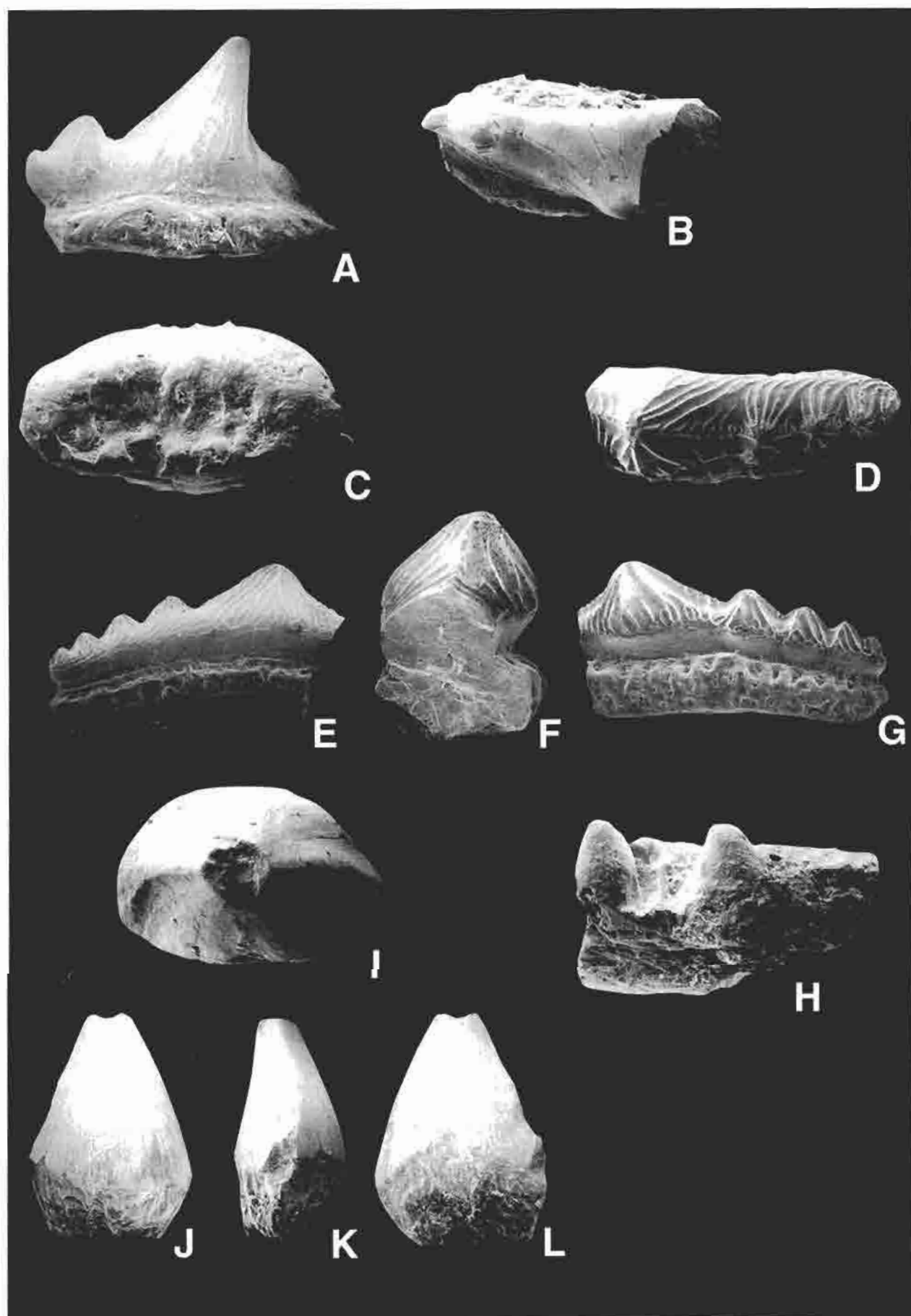of the root. However, one tooth, from bed R22, on which

Fig. 6. – **A-C:** Tooth of *'Hybodus' minor* (MALS 1998.2.16) in A: lingual, B: apical, and C: basal view. **D-G:** Tooth of *Synechodus rhaeticus* (MALS 1998.2.14) in D: apical, E: labial, F: ?mesial or ?distal, and G: lingual view. **H:** Jaw fragment of a sphenodont (MALS 1998.2.37) in lingual view. **I-L:** Premaxillary tooth of an ornithischian dinosaur (MALS 1998.2.39) in I: apical, J: labial, K: ?mesial or ?distal, and L: lingual view. – All scale bars = 0.5 mm.

all the cusps are broken, shows a root with a series of open vascular canals at the base of the labial face, giving its margin a corrugated appearance. This feature could be the result of wear of the basal labial part of the root. In lingual view, the root shows a row of large vascular foramina, situated in the upper part of the lingual face. In labial view, the root is shallow compared to the height of the crown.

Discussion: These teeth agree with the description of those of *Hybodus minor* given by DUFFIN (1993) although the recent study of the enameloid ultrastructure has demonstrated that the teeth of *'Hybodus' minor* belong to a neoselachian, and not a hybodont shark (CUNY 1998; CUNY et al. 1998; GODEFROIT et al. 1998). Teeth of *'Hybodus' minor* possess all but one of the diagnostic characters of the Synechodontiformes, as defined by DUFFIN & WARD (1993), the only difference being that the open vascular canals in the basal face of the root are roofed labially. The vascularization of the root of *'H.' minor* is, nevertheless, very similar to that of typical Synechodontiformes, with a series of basal vascular canals (DUFFIN & WARD 1993), and if the basal labial part of the root happens to be worn, the root vascularization show no difference with that of a typical Synechodontiformes. *'H.' minor* is therefore included here in the Synechodontiformes, and the diagnosis of this order given by DUFFIN & WARD (1993) is amended as follows:

Synechodontiformes: "the basal face of the root has a series of open vascular canals, which may be roofed labially, and which shallow and terminate lingually" instead of "The basal face of the root has a series of open vascular canals originating labially and shallowing and terminating lingually".

It should also be noted that the character: "The lingual face of the root is convex and lingually displaced", given by DUFFIN & WARD (1993), is primitive for the basal neoselachian sharks (CUNY 1998).

Inside the Synechodontiformes, *'Hybodus' minor* is probably closer to the Palaeospinacidae (teeth with a moderately high central cusp, flanked by lateral cusplets and never flanked with low blades, basal root face arcuate to a variable degree, with deep open vascular canals in the central depression; see DUFFIN & WARD 1993) than to the Orthacodontidae, but as this genus appears primitive, at least in the vascularization of its root, its familial assignment is still problematic. *'H.' minor* may prove to belong to the genus *Rhomphaiodon* DUFFIN 1993, in a family of its own (CUNY & EDWARDS in prep.).

Class Reptilia LAURENTI 1768
Subclass Diapsida OSBORN 1903
Subdivision Archosauria COPE 1869
Superorder Dinosauria OWEN 1842
Order Ornithischia SEELEY 1888
Figs. 6I-L, 7A-D

Materials: One tooth from bed R11 (MALS 1998.2.39).

Description: The tooth is 1.3 mm high and 1.1 mm wide at its base. In lateral view, the outline of the crown is low and triangular-shaped (Figs. 6J, L, 7C, D). In apical view, the crown appears to be asymmetrical, the labial side being more developed than the lingual one (Figs. 6I, 7B). Mesial and distal edges have developed thick keels, particularly clear in lingual view. The distal keel is denticulated (around 4 denticles per mm); the denticles are coarse and poorly preserved (Figs. 6K, 7A). The crown shows no cingulum, and its enamel appears to lack ornamentation, with only some cracks at the base which are attributed to the mode of preservation. The base of the tooth is poorly preserved, making it difficult to determine if there is a well-developed neck separating the crown from the root. There is no preserved wear facet.

Discussion: This tooth was previously misidentified by one of us (G.C.) as belonging to a phytosaur (CUNY 1993, 1995b). The presence of coarse denticles is suggestive of a herbivorous adaptation (e.g. GALTON 1986; HUNT & LUCAS 1994). The principal latest Triassic herbivorous groups are aetosaurs, prosauropods and ornithischians; the latest rhynchosaurs are early Norian in age (HUNT & LUCAS 1991). Aetosaur teeth lack denticles, and this tooth differs from those of prosauropods in being asymmetric in anterior/posterior view (HUNT & LUCAS 1994: fig. 12.3). The French tooth is very similar to premaxillary teeth referred to early ornithischian dinosaurs (e.g., HUNT 1989; HUNT & LUCAS 1994). Similar features include (compare HUNT & LUCAS 1994: figs. 12.4A-F, 12.5C-F, 12.7F, 12.8A, C): (1) asymmetrical in anterior/posterior view; (2) slightly recurved in lateral view; (3) in lingual view, the crown is slightly convex with a narrow sulcus dividing the denticulated margin from the main body of the tooth; the sulcus decreases in prominence towards the apex; (4) the lingual surface is slightly incurved and; (5) the labial surface of the tooth is more convex than the lingual. The possession of this suite of characters strongly suggests that the tooth is the premaxillary tooth of an ornithischian.

There are relatively few late Triassic ornithischians (HUNT 1991; GODEFROIT & CUNY 1997) to compare with the French tooth, and all those represented by premaxillary teeth are from North America (HUNT & LUCAS 1994). The new tooth differs from the premaxillary teeth of: *Revueltosaurus*, in being wider and lower in lateral view, i.e., closer to an equilateral triangle in shape (compare HUNT 1989: pl. 8, figs. E-F); *Galtonia*, in that in anterior/posterior view, the base is less bulbous (compare HUNT & LUCAS 1994: fig. 12.4A) and; *Pekinosaurus*, in being much less bulbous in anterior/posterior view (compare
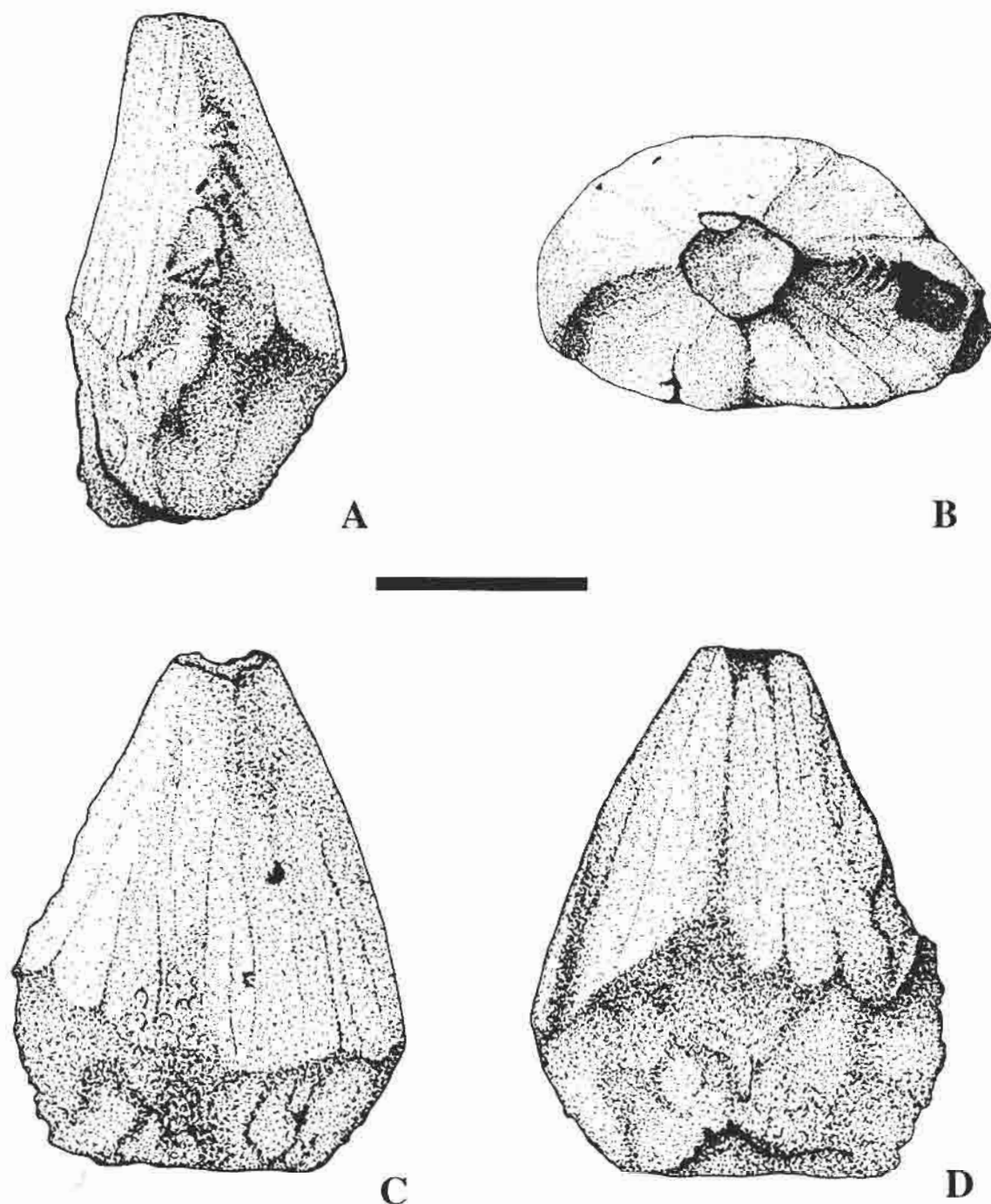
Fig. 7. Premaxillary tooth of an ornithischian dinosaur (MALS 1998.2.39) in A: ?mesial or ?distal, B: apical, C: labial, and D: lingual view. – Scale bar = 0.5 mm.

HUNT & LUCAS 1994: fig. 12.5F), and in that the lingual sulci extend much lower down the crown (compare HUNT & LUCAS 1994: fig. 12.5D). Undescribed premaxillary teeth of the late Carnian *Tecovasaurus* also differ from the French tooth (A.H. pers. obs.). The early Norian *Lucianosaurus* is only known from maxillary/dentary teeth (HUNT & LUCAS 1994). Some ornithischian teeth have also been described from the French Upper Triassic at Saint-Nicolas-de-Port (Lorraine), but they are different from the one described here; the ornithischian teeth

of type 1 and 2 from Saint-Nicolas-de-Port are ornamented on the lingual side, while those of type 3 are much lower than the one from Lons-le-Saunier (GODEFROIT & CUNY 1997). These teeth are, however, probably dentary/maxillary teeth, making comparisons difficult.

In conclusion, the new tooth undoubtedly represents the premaxillary tooth of an ornithischian and it differs from all other known ornithischian premaxillary teeth. It is possible that it represents the premaxillary tooth of *Lucianosaurus*, currently known only from other denti-

tion. However, the much greater age of the North American form makes this unlikely; no Late Triassic ornithischian teeth are currently known from two successive stages, probably reflecting the rapid early diversification of this group. Therefore, it is likely that the new tooth represents a new genus of ornithischian.

Discussion

In Western Europe, microremains are the most common vertebrate fossils found at the top of the Triassic (CUNY 1993), providing most of the evidence concerning faunal evolution at the Triassic/Jurassic boundary, and allowing detection of rare components of the fauna. Identification of microremains is difficult, but may be aided by the study of the enameloid ultrastructure of isolated teeth.

The ultrastructure of the enameloid as a taxonomic criterion

Teeth of 'Hybodus' minor are so-called because of their superficial similarity to hybodont teeth but the presence of triple-layered enameloid indicates that this taxon undoubtedly belongs to the Neoselachii. However, our knowledge of the structure of the enameloid of shark teeth is still in its infancy, and some types of enameloid are difficult to interpret. The teeth of Synechodus rhaeticus described above are demonstrative of this fact. Although unusual, their enameloid appears different from what can be observed among hybodont sharks (see above) and as it is triple-layered, it strongly suggests neoselachian affinities. The main deviations from the typical triple-layered enameloid in extant non-batoid neoselachian sharks are linked to a durophagous diet, as exemplified by Heterodontus (REIF 1973). Study of posterior teeth of Heterodontus portusjacksoni by REIF (1973) revealed an enameloid made of only two layers, an external SCE and an internal tangled-fibred enameloid (TFE). The PFE, resistant to tensile stresses (PREUSCHOFT et al. 1974; REIF 1978), is of little use in crushing teeth and tends to disappear. Posterior teeth of Heterodontus francisci studied by G.C. show a more reduced SCE than that figured in Heterodondus portusjaksoni by REIF (1973), suggesting an important variation in the enameloid ultrastructure at specific level. The enameloid ultrastructure of Synechodus rhaeticus teeth from Habay-la-Vieille was therefore interpreted as a neoselachian enameloid, highly adapted for a crushing diet, with a well developed single crystallite enameloid (SCE, but this included the layer of parallel bundles of fibres described above) and a reduced tangled-fibred enameloid (TFE) (CUNY 1998). However, this situation is almost the opposite of the one observed in Heterodontus where the TFE forms the main part of the enameloid. Synechodus rhaeticus may therefore represent a different mode of adaptation to a durophagous diet among neoselachian sharks. The presence of radial fibres in between the bundles of fibres parallel to the surface in the middle layer suggests

it is indeed a PFE (REIF 1973). The fact that the main bundles are quite indistinct may indicate partial loss of this layer which would have subsequently become a SCE layer, resistant to compressive stresses (PREUSCHOFT et al. 1974). However, this does not explain the unusual orientation of the bundles, nor the presence of a single layered radial-bundled enameloid in some part of the teeth of S. rhaeticus. Radial-bundled enameloid seems, nevertheless, to be quite common among chondrychthyans (LUND 1989).

Teeth of three species of Synechodus (S. incrementum, S. multinodosus, S. volaticus) have also been recently described from the Upper Triassic of Canada (JOHNS et al. 1997), and these authors provide some sections of the enameloid of the teeth. Teeth of S. multinodosus and S. volaticus show a well developed PFE, while the enameloid of the S. incrementum teeth is more unusual. The PFE figured by JOHNS et al. (1997: pl. 7, figs. 1-3) seems to be recrystallized and may be an artefact. The other sections provided show bundles of fibres which appear to be preferentially oriented perpendicular to the surface, in a way quite similar to that which have been observed in the teeth of Synechodus rhaeticus from Lons-le-Saunier. As no illustrations of etched surfaces of the teeth were provided, it is not possible to assess if S. incrementum, like S. rhaeticus, possesses a PFE with bundles perpendicular to the axis of the crown. Nevertheless, teeth of S. incrementum are very similar morphologically to those of S. rhaeticus, and these two species are probably closely related. Whether or not they should be assigned to the genus Synechodus requires a better knowledge of the variation of the enameloid ultrastructure among the genus Synechodus, and among synechodontiform sharks.

Evolution of the faunas during the Rhaetian transgression

Some general trends may be noted across the studied section at Lons-le-Saunier. In bed R11, the shark fauna is dominated by the durophagous hybodont Lissodus minimus, while neoselachians represent only 8% of the total number of shark teeth, and are mainly represented by 'Hybodus' minor. In bed R22, however, neoselachians constitute 25% of the total number of shark teeth and are represented mainly by the quite peculiar durophagous form Synechodus rhaeticus (Fig. 8). Among osteichthyes, 'Birgeria' type teeth remain the commonest teeth throughout the 3 fossiliferous beds, although they show a decrease in abundance from bed R11 to bed R22. Among durophagous forms, Sargodon tomicus increases in abundance from bed R11 (7% of the total bony fish teeth) to bed R22 (30% of the total), and is the only one to reach bed R22 (Fig. 9). This suggests a re-organization of the durophagous faunas throughout the section, with the development of Synechodus rhaeticus and Sargodon tomicus. These observations are of little value, as the preservation and study of vertebrate microremains could suffer considerable bias, although some of the ten-
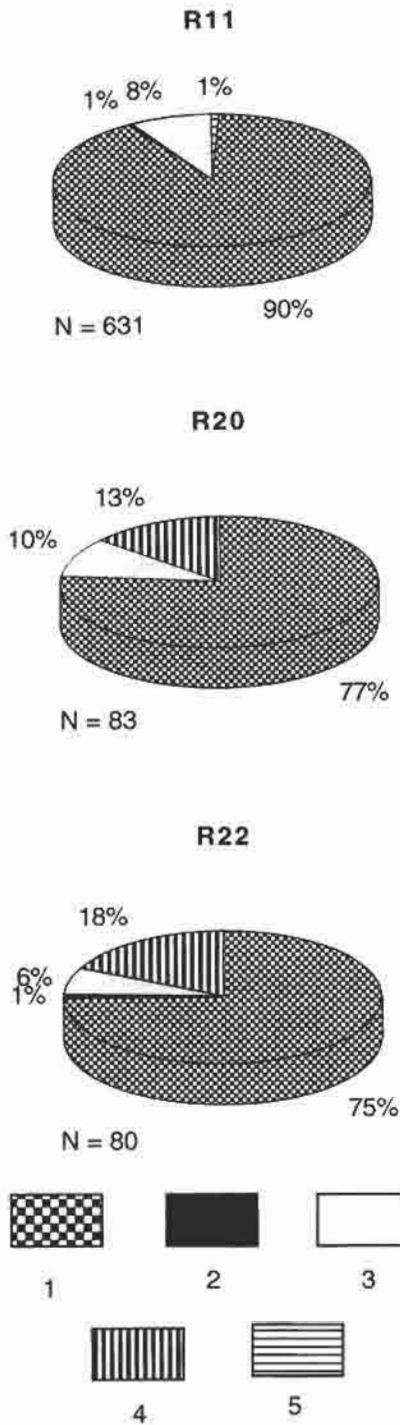
R11

N = 631

R11

N = 181

R20

N = 83

R20

N = 37

R22

N = 80

R22

N = 64

Fig. 8. Distribution of fossil shark teeth in each fossiliferous bed. 1: *Lissodus minimus*, 2: *Pseudodalatias barnstonensis + Pseudocetorhinus pickfordi*, 3: *'Hybodus' minor*, 4: *Synechodus rhaeticus*, 5: *Hybodus cloacinus*. Although *Pseudodalatias barnstonensis* and *Pseudocetorhinus pickfordi* are not related to each other, they have been considered together for clarity, as these teeth are rare in the sediment. N: total number of fossil shark teeth recovered in each bed.
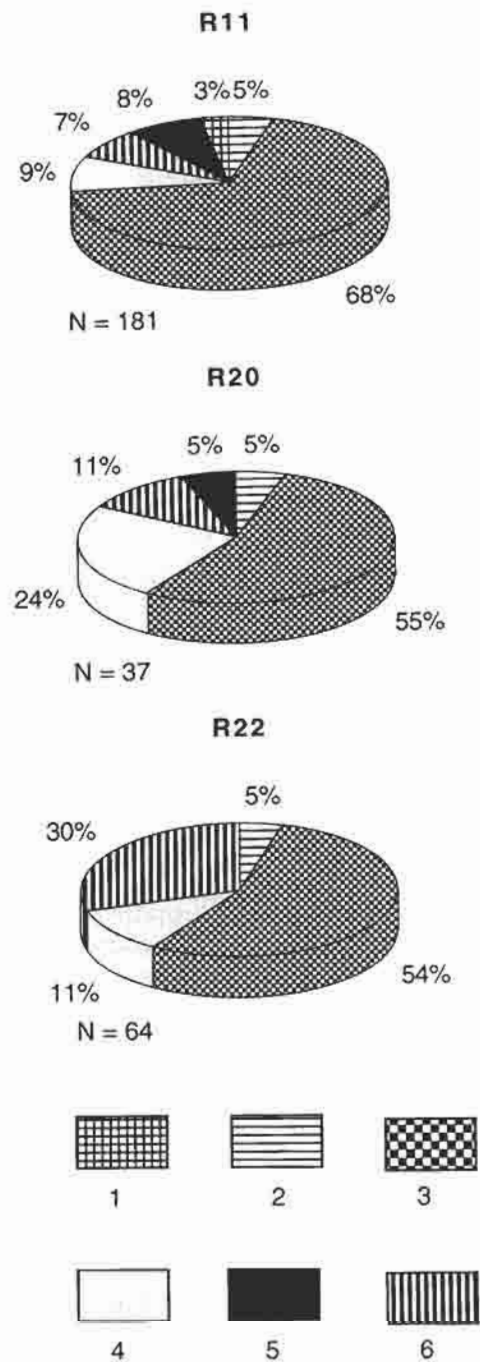
Fig. 9. Distribution of fossil actinopterygian teeth in each fossiliferous bed. 1: indeterminate Actinopteri, 2: *'Saurichthys'* type teeth, 3: *'Birgeria'* type teeth, 4: *'Gyrolepis'* type teeth, 5: indeterminate Neopterygii, 6: *Sargodon tomicus*, N: total number of fossil teeth recovered in each bed.

dencies described here seem to be repeated elsewhere. The progressive domination of *Sargodon tomicus* among durophagous Osteichthyes is confirmed in other sites in the Jura area (CUNY et al. 1994; CUNY 1995b), although

this fish remains rare in the Westbury Formation in Great Britain (M. CURTIS pers. com., G.C. pers. obs.). A drop in abundance of *'Birgeria'* type teeth was also noticed in the Westbury Formation by M. CURTIS (pers. com.). The drop

in abundance of *Lissodus minimus*, and the increase in abundance of neoselachian sharks during the Rhaetian transgression was also observed in the Westbury Formation, where it appears to be much more important (CURTIS, pers. com.). *Sargodon tomicus* is a successful newcomer from the Tethyan realm, where it is known since the Norian (TINTORI 1981, 1983), invading the Germanic realm with the Rhaetian transgression. *Synechodus rhaeticus* is not known before the beginning of the Rhaetian transgression, in Europe or elsewhere. Its appearance, like that of some primitive neoselachian sharks, may be directly related to the Rhaetian transgression over western Europe, although non-durophagous species such as '*Hybodus*' *minor* were well represented in the German realm since the Norian (CUNY 1998). Among the terrestrial component, the ornithischian dinosaur is one of the most ancient known in Europe (see GODEFROIT & CUNY 1997 for a complete review of the Triassic ornithischians), and its similarities with older North American forms may indicate an American origin for the European forms. However, ornithischian dinosaurs probably reached Europe before the Rhaetian transgression, which isolated the Western European archipelago from other landmasses (GODEFROIT & CUNY 1997; GODEFROIT et al. 1998). The diversity of the ornithischians from Saint-Nicolas-de-Port, a site slightly older than Lons-le-Saunier, seems to confirm this hypothesis, although detailed data about the evolution of the species represented by vertebrate microremains during the Rhaetian transgression are patchy, and no firm conclusion can be reached. Detailed study of Belgian sites like Habay-la-Vieille, located between the Jura area and British sites, would probably provide valuable data to elucidate the pattern of the evolution of vertebrate faunas in Western Europe at the Triassic/Jurassic boundary.

Conclusion

The study of the vertebrate microremains from a palynologically dated Rhaetian section at Lons-le-Saunier reveals variations in the faunal composition at the base of the Rhaetian. Major changes are seen among the durophagous marine fauna, with the dominance of *Sargodon tomicus* among bony fishes, and the development of neoselachian sharks. Study of the ultrastructure of isolated shark teeth enameloid allows recognition of the typical neoselachian pattern in teeth presumed to be of hybodont affinity ('*Hybodus*' *minor*), but also reveals an unusual, and previously unknown, pattern which remains difficult to interpret (*Synechodus rhaeticus*). Vertebrate microremains also allow recognition of small terrestrial vertebrates, among them one of the oldest teeth in Europe attributable to an ornithischian dinosaur. However, the data concerning the early radiation of Ornithischia in Europe are currently very fragmentary, and new discoveries are needed before a convincing hypothesis can be proposed.

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