

## PRIMITIVE NEOSELACHIAN SHARKS : A SURVEY.

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**Abstract :** A study of the ultrastructure of the enameloid of isolated teeth demonstrates that the neoselachian sharks, characterized by a triple-layered enameloid, radiated just after the Carnian, at the same time as some "experimental", poorly known sharks (*Vallisia*, *Raineria*, *Pseudodaltias* and *Doratodus*). Most of the Triassic neoselachian teeth share a hybodont-like architecture of the crown and a well-developed lingual torus in the root. These latter can be traced back at least in the Early Triassic. The clade *Eunemacanthus* + *Amelacanthus* + *Hopleacanthus* + *Acronemus* + Neoselachii may have appeared as far back as the Carboniferous. Isolated Palaeozoic teeth belonging to *Mcmurdodus* and *Anachronistes* may not belong to neoselachian sharks. Most likely, these isolated teeth represent the result of a convergence phenomenon in tooth morphology and vascularisation.

*Key words:* Neoselachii, early evolution, Palaeozoic, Triassic, enameloid ultrastructure.

### Une revue des néosélaciens primitifs (Chondrichthyes : Elasmobranchii).

**Résumé :** L'étude de l'ultrastructure du pseudo-émail de dents isolées montre que les néosélaciens, dont les dents sont caractérisées par la possession d'un pseudo-émail à trois couches superposées, ont connu une importante radiation juste après le Carnien, en même temps que des requins plus "expérimentaux" dont les relations de parentés demeurent un mystère comme *Vallisia*, *Raineria*, *Pseudodaltias* et *Doratodus*. La plupart de ces dents de néosélaciens du Trias supérieur montrent une architecture de la couronne très proche de celle des dents d'hybodontes et une projection linguale très nette de leur racine. Cette lignée remonte au moins au Trias inférieur. L'ensemble *Eunemacanthus* + *Amelacanthus* + *Hopleacanthus* + *Acronemus* + Neoselachii est monophylétique et l'apparition de ce clade remonte au moins au Carbonifère. Les dents isolées de *Mcmurdodus* et d'*Anachronistes* trouvées dans le Paléozoïque, malgré des similitudes d'apparences, pourraient ne pas appartenir à de vrais Neoselachii mais semblent plutôt être le résultat de phénomènes de convergence de la morphologie et du système de vascularisation de ces dents.

*Mots clés :* Neoselachii, évolution, Paléozoïque, Trias, ultrastructure de l'émail.

### INTRODUCTION

Two years ago, I made a preliminary survey of the evolution of French vertebrate faunas across the Triassic-Jurassic boundary (Cuny, 1995c). Concerning the selachians, I stated that "...a study of the enamel ultrastructure of their (Hybodontidae) teeth could reveal that some *Hybodus* teeth from various stages belong in fact to neoselachians....It thus appears that the diversity of the neoselachians during the Norian may have been underestimated". Indeed, according to Reif (1973), isolated teeth of neoselachian sharks can be recognized on the basis of

the structure of their enameloid (fig. 1), which is formed of three distinct layers: an external shiny-layered enameloid (SLE) composed of thin apatite crystals randomly oriented, a central parallel-fibred enameloid (PFE) formed mainly by surface-parallel apatite fibre bundles running in a basal-apical direction, and an inner tangled fibred enameloid (TFE) where the above-mentioned fibres become randomly oriented. Recent studies of the enameloid of Upper Triassic shark teeth have shown a triple-layered enameloid to occur in teeth previously thought to be of hybodont affinities. The abundance of neoselachian sharks during the Upper Triassic has therefore been under-

estimated and, for the first time in their history, they appeared to be well represented in the faunas. On the other hand, the Palaeozoic fossil record of the Neoselachii remains scarce and intriguing. The evolution of the group, from their first possible appearance in the Early Devonian to their first noticeable radiation in the Upper Triassic, remains poorly known. The phylogenetic position of most of the fossils, which consists of isolated teeth or fin-spines are still unclear. The present paper is intended as a quick survey of what we know (and don't know!) about the early evolution of the Neoselachii. This review will emphasize the study of the enameloid of the teeth.

The following abbreviations are used in the text: BRSMG: Geology Department, Bristol City Museum, BGM: Bath Geology Museum, GPIT: Department of Geology and Palaeontology, University of Tübingen, IRSNB: Institut Royal des Sciences Naturelles de Belgique, SMNS: Staatliches Museum für Naturkunde in Stuttgart, SNP: Saint-Nicolas-de-Port.

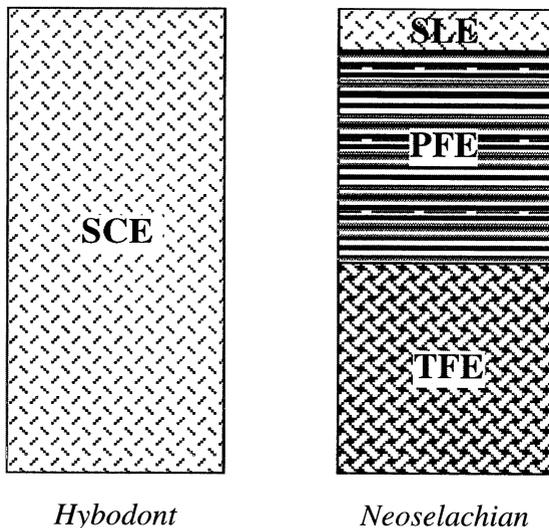


Fig. 1: Diagrammatic section of the enameloid in hybodont and neoselachian sharks. SCE: single crystallite enameloid. SLE: shiny layered enameloid. PFE: parallel fibred enameloid. TFE: tangled fibred enameloid.

Coupe schématique du pseudo-émail chez un hybodont et chez un néosélacien. SCE: pseudo-émail à cristaux simples. SLE: couche de pseudo-émail brillante. PFE: pseudo-émail à fibres parallèles. TFE: pseudo-émail à fibres enchevêtrées.

## EARLY STAGES IN THE EVOLUTION OF THE NEOSELACHIAN SHARKS.

The Palaeozoic and early Mesozoic fossil record of neoselachian sharks consists mainly of isolated teeth, dermal denticles and fin-spines. Therefore, the details of the early evolution of this group are poorly known. The first neoselachian shark may be as old as the Early-Middle Devonian, and is represented by some isolated teeth from Western Queensland (Australia) and attributed to *Mcmurdodus whitei* (Turner & Young, 1987). Another species, *Mcmurdodus featherensis*, is also known by a single tooth from the Middle-Late Devonian of Antarctica (see Turner & Young, 1987). The teeth of this genus are strikingly similar to those of the Hexanchidae, but the first record of this family does not occur until the Lower Jurassic (Cappetta, 1987). As the structure of the enameloid of the teeth of *Mcmurdodus* has not been studied, and taking into account the stratigraphical gap from the first Hexanchidae, it is very difficult to state whether *Mcmurdodus* is indeed the oldest known neoselachian. The similarity may be the result of a convergence in tooth morphology (Cappetta *et al.*, 1993).

The next oldest occurrences of possible neoselachian teeth are from the British Lower Carboniferous with the genus *Cooleyella* (Duffin & Ward, 1983). This genus is also known in the North American and Brazilian Upper Carboniferous (Duffin *et al.*, 1996; Gunnell, 1933) as well as in the North American Permian (Duffin & Ward, 1983). Duffin and Ward (1983) stated that "*Anachronistes* (= *Cooleyella*) is a neoselachian shark because it possesses a conical central cusp, well-developed lateral blades and a basal flange, a V-shaped basal face of the root, and a typical neoselachian root vascularization (hemiaulacorrhize)". However, these teeth lack an enameloid cover, which is quite a problematic feature. Recent phylogenetic hypotheses accept the Hybodontoida as the sister-group of the Neoselachii (Maisey, 1984; Gaudin, 1991) and the structure of the enameloid in some Upper Triassic Neoselachii may suggest that it is derived from a more primitive single crystallite enameloid (SCE). There is therefore little support for Duffin and Ward's hypothesis concerning the presence of unenamelled teeth in primitive neoselachians. A secondary loss of the enameloid cover is also

problematic as there is no other example of such a loss across the whole lineage, and it is difficult to justify this in mechanical terms.

Moreover, a conical central cusp flanked by lateral blades seems to be present in non-neoselachian sharks (*Pseudodalatias*, *Doratodus*, see below), while Duffin and Ward (1983) noted that a basal flange is also present in the hybodont *Steinbachodus* (see below). Finally, the hemiaulacorhize state is, as far as I know, unknown outside the Neoselachii but, given the present state of knowledge, convergence cannot be ruled out. All in all, the arguments to consider *Cooleyella* a true neoselachian are rather weak (Thies & Reif, 1985; Turner & Young, 1987), and the phylogenetic position of this genus remains unclear.

*Hopleacanthus richelsdorfensis* is quite a well known genus from the Permian of Germany (Schaumberg, 1982). It 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: notochordal sheath segment calcified anteriorly; fin-spines with a mantle of shiny enameloid and lacking posterior tubercles; and 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 however quite unclear. The drawing of the vertical section of one of them (Schaumberg, 1982 : fig. 2) was made according to a single abraded scale (Schaumberg, pers. com.) and a new study of the dermal skeleton of this genus would be welcome. Two teeth of this genus are known, but the ultrastructure of their enameloid was not studied. Until a reassessment of the structure of the teeth and dermal denticles is made, the exact affinities of *Hopleacanthus* will be difficult to elucidate. The character "fin-spines with a mantle of shiny enameloid and lacking posterior denticles" also appears in the Carboniferous genera *Amelacanthus* and *Eunemacanthus*, known only from fin-spines (Maisey, 1982).

The earliest unequivocal neoselachian tooth is known from the Lower Triassic rocks 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*. *Palaeospinax* is moreover a *nomen dubium* (Duffin and Ward, 1993; Thies 1993), and if this tooth does belong to a palaeospinacid, it should therefore be attributed to the genus *Synechodus*. Quite similar teeth have also recently been reported from the Middle Triassic strata of Nevada (USA) as ?*Palaeospinax* sp. by Rieppel *et al.* (1996). The roots of these teeth are poorly preserved and the vascularization system cannot be properly observed. It is impossible, for the same reasons as those given above, to assess whether these teeth belong to a true palaeospinacid. Moreover, the lateral cusplets appear to be well separated from the main cusp, which according to Cappetta (1992) and Duffin and Ward (1993), is a characteristic of *Paraorthacodus* rather than of *Synechodus* (the latter including teeth formerly described as *Palaeospinax* teeth). The roots of these North American teeth are projected lingually and perpendicular to the crown, which may indicate neoselachian affinities (see below). The exact relationships between the Nevada teeth and the neoselachians, as well as for the Turkish tooth, cannot be assessed at the present time.

*Acronemus tuberculatus*, from the Middle Triassic of Monte San Giorgio (Switzerland), was first considered as a ctenacanth shark (Rieppel, 1982). Maisey (1984) pointed out two characters indicating some affinities of this genus with the neoselachian sharks: fin-spines with an ornament of shiny enamelled lateral tubercles and anterior keel, and an absence of posterior denticles on the concave posterior wall; and body dermal denticles of the non-

growing, placoid type with widely spaced longitudinal striae. However, the dermal denticles were not described in detail by Rieppel (1982), and very similar dermal denticles seem to occur in *Hopleacanthus*. Moreover, the teeth display only a single crystallite enameloid (SCE), which would exclude this genus from the Neoselachii. A secondary adaptation to a crushing diet would however explain the loss of the triple layered enameloid in a neoselachian, as is seen in the Rajiformes and in the posterior teeth of *Heterodontus*. However, there is usually a remnant of the tangled fibred enameloid, while, according to Rieppel (1982), this is not the case in *Acronemus*. *Acronemus* does not appear to be a true neoselachian, but *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: "fin-spines with an ornament of shiny enamelled lateral tubercles and anterior keel and without any posterior denticles on the concave posterior wall" is a primitive character for the Neoselachii.

The genus *Nemacanthus* is based solely on fin-spines of a similar structure than those of *Acronemus* and were reported in the Lower Triassic of Spitzbergen (*Nemacanthus* sp., Stensiö, 1921), East Greenland (*Nemacanthus* sp., Stensiö, 1932) and Idaho, U.S.A. (*Nemacanthus* (*Cosmacanthus*) *elegans*, Evans, 1904) and is common in the Upper Triassic of Western Europe (*Nemacanthus monilifer*; see below). The affinities of this genus are discussed later. The neoselachian fossil record from the Devonian up to the Middle Triassic remains sparse, with a low diversity and most of the fossils having uncertain phylogenetic positions. It is not even certain that the remains belong to true neoselachians. We have to wait until the Upper Triassic to see more diversified neoselachian faunas.

#### A SURVEY OF THE POSSIBLE NEOSELACHIAN SHARKS FROM THE UPPER TRIASSIC.

Until recently, the neoselachian sharks were known by six species in the uppermost Triassic (Norian + "Rhaetian"), all restricted to Europe : *Nemacanthus monilifer* Agassiz, 1837; *Hueneichthys costatus* Reif, 1977; *Reifia minuta* Duffin, 1980;

*Vallisia coppi* Duffin, 1982; *Synechodus rhaeticus* (Duffin, 1982); and *Rhomphaiodon nicolensis* Duffin, 1993.

*Nemacanthus monilifer* is known solely from isolated fin spines, but is a common species in the Upper Triassic of Western Europe. It has been reported in Great Britain (Westbury Formation, Storrs 1994), France (Saint-Nicolas-de-Port, Cuny & Ramboer, 1991 ; Varangéville, Godefroit, 1997; Boisset, Cuny, 1993 a ; and Provenchères-sur-Meuse, Cuny, 1995b), Belgium (Habay-la-Vieille, Duffin *et al.*, 1983), Luxembourg (Medernach, Delsate, 1995), Italy (Lombardy, Boni, 1937) and Germany (Wurttemberg, Boni, 1937; Schmidt, 1928). The affinities of this genus were, for a long time, unclear. Maisey (1975) stated that "*Nemacanthus* is a slightly earlier euselachiform shark than *Palaeospinax*, or else a ctenacanthiform closely allied to primitive Euselachiformes (i.e. Neoselachii)" and later (Maisey, 1977) considered it as "closely allied to *Palaeospinax* and may represent an immediate ancestor". Cappetta (1987) included it in the family Palaeospinacidae. However, as quoted above, the characters used by Cappetta to include it in the family Palaeospinacidae seem to be primitive for the Neoselachii. Cuny and Ramboer (1991) and Cuny (1995b) considered it as a derived ctenacanthoid. This assertion was based on the concave posterior wall of the spine, the central cavity displaced backwards and the presence of a row of hook-like denticles on the posterolateral margins. This condition is very similar to that of *Ctenacanthus* (Maisey, 1981; Rieppel, 1982) and leads me to accept a ctenacanth ancestry for the neoselachian sharks, as suggested by Maisey (1975, 1977). In contrast, recent analyses of the phylogeny of the chondrichthyans (Gaudin, 1991 ; Maisey, 1984) indicate that the sister-group of the Neoselachii is the Hybodontoidae. That means that the similarities between the dorsal fin spines of *Ctenacanthus* and *Nemacanthus* are based on primitive characters only, without any phylogenetic significance (Maisey, 1984). The presence of an enamelled ornamentation would preclude *Nemacanthus* from belonging to the Ctenacanthoidae (Maisey, 1982), but would remain a primitive character for the Neoselachii. Whether *Nemacanthus* is a true neoselachian or belongs to its sister-group (see above) appears impossible to prove on the basis of fin-spines alone.

*Hueneichthys costatus* is known from a single tooth (GPIT 1510) found in the German Rhaetic near Stuttgart (Reif, 1977). The root of the tooth is not preserved and the crown is tricuspid and lacks any specific characters. According to the external shape only, this tooth could hardly be recognized as a shark tooth (Huene, 1933). It was the ultrastructure of the enamel which allowed Reif (1977) to recognize that this fossil belongs to a neoselachian shark. The tooth shows a SLE and a PFE. No TFE was found by Reif, but as the tooth was unique, no section was made. It is therefore possible that a TFE exists below the PFE. According to Reif, the most important characteristic of this tooth is the presence of an additional layer of fibres in the PFE at the level of the ridges ornamenting the crown. The fibres of this extra layer run in a horizontal direction parallel to the surface. This feature is unknown in any other neoselachian sharks.

*Reifia minuta* is known from five isolated, minute teeth (SMNS 50.200 to 50.204) found in the Lower Norian of Germany (Duffin, 1980). The enameloid is imperfectly known, but seems to display at least a PFE and a TFE, although an SLE could also have been present (Duffin, 1980). The TFE appears quite peculiar, being made of single, randomly oriented crystallites, rather than true fibers (Duffin, 1980 : fig. 3e, 3f). This structure is very reminiscent of that described by Duffin (1993b) in *Rhomphaiodon nicolensis* (see below). Based on the overall morphology of the teeth, Duffin (1980) suggested that *Reifia* was a member of Galea (*sensu* Shirai, 1996) closer to the Orectolobiformes than to the Carchariniformes. Cappetta (1987) pointed out, however, that the teeth of *Reifia* lack the lingual enameloid protuberance at the base of the crown and the labial apron, which are characteristic of the Orectolobiformes. He favoured a closer relationships with the Carchariniformes rather than with the Orectolobiformes. However, the same author also pointed out the resemblance of the teeth of *Reifia* to those of some Batomorphii like Sclerorhynchidae, which could indicate squalean affinities rather than galean. The main problem is that the teeth of *Reifia* lack apomorphic characters at the level of the crown and the vascularization of the root appears quite primitive. It is anaulacorhize, but with a reduction in the number of foramina on the lingual side of the root. There is just one centro-lingual foramen flanked by a margino-lingual foramen on each

side. This arrangement is quite reminiscent of the Casier's (1947) squatinoid type, but a central foramen on the basal face is lacking. It is therefore difficult to assess whether the relationships of *Reifia* are with the Squalea or the Galea.

*Vallisia coppi* is known from seven isolated teeth (BRSMG Cc 400 to 404, BGM CD 59, 60) found in the Westbury Beds (Penarth Group, Somerset) and in fissure fillings (Holwell, Somerset) (Duffin, 1982b). This species was also found in Belgium near the village of Hachy, close to Habay-la-Vieille, but no description has been published (Duffin *et al.*, 1983). The crown morphology of this genus is unique among neoselachians, and the superficial resemblances to Orectolobiformes and Heterodontiformes seem to be the result of convergence (Duffin, 1982b; Cappetta, 1987). Duffin (1982b, 1983) suggested batoid affinity for this genus, based mainly on the holaulacorhize root morphology of the teeth. However, Duffin (1982b) stated that some teeth have a rhinobatoid-type vascularization, while others have a scyliorhinoid-type pattern. According to Casier (1947) however, these two types of vascularization arose independently. The scyliorhinoid-type is restricted to Galea while the rhinobatoid-type is only found among Rajiformes. Recent cladistic analysis of the extant elasmobranchs (Shirai, 1996; De Carvalho, 1996) put the Rajiformes into the Squalea, and support Casier's hypothesis that the two types of vascularization arose independently. The appearance of both types of vascularisation in *Vallisia* may suggest a rather different evolution of the vascularization system than that seen in modern elasmobranchs. The presence of partially roofed grooves in some teeth, unknown in modern holaulacorhize teeth, would also suggest the same. This may indicate that *Vallisia* shares no affinity with the modern elasmobranchs, neither Squalea nor Galea. As the structure of the enameloid has not yet been studied, it is difficult to prove that *Vallisia* is a real neoselachian.

*Synechodus rhaeticus* was first named as *Palaeospinax rhaeticus* by Duffin in 1982a on the basis of several fin-spines from the Westbury Beds of Aust Cliff (South Gloucestershire, England) and in the fissure fillings at Holwell (Somerset, England). The presence of fin-spines and teeth of *Palaeospinax* was however noticed as early as 1889 by Woodward, although the teeth mentioned by this latter author do

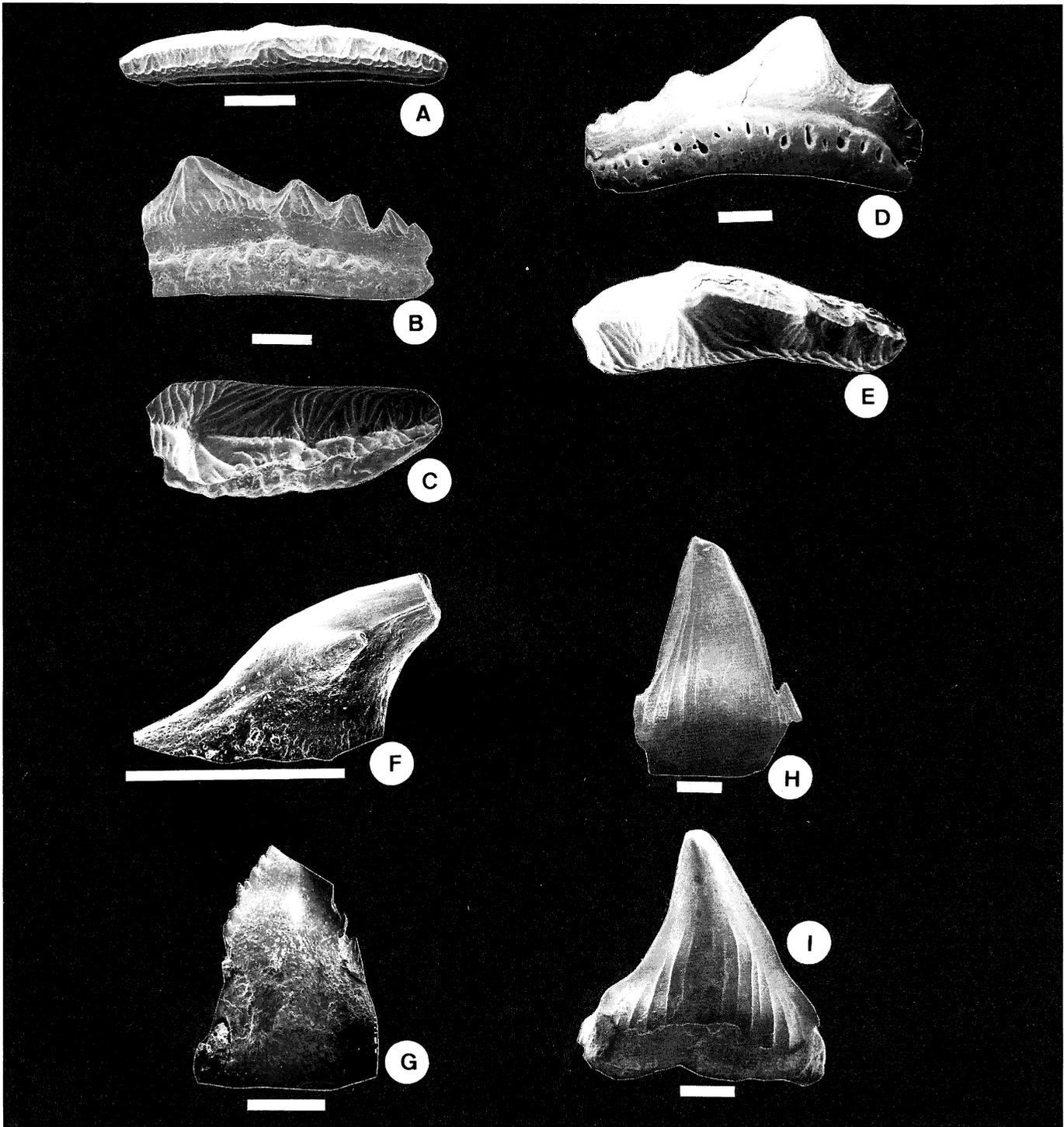


Fig. 2: A-E: Teeth of cf. *Synechodus rhaeticus* from the Rhaetic in A,C,E: apical and B,D: lingual views. A: Posterior and D,E: lateral teeth from Habay-la-Vieille (Belgium). B,C: Lateral tooth from Lons-le-Saunier (Jura, France). F-G: Teeth of *Pseudodalatias barnstonensis* from the Rhaetic of Saint-Germain-les-Arlay (Jura, France). F: Upper tooth in lateral view and G: lower tooth in labial view. H,I : Teeth of the new species from Grozon in labial views. H: Anterior tooth and I: lateral tooth. All scale bars represent 1 mm.

A-E: dents de cf. *Synechodus rhaeticus* provenant du rhétien en vues A,C,E: apicales et B,D: linguales. A: Dent postérieure et D,E: latérale provenant d'Habay-la-Vieille (Belgique). B,C: Dent latérale provenant de Lons-le-Saunier (Jura, France). F-G: Dents de *Pseudodalatias barnstonensis* provenant du rhétien de Saint-Germain-les-Arlay (Jura, France). F: Dent supérieure en vue latérale et G: dent inférieure en vue labiale. H,I : Dents de la nouvelle espèce de Grozon en vues labiales. H: Dent antérieure et I: dent latérale. Toutes les barres d'échelles représentent 1 mm.

not seem to belong to *Palaeospinax*, but to a hybodontiform shark (Duffin, 1982a). In 1993 Duffin and Ward claimed that the name *Palaeospinax* has to be restricted to a single specimen of *Palaeospinax priscus* with no character of taxonomic value and is thus a *nomen dubium* (for a review of the *Palaeospinax* problem, see Cappetta, 1987, 1992 and Thies, 1991, 1992, 1993). They move the species *rhaeticus* into the genus *Synechodus*. Teeth of “*Palaeospinax rhaeticus*” have been cited in the “Rhaetian” of Habay-la-Vieille (Belgium) by Delsate and Lepage (1991). These authors provide rather poor illustrations and no real description of these teeth. They seem to be characterized by rather low cusps. The accessory cusps are not well separated from each other or from the main one. The crown is densely ornamented with ascending ridges. At the base of the labial face of the crown, the ornamentation appears to be reticulate. The root shows a pseudopolyaulacorhize vascularization. I have also found rather similar teeth (fig. 2B, C) in the “Rhaetian” of Lons-le-Saunier (Jura, France). Preliminary study of the enameloid of some teeth from Habay-la-Vieille (fig. 2A, D, E) and Lons-le-Saunier has revealed a thick layer of SCE (fig. 3A). Below, there is a layer of TFE, made of entangled bundles of fibres of apatite crystallites (fig. 3B). This structure appears very similar to that described by Reif (1973) in *Heterodontus* although the thickness of the TFE is much more reduced in the Triassic teeth than in this latter genus. This structure could indicate a specialization toward a crushing dentition, as the SCE is resistant to compressive stresses while the PFE is resistant to tensile stresses (Preuschoft *et al.*, 1974). This is in accordance with the low profile of the studied teeth. However, no formal description of the teeth of *Synechodus rhaeticus* is currently available in the literature (this should be done shortly, C. Duffin, pers. comm.) and the interpretation of these results remains therefore problematic. The cyclopondylous vertebrae reported in the Penarth Group in Great Britain are often associated with *Synechodus rhaeticus*, since calcified vertebrae are unknown in ctenacanthiform and hybodontiform sharks (Woodward, 1889; Maisey, 1977; Duffin, 1982a; Storrs, 1994). The phylogenetic position of the Palaeospinacidae (*Synechodus (Palaeospinax)* + *Paraorthacodus*) remains much disputed. This family is sometimes considered as the sister-group of the

other Neoselachii (De Carvalho, 1996), or as basal Galea (Maisey, 1985, Cappetta, 1987), or as the sister-group of the Squalea (Duffin & Ward, 1993). The latter hypothesis is based only on dental characters, however. Such different interpretations highlight our lack of knowledge concerning primitive Neoselachii.

*Rhomphaiodon nicolensis* is known from hundreds of teeth found in the French locality of Saint-Nicolas-de-Port, which is better known for having yielded numerous teeth of early mammals. These teeth are housed in the collection of the Institut Royal des Sciences Naturelles de Belgique (SNP 1000 to 1005, SNP 1008 and hundreds of uncatalogued teeth) (Duffin, 1993b). *Rhomphaiodon* may also be present in the Knollenmergel of Halberstadt (Germany, Duffin, 1993b) and this genus has been cited at Varangéville, a locality a few kilometres east of Saint-Nicolas-de-Port, by Godefroit (1997). This latter author has provided no description nor illustration of the teeth however. Morphologically, the teeth of *Rhomphaiodon nicolensis* are quite similar to those of “*Hybodus*” *minor*, a common species in the Upper Triassic of Western Europe. Teeth of “*Hybodus*” *minor* are generally more squat and less elongate in overall shape than those of *Rhomphaiodon nicolensis*, with better developed ridges on the lingual side of the crown. Teeth from juvenile *Rhomphaiodon nicolensis* also show higher lateral cusplets than in juvenile “*Hybodus*” *minor* (Duffin, 1993b). According to Duffin (1993b), the enameloid of the teeth of *Rhomphaiodon* possess a unique triple-layered structure with a surface SLE, a central PFE and a basal layer of haphazard single crystallite enameloid. This latter layer appears strikingly similar to the basal layer of the teeth of *Reifia minuta* (compare Duffin, 1980, fig. 3e, 3f and Duffin, 1993b, Pl.4, fig. 2). I have studied the enameloid of one tooth from Saint-Nicolas-de-Port, and I have found the remnants of a surface SLE, a central PFE (fig. 3C) and a typical TFE made of entangled bundles of fibres of apatite (fig. 3D). This latter layer was only found in the upper third of the cusps. On the other hand, I was unable to demonstrate the existence of a basal layer of haphazard single crystallite enameloid like that illustrated by Duffin (1993b). These results may indicate that at least two different species of neoselachian sharks co-existed in Saint-Nicolas-de-Port but more work is required to reach a firm conclusion.

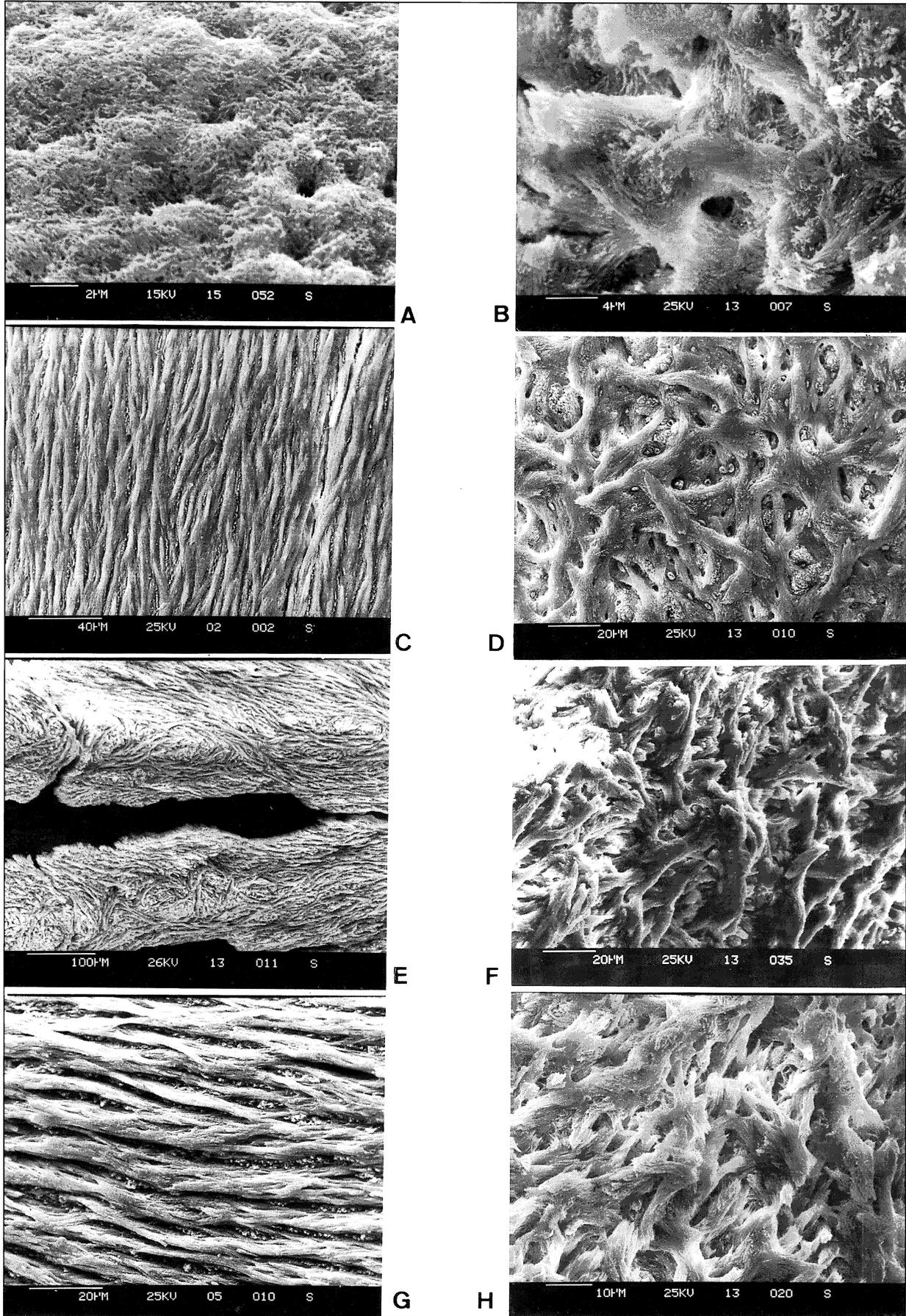


Fig. 3

Fig. 3 : A-B: cf. *Synechodus rhaeticus* from the Rhaetic. A: Thick SCE-like layer at the surface of a tooth from Habay-la-Vieille (Belgium), etched 30s in 10% HCl. B: Inner TFE in a tooth from Lons-le-Saunier (Jura, France), etched 10mn 35s in 10% HCl. C-D: "*Hybodus*" *minor* (?) from Saint-Nicolas-de-Port (Meurthe-et-Moselle, France). C: PFE in a tooth etched 50s in 10% HCl and D: TFE at the apex of a tooth etched 5mn 50s in 10% HCl. E-F: New Grozon species. E: Appearance of the TFE at the level of the ridge of a tooth etched 2mn 50s in 10% HCl and F: TFE at the apex of a tooth etched 5mn 20s in 10% HCl. G-H: "*Pseudocetorhinus pickfordi*" from the Rhaetic of Habay-la-Vieille. G: PFE in a tooth etched 40s in 10% HCl and H: TFE at the apex of a tooth etched 6mn 40s in 10% HCl. All the photographs represent the surface of the teeth after etching.

A-B: cf. *Synechodus rhaeticus* provenant du rhétien. A: Epais niveau ressemblant à un SCE à la surface d'une dent provenant d'Habay-la-Vieille (Belgique), attaquée 30s dans de l'HCl dilué à 10%. B: TFE interne dans une dent provenant de Lons-le-Saunier (Jura, France), attaquée 10mn 35s dans de l'HCl dilué à 10%. C-D: "*Hybodus*" *minor* (?) provenant de Saint-Nicolas-de-Port (Meurthe-et-Moselle, France). C: PFE dans une dent attaquée 50s dans de l'HCl dilué à 10% et D: TFE à l'apex d'une dent attaquée 5mn 50s dans de l'HCl dilué à 10%. E-F: nouvelle espèce de Grozon. E: Apparition du TFE au niveau d'une ride d'ornementation sur une dent attaquée 2mn 50s dans de l'HCl dilué à 10% et F: TFE à l'apex d'une dent attaquée 5mn 20s dans de l'HCl dilué à 10%. G-H: "*Pseudocetorhinus pickfordi*" provenant du Rhaetic d'Habay-la-Vieille. G: PFE dans une dent attaquée 40s dans de l'HCl dilué à 10% et H: TFE à l'apex d'une dent attaquée 6mn 40s dans de l'HCl dilué à 10%. Toutes les photographies ont été prises en surface après attaque à l'acide.

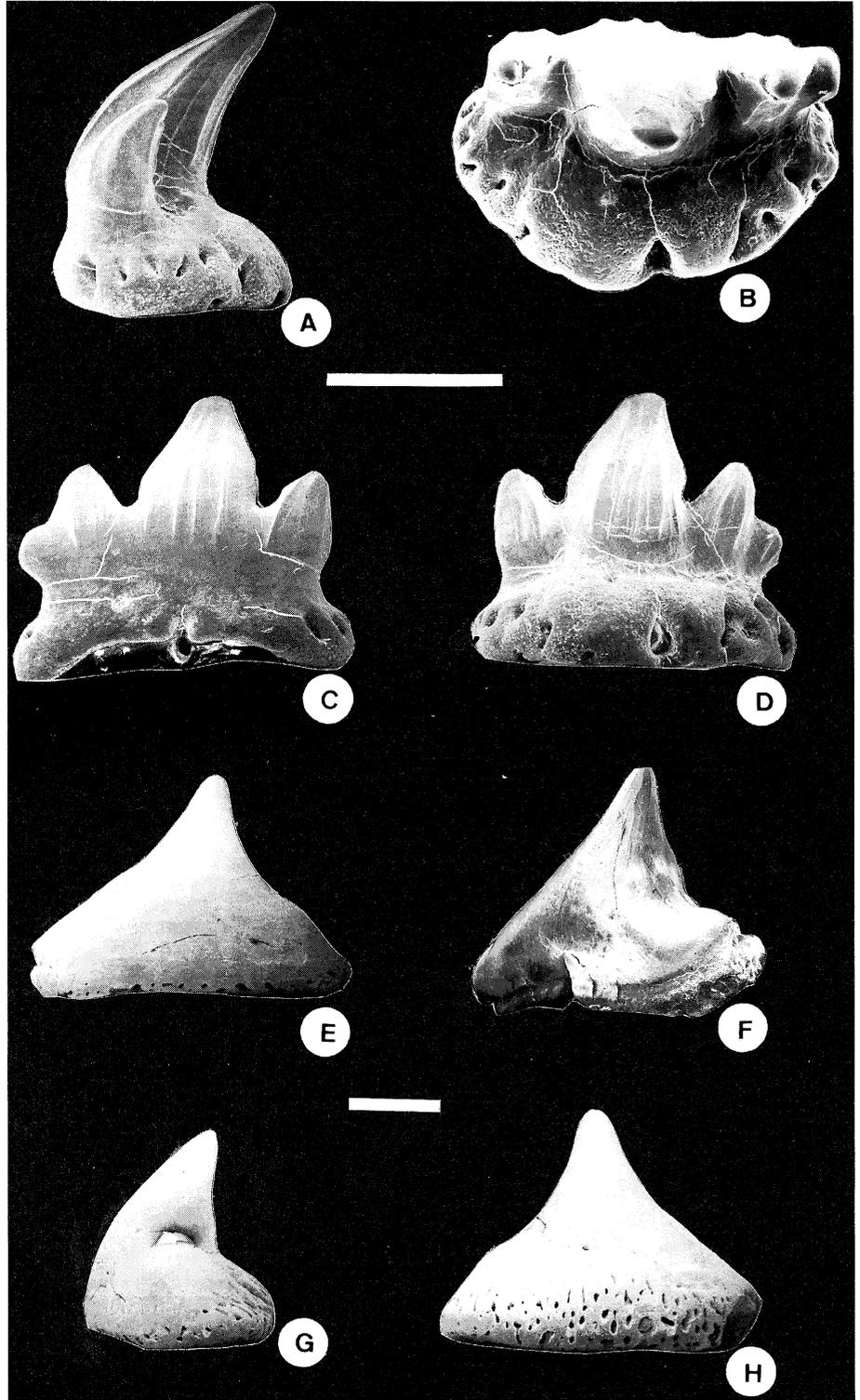


Fig. 4: A-D: Tooth of "*Hybodus*" *minor* from the Rhaetic of Aust (South Gloucestershire, England) in A: lateral, B: apical, C: labial and D: lingual view. E-H: Teeth of "*Pseudocetorhinus pickfordi*" from the Rhaetic in E,F: labial, G: lateral and H: lingual views. E,G,H from Habay-la-Vieille (Belgium) and F from Saint-Germain-les-Arlay (Jura, France). All scale bars represent 1 mm.

Fig. 4: A-D: Dent d'"*Hybodus*" *minor* provenant du rhétien d'Aust (South Gloucestershire, Angleterre) en vues A: latérale, B: apicale, C: labiale et D: linguale. E-H: Dents de "*Pseudocetorhinus pickfordi*" provenant du rhétien en vues E,F: labiales, G: latérale et H: linguale. E,G,H provient d'Habay-la-Vieille (Belgique) et F de Saint-Germain-les-Arlay (Jura, France). Toutes les barres d'échelle représentent 1 mm.

Three other species from the Upper Triassic of Northwestern Europe have problematic affinities and should be discussed here : *Doratodus* cf. *tricuspidatus* Schmid, 1861; *Pseudodalatias barnstonensis* (Sykes, 1971); and *Raineria osswaldi* Cappetta, 1987.

*Doratodus tricuspidatus* was originally described by Schmid (1861) from the Lower Keuper outcropping near Jena (Germany) but the type series of teeth seem to have been lost (Duffin, 1981). Similar teeth have also been reported in the Muschelkalk of Lorraine (France) by Sauvage (1883) and from the Lower Norian of Southwestern Germany (*Doratodus* cf. *tricuspidatus*, Seilacher, 1943). The enameloid of these teeth is formed by a SCE which suggests hybodont affinities for this genus (Duffin, 1981). Duffin (1981) and Cappetta (1987) noted, however, that the morphology of these teeth is very different from that of any other hybodonts. The tooth crown is strongly differentiated from the root, and a crown/root junction deeply incised around the whole tooth is reminiscent of the neoselachian condition (Duffin, 1981). The root morphology is unknown. While the structure of the enameloid precludes *Doratodus* from being a Neoselachii, it does not seem to be a hybodont shark either.

*Pseudodalatias barnstonensis* was first named as *Dalatias barnstonensis* by Sykes (1971) on the basis of isolated teeth. The dentition of this genus, with a strong dignathic heterodonty, shows remarkable convergence with that of the extant *Dalatias* (Squalea: Dalatiiformes: Dalatiidae) (fig. 2F, G). Later, however, Reif (1978a) showed that these teeth belong to a new genus which he named *Pseudodalatias* and for which he erected a new family: Pseudodalatiidae. This new family is characterized by teeth having a thin layer of a peculiar SCE, with crystals perpendicular to the tooth surface in the inner part of the enameloid layer but parallel to the surface, with a basal-apical direction in the outer part. Underneath the enameloid there is a thin layer of orthodentine. The rest of the crown and the whole root are formed by trabecular, acellular bone, a unique condition among advanced elasmobranchs (Reif, 1978a). Reif (1978a) very tentatively attributed this family to the Hybodontoidae, but there are no convincing arguments to do so (Cappetta, 1987). *Pseudodalatias barnstonensis* is quite a common

species, reported in the Rhaetic of Great Britain (Westbury Formation, in at least nine localities: Barnstone, Aust, Axminster, Blue Anchor Point, Westbury, Penarth, Lavernock, Lincolnshire, Leicestershire and Holwell : Sykes, 1974; Storrs, 1994), Belgium (Habay-la-Vieille : Duffin *et al.*, 1983; Attert, *et al.*, 1993), and the French Jura (Lons-le-Saunier : Cuny, 1995a,c ; Saint-Germain-les-Arlay : Cuny *et al.*, 1994; Boisset : Cuny, 1993a). *Pseudodalatias barnstonensis* was also reported from the Norian of Lombardy (Italy : Tintori, 1980), but, strangely, only lower teeth in connection were found, and no upper teeth. Moreover, the tooth described by Henry (1876) as *Hemipristis lavigniensis* in the Rhaetic of Lavigny (Jura, France) may also represent a lower tooth of *Pseudodalatias* (Cuny, 1993b, but see Duffin, 1981). I have studied the ultrastructure of the enameloid of some teeth from Aust, Habay-la-Vieille and Lombardy. The enameloid layer (fig. 6A) is indeed very thin, but so far, I am unable to confirm, or deny, Reif's observations. The affinities of this genus remain, however, poorly understood (Duffin, 1981; Cappetta, 1987; Storrs, 1994; Cuny, 1995c). As is the case for *Doratodus*, the teeth of *Pseudodalatias* show, in their overall shape, many similarities with those of neoselachians, but the structure of the teeth appears very different, which strongly suggests convergence. The relationship of *Doratodus* and *Pseudodalatias* with hybodonts is poorly supported and the hypothesis that they belong to a different, new and ephemeral group cannot be dismissed. From the Carnian to the end of the Rhaetic, marine faunas were strongly modified (Benton, 1991), with the appearance of the Teleostei and the explosive radiation of the Neopterygii (Dapediidae, Semionotidae, Macrosemiidae, Pycnodontiformes, Caturidae) (Gardiner, 1993; Patterson, 1993; Tintori, 1996). In Europe, the Rhaetic transgression represented a way for the Tethyan marine faunas to invade western Europe. The shallow sea covering the area was a good environment for the radiation of new lineages. This could explain the appearance at that time of some ephemeral sidebranch shark lineages (*Vallisia?*, *Doratodus*, *Pseudodalatias*, *Raineria?*), quickly replaced by true neoselachians.

*Raineria osswaldi* is known only by an almost complete rostrum from the Rhaetic of Austria. It was referred to as *Raineria* nov. gen. by Osswald (1928),

who did not give a species name to the specimen. Cappetta (1987) has proposed *Raineria osswaldi*. The elongated rostrum of this species is quite similar to that of the Pristiophoridae, Sclerorhynchidae and Pristidae and shows dermal denticles of the placoid morphotype (Duffin, 1981; Cappetta, 1987). This led Duffin (1981) and Thies and Reif (1985) to consider *Raineria* as a neoselachian shark. Cappetta (1987) pointed out, however, that the oldest members of the three families Pristiophoridae, Sclerorhynchidae and Pristidae did not appear before the Albian and the elongated rostrum of *Raineria* would therefore be the result of convergence. Moreover, contrary to the more recent families, the rostrum possesses sharp lateral edges, probably devoid of rostral teeth (Cappetta, 1987). Placoid scales appear in all Neoselachii and pre-Rhaetic Hybodontoida according to Reif (1978b). However the distribution of this character is insufficiently known to allow its use for taxonomic purposes (see above in *Acronemus* and *Hopleacanthus* for example). Cappetta (1987) stated that "It is not impossible that the rostrum of *Raineria* belongs to the selachian of doubtful affinities.... *Pseudodalatias* Reif." and so he considers it as a possible Hybodontoida. There is no direct evidence of the association of *Raineria* and *Pseudodalatias*. The latter is known in the Rhaetic of Great Britain, Belgium and France, and in the Norian of Lombardy, but was never recorded in the Rhaetic of Austria. Moreover, Cappetta (1987) also pointed out some similarities in the shape of the teeth of *Reifia minuta* to those of the Sclerorhynchidae, but he did not consider an association *Reifia/Raineria*. Without more complete material, it is impossible to state the real affinities of *Raineria*.

Duffin (1981) considers that *Steinbachodus estheriae* Reif, 1980 approaches the neoselachian condition as its teeth show considerable differentiation of the crown. The root is of hybodontid organisation and vascularisation, and the crown displays only a SCE (Reif, 1980). Cappetta (1987) pointed out, moreover, similarities between the anterolateral teeth of *Steinbachodus* and those of *Polyacrodus*. I agree with Cappetta that *Steinbachodus* is a true hybodontoid.

## NEW DATA ABOUT UPPER TRIASSIC NEOSELACHIAN SHARKS.

I have recently undertaken a systematic survey of the ultrastructure of the enameloid of isolated teeth from the Upper Triassic of Western Europe. This leads to the recognition of triple-layered enameloid in species hitherto thought to belong to the Hybodontoida. There is "*Hybodus*" *minor*, and also a species not yet officially named, but appearing sometimes as "*Pseudocetorhinus pickfordi*" (Delsate & Lepage, 1991; Cuny, 1993b), and usually considered to be a hybodont. There is also a new species, which will be described in detail elsewhere, from Grozon, in the French Jura.

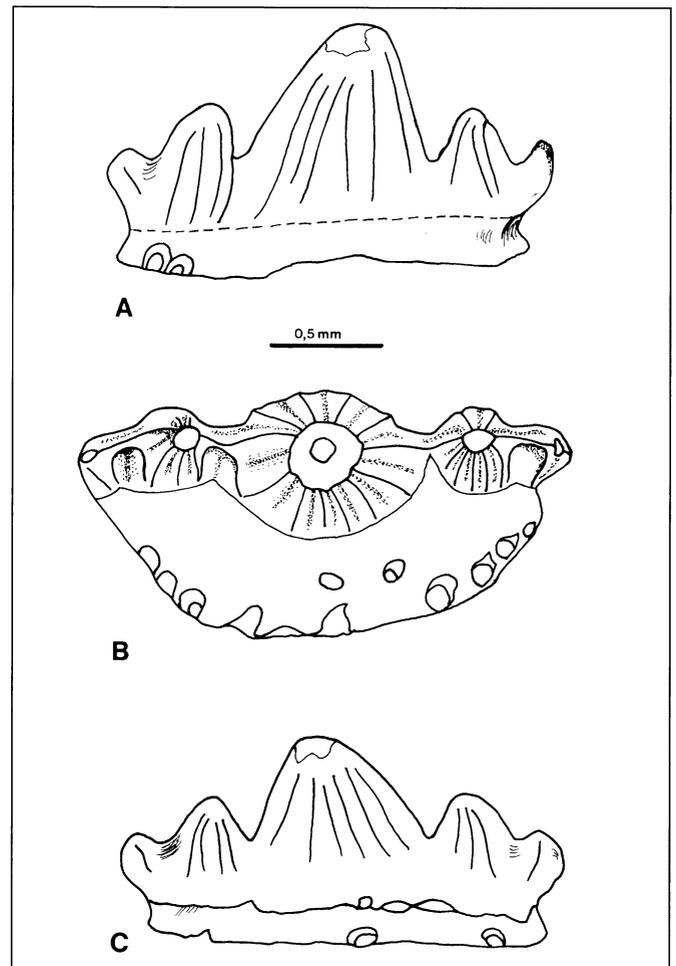


Fig. 5: Tooth of "*Hybodus*" *minor* from the Rhaetic of Saint-Germain-les-Arley (Jura, France) in A: labial, B: apical and C: lingual views.

Fig. 5: Dent d'"*Hybodus*" *minor* provenant du rhétien de Saint-Germain-les-Arley (Jura, France) en vues A: labiale, B: apicale et C: linguale.

Teeth of "*Hybodus*" *minor* from Aust (Westbury Formation, England, fig. 4A-D), Habay-la-Vieille (Grès de Mortinsart, Belgium), Medernach (Steinmergelgruppe, Luxembourg), Syren (Rhaetic, Luxembourg), and Saint-Germain-les-Arlay (Groupe des calcaires marneux et des "schistes noirs" du Rhétien, France, fig. 5) have been studied. All these teeth show a triple-layered enameloid with surface SLE (fig. 6B, C, D), a middle PFE (fig. 6E, F, G) and an internal TFE (fig. 6H). J. Day has independently reached similar conclusions with teeth of "*Hybodus*" *minor* coming from Aust (J. Day, pers. com.). However, some important differences exist in the layering of "*Hybodus*" *minor*. At the level of the ridges ornamenting the crown, the SLE is thicker than in other parts of the crown (fig. 6C, D). Below this thick SLE, the PFE shows an unusual feature as the bundles of fibres show a change in orientation, becoming perpendicular to the axis of the ridges rather than being oriented in a basal-apical direction (fig. 6E, G). This is very similar to the condition described in *Hueneichthys costatus* by Reif (1977, see above). However, there is not a true extra layer, but a gradual change of orientation of the bundles of fibres at the level of each ridge. This could also be the case in *Hueneichthys costatus* as the detail of the structure in the figure provided by Reif (1977, fig. 4) is masked by numerous radial fibres. The TFE layer was shown to exist with certainty only in teeth coming from Aust, Syren, and Saint-Germain-les-Arlay. Teeth from Habay-la-Vieille and Medernach have not yet been checked in this regard. When the surface of the teeth is etched with diluted HCl, TFE seems to be restricted to the upper third of the crown only, as in the teeth from Saint-Nicolas-de-Port (see above). It is possible that the species "*Hybodus*" *minor*, difficult to distinguish from *Rhomphaiodon nicolensis* on a morphological basis, is also present at this site. Some sections made in teeth from Aust show, however, that a TFE also exists at the base of the crown. The reason why this basal TFE never show up with surface etching, while the apical one do, is unclear. There may have been a problem with the preparation of the teeth and further work is needed to check this.

The vascularisation of the teeth of "*Hybodus*" *minor* is also interesting. As noted earlier by several authors, the root of "*Hybodus*" *minor* is lingually projected (Woodward, 1889; Maisey, 1977; Duffin,

1993a, Storrs 1994; Cuny *et al.*, 1994; Cuny, 1995b), forming what Maisey (1975, 1977) called a lingual torus (figs. 4A, B, 5B). On the lingual face, the root is penetrated by numerous, small, irregularly distributed vascular foramina (fig. 4B, D).

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Fig. 6: A: *Pseudodalatias barnstonensis*, Rhaetic of Habay-la-Vieille, Belgium, tooth etched 10s in 10% HCl. Ultrastructure of the enameloid showing single, randomly oriented crystallites of apatites. B-H: "*Hybodus*" *minor*. B: Remnant of the SLE at the surface of a tooth etched 5s in 10% HCl. C: Thick SLE at the level of a ridge ornamenting the surface of the crown, tooth etched 20s in 10% HCl. The SLE has disappeared from the other part of the crown, showing the underlying PFE. D: Thick SLE at the level of the cutting edge of a tooth etched 10s in 10% HCl. E: Ridge at the surface of the crown of a tooth etched 1mn in 10% HCl, with the SLE removed, showing the change in orientation of the bundles of fibres of the PFE. F: PFE at the surface of the crown of a tooth etched 30s in 5% HCl + 1mn in 10% HCl. G: PFE at the level of the ridges of a tooth etched 35s in 10% HCl. H: Inner TFE at the apex of a tooth etched 6 mn in 10% HCl. B,G from the Rhaetic of Saint-Germain-les-Arlay (Jura, France), C from the Norian of Medernach (Great-Duchy of Luxemburg), D,H from the Rhaetic of Aust (South Gloucestershire, England), E from the Rhaetic of Syren (Great-Duchy of Luxemburg), F from the Rhaetic of Habay-la-Vieille (Belgium). All the photographs represent the surface of the teeth after etching.

Fig. 6: A: *Pseudodalatias barnstonensis*, rhétien d'Habay-la-Vieille, Belgique, dent attaquée 10s dans de l'HCl dilué à 10%. Ultrastructure du pseudo-émail montrant des cristaux simples, orientés au hasard. B-H: "*Hybodus*" *minor*. B: Restes du SLE à la surface d'une dent attaquée 5s dans de l'HCl dilué à 10%. C: SLE épaissi au niveau d'une ride d'ornementation de la couronne d'une dent attaquée 20s dans de l'HCl dilué à 10%. Le SLE a disparu sur les autres parties de la couronne, découvrant le PFE sous-jacent. D: SLE épaissi au niveau de la carène d'une dent attaquée 10s dans de l'HCl dilué à 10%. E: Ride d'ornementation à la surface d'une dent attaquée 1mn dans de l'HCl, et dont le SLE a été enlevé, montrant le changement d'orientation des faisceaux de fibres du PFE. F: PFE à la surface d'une dent attaquée 30s dans de l'HCl dilué à 5% et 1mn dans de l'HCl dilué à 10%. G: PFE au niveau d'une ride d'ornementation d'une dent attaquée 35s dans de l'HCl dilué à 10%. H: TFE interne à l'apex d'une dent attaquée 6 mn dans de l'HCl dilué à 10%. B,G provenant du rhétien de Saint-Germain-les-Arlay (Jura, France), C du Norien de Medernach (Grand-Duché de Luxembourg), D,H du rhétien d'Aust (South Gloucestershire, Angleterre), E du rhétien de Syren (Grand-Duché de Luxembourg), F du rhétien d'Habay-la-Vieille (Belgique). Toutes les photographies ont été prises en surface après attaque à l'acide. ►

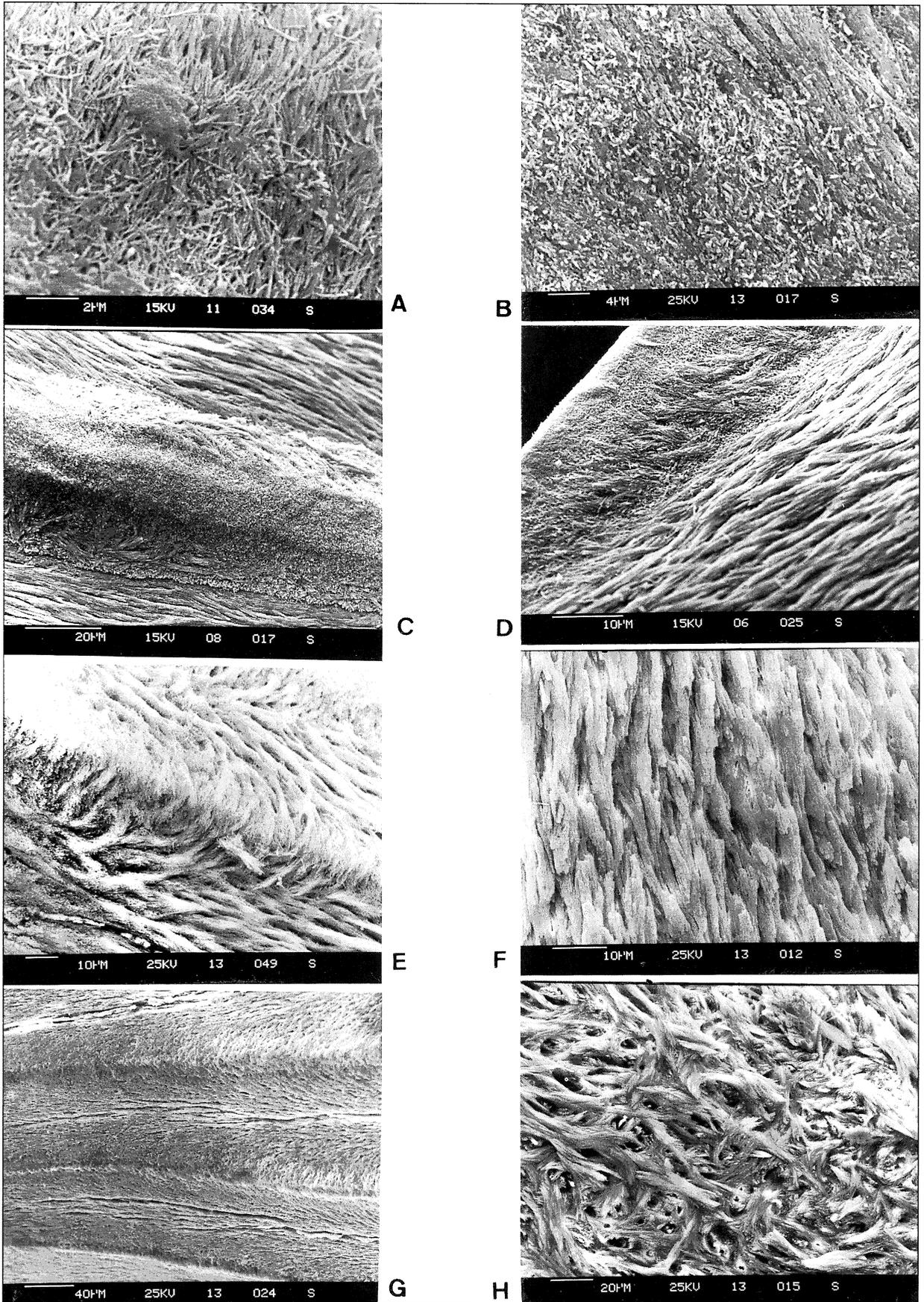


Fig. 6

The basal face is convex, with a depression oriented mesio-distally and situated just under the base of the crown. In this depression, there are some, fewer than ten on average, open vascular canals. These canals become covered lingually and labially and their openings on the labial side appear relatively large, near the base of the root. In some teeth however, there is a very well-developed central foramen, corresponding to Casier (1947)'s "foramen médio-externe" (fig. 4C). When the anterior part of the root is worn away, which happens quite often, the base of the labial face appears corrugated, as in the *Synechodontiformes* (Duffin & Ward, 1993; see the figures 10, 11 & 12 provided by Duffin, 1993a). It is probable that the pseudopolyaulacorhize state of the *Synechodontiformes* arose from a "*Hybodus*" *minor*-like anaulacorhize state. The appearance of the central depression in the teeth of "*Hybodus*" *minor* favoured the appearance of open canals in the central part of the root. The disappearance of the labial "wall" on the basal face of the root will allow these open canals to reach the labial side of the root, giving Cappetta's (1987) pseudopolyaulacorhize state. "*Hybodus*" *minor* now appears to be closely related to the Palaeospinacidae.

A new species recently found at Grozon (Cuny *et al.*, in press) displays the same structure of the enameloid as in "*Hybodus*" *minor* (fig. 3E, F). Both species are found together at this site, but the teeth of the new species differ from those of "*Hybodus*" *minor* by the more labiolingually compressed cusps with well-developed cutting edges and the absence of lateral cusplets (fig. 2I). Very reduced cusplets appear in the more anterior teeth only (fig. 2H). The root is projected lingually, but no open vascular canals were observed. The anaulacorhize vascularisation of the root appears more primitive than that of "*Hybodus*" *minor*.

I have studied the ultrastructure of the enameloid of teeth of "*Pseudocetorhinus pickfordi*" from Habay-la-Vieille (fig. 4E, G, H) only, although these teeth are also known to appear at Aust (pers. obs., Duffin, pers. com.), Holwell (Duffin, pers. com.), Syren (Cuny *et al.*, 1997), Attert (Duffin & Delsate, 1993) and Saint-Germain-les-Arlay (Cuny *et al.*, 1994) (fig. 4F). As these teeth will soon be described and officially named by C. Duffin (pers. com.), I shall not give a complete description of them here. The

teeth of Habay-la-Vieille show a triple-layered enameloid, but it is quite different from that of the two above-mentioned taxa. Firstly, the surface of the crown is mainly smooth. Therefore, the peculiar structure associated with the ridges in the above-mentioned taxa do not appear. Secondly, the SLE appears thicker than in the teeth of "*Hybodus*" *minor* or *Rhomphaiodon nicolensis*. In these taxa, a bath of five seconds in diluted HCl 10% is enough to remove most of the SLE, while in teeth of "*Pseudocetorhinus pickfordi*", 20 seconds are necessary to see the PFE (fig. 3G) appear near the apex of the crown, suggesting that the SLE is even thicker at the base of the crown. Taking into account this unusual thickness, it is unclear whether or not this SLE is homologous to that in modern neoselachians. In the latter, this layer is very thin and seems only to prevent cracks appearing in the PFE. It may have appeared secondarily. On the other hand, the thick layer in "*P. pickfordi*" could be a remnant of the primitive SCE of the Hybodontoidae. The appearance and development of the SLE in modern sharks is far from being fully understood and much more work is needed before a convincing hypothesis is reached. The TFE (fig. 3H) has been found in the upper third of the teeth only, as in "*Hybodus*" *minor*. The roots of the teeth of "*P. pickfordi*" are projected lingually (fig. 4G), but show an anaulacorhize state of vascularization, without any open canals. Foramina are randomly distributed on the whole surface of the lingual face of the root (fig. 4H) and at the base of the labial face (fig. 4E).

It is striking that in the Upper Triassic teeth possessing a triple-layered enameloid in which the root is well-preserved (*Synechodus rhaeticus*, *Rhomphaiodon nicolensis*, "*Hybodus*" *minor*, "*Pseudocetorhinus pickfordi*", and the new species from Grozon), all show a root 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 Ctenacanthoidae (Maisey, 1975) and to a lesser extent among Hybodontoidae, 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 Hybodontoidae is a derived character, and that the primitive Neoselachii have retained the primitive condition.

The Ctenacanthoidea, on the other hand, seem to have almost vanished by Upper Triassic times (Cappetta, 1987), and a revision of the teeth attributed to the ctenacanth *Phoebodus* in the Upper Triassic would certainly prove to be useful, as the real affinities of these teeth appear unclear (Cappetta, 1987). The crown morphology is extremely similar in hybodonts and primitive neoselachians. 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 Hybodontoida and those of primitive Neoselachii.

### "HYBODUS" MINOR AND NEMACANTHUS MONILIFER.

The hypothesis that the fin-spines of *Nemacanthus monilifer* and the teeth of "*Hybodus*" *minor* belong to the same animal is an old idea appearing sporadically in the literature (Woodward, 1891; Sauvage, 1907; Priem, 1908; Maisey, 1977; Storrs, 1994; Cuny, 1995b). The main problem with this hypothesis, however, is that the teeth, although sometimes considered unusual for a hybodont (Maisey, 1977; Storrs, 1994), were thought to belong to a hybodont (Duffin, 1993a), while *Nemacanthus monilifer* was supposed to share affinities with either Ctenacanthoidea or Neoselachii (see above). The present work proves that the teeth of "*Hybodus*" *minor* did not belong to a hybodont, but to a neoselachian shark, with a vascularisation of the root more primitive than in *Synechodus* (including *Palaeospinax*, see above). Interestingly, the fin-spines of *Nemacanthus monilifer* also appear more primitive than those of *Synechodus* (Maisey, 1977). These teeth and fin-spines appear, moreover, to be associated on an almost regular basis in Belgium (Duffin *et al.*, 1983), France (Cuny, 1995b), Germany (Schmidt, 1928), Great Britain (Woodward, 1891; Storrs, 1994), and Luxembourg (Duffin, 1993a; Delsate, 1995; Cuny *et al.*, 1997). Some exceptions can be explained as follows.

The absence of *Nemacanthus monilifer* in sites like Saint-Germain-les-Arlay (Cuny *et al.*, 1994) or Attert (Duffin & Delsate, 1993) seems to be directly related to the sorting of the sediment, these two sites having yielded millimetre-scale remains only. The

presence of "*Hybodus*" *minor* at Saint-Nicolas-de-Port, where fin-spines of *Nemacanthus monilifer* are known (Cuny & Ramboer, 1991), could not be ruled out at the present time, but need further investigation (see above). The species "*H.*" *minor* has to be removed from the genus *Hybodus*, but before a new genus is created, it would be worth carefully investigating a possible synonymy between *Nemacanthus monilifer* and "*Hybodus*" *minor*.

If confirmed, this synonymy will demonstrate that *Nemacanthus* is a primitive neoselachian, with no apomorphic characters in the fin-spines. On the other hand, *Hybodus minor* will be based on fin-spines only (Agassiz, 1833-43). As these fin-spines could also belong to the genus *Lissodus*, *Hybodus minor* is therefore a *nomen dubium*.

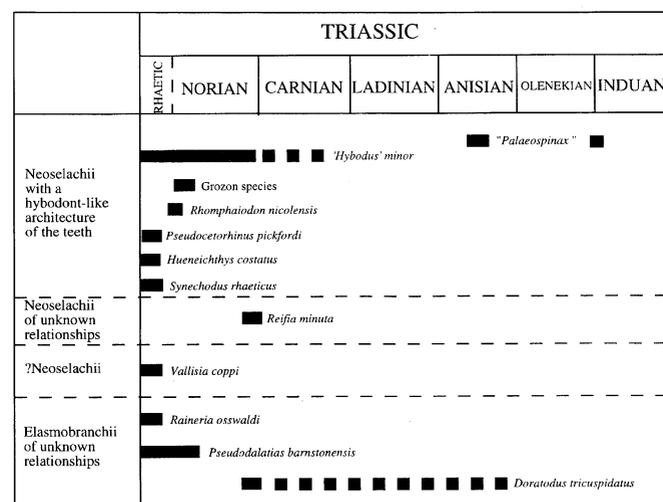


Fig. 7: Stratigraphic distribution of the Neoselachii and possibly related sharks in the Triassic showing the dramatic radiation of the group after the Carnian (*Nemacanthus monilifer* have been excluded because of a possible synonymy with "*Hybodus*" *minor*).

Fig. 7: Répartition stratigraphique des Neoselachii ainsi que des requins pouvant leur être apparentés durant le Trias montrant leur nette radiation après le Carnien (*Nemacanthus monilifer* n'a pas été pris en compte car il pourrait s'agir du même animal qu'"*Hybodus*" *minor*).

## CONCLUSION

The Upper Triassic (Norian + "Rhaetian") of Western Europe has yielded at least seven different neoselachian species :

- *Hueneichthys costatus*
- *Reifia minuta*
- *Synechodus rhaeticus*
- *Rhomphaiodon nicolensis*
- "*Hybodus*" *minor* / *Nemacanthus monilifer*  
(which could represent the same animal)
- new Grozon species
- "*Pseudocetorhinus*" *pickfordi*"

among which three (*Synechodus rhaeticus*, "*Pseudocetorhinus pickfordi*", and the new Grozon species) are still waiting a complete description. Some species (*Synechodus rhaeticus*, "*Hybodus*" *minor* ? *Nemacanthus monilifer* and "*Pseudocetorhinus pickfordi*") are quite common, reflecting the growing importance of the Neoselachii in the post-Carnian ecosystem (fig. 7). All of them share a similar ultrastructure of the enameloid, with at least a surface SLE and a middle PFE. The SLE often appears thicker than in extant neoselachians (at the level of the ridges in "*Hybodus*" *minor* and the new Grozon species, on the whole crown in "*Pseudocetorhinus pickfordi*" and *Synechodus rhaeticus*) and very similar in structure to the SCE of the Hybodontoida. It is possible that this Triassic SLE is not homologous to the SLE of the extant sharks, but represents a remnant of the primitive SCE that we find for example in *Acronemus*. In *Synechodus rhaeticus*, however, the thickness of the SLE in the posterior teeth appears to be a secondary adaptation towards a crushing diet. The TFE appears more variable in structure, consisting of single, randomly oriented crystallites in *Reifia* and *Rhomphaiodon*, or displaying the modern pattern (randomly oriented bundles of fibres) in *Synechodus rhaeticus*, "*Hybodus*" *minor*, "*Pseudocetorhinus pickfordi*", and the new Grozon species. TFE remains unknown in *Hueneichthys*.

Most of these teeth appear rather primitive in appearance, with a crown shape rather similar to the typical hybodont pattern (cusps rather blunt and moderately compressed labio-lingually, with lateral cusplets not well separated from the main cusp, crown often heavily ornamented) and retaining a well-developed lingual torus in the root. It is possible

that *Hueneichthys costatus*, *Rhomphaiodon nicolensis*, *Synechodus rhaeticus*, "*Hybodus*" *minor*, "*Pseudocetorhinus pickfordi*", and the new Grozon species are closely allied, but this hypothesis is based on primitive characters only. If true, this lineage would have been appeared at least in the Lower Triassic (Thies, 1982). The phylogenetic position of *Reifia minuta* is unclear. Together with the Neoselachii, the post-Carnian faunas show the appearance of strange, ephemeral forms such as *Doratodus*, *Pseudodalatias*, *Raineria*, and *Vallisia*. *Vallisia* may be a true neoselachian, but the three other genera appear to belong neither to the Neoselachii, nor to the Hybodontoida. The major change in the selachian faunas at the Carnian/Norian boundary is not restricted to Europe, as shown by the study of dermal denticles in Canada (Johns, 1996). However, dermal denticles do not allow analysis of this change from a taxonomic point of view. Before the Triassic, the evolution of the Neoselachii is hardly known. The Middle Triassic *Acronemus* shares the primitive structure of its fin-spines with the Neoselachii (mantle of shiny enameloid and lack of posterior denticles), but the absence of a triple-layered enameloid in its teeth precludes its assignment to the Neoselachii.

The character "mantle of shiny enameloid and lack of posterior denticles in the fin-spines" is therefore a synapomorphy for *Eunemacanthus* + *Amelacanthus* + *Hopleacanthus* + *Acronemus* + Neoselachii, which therefore represents a clade whose appearance can be traced back into the Carboniferous.

If *Hopleacanthus* possesses teeth with a triple-layered enameloid, it will be considered as a true neoselachian, but the exact relationships among *Eunemacanthus*, *Amelacanthus*, *Acronemus* and the Neoselachii are impossible to assess because of the fragmentary nature of their fossil record. Finally, the isolated Palaeozoic teeth attributed to the Neoselachii (*Mcmurdodus* and *Anachronistes*) appear quite specialized when compared to most of the Triassic teeth which possess a hybodont-like architecture of the crown and a well-developed lingual torus in the root. This would suggest, but not prove, that they are more likely the result of a convergence phenomenon than true neoselachian teeth.

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## NOTE ADDED IN PROOF.

Since the submission of this manuscript, teeth of *Synechodus rhaeticus* have been described (Duffin, 1998b) but additional studies of the enameloid of teeth from Lons-le-Saunier and Holwell (Cuny, submitted) have revealed a more complex structure than the one described above. There are indistinct bundles of fibres perpendicular to the surface or parallel to it but perpendicular to the axis of the tooth. As these patterns are different from the usual neoselachian pattern, the exact relationships of *Synechodus rhaeticus* are still enigmatic. Teeth of *Pseudocetorhinus pickfordi* have also been described by Duffin (1998a) as a lamniform neoselachian shark, close to the extant basking shark, *Cetorhinus maximus*. Teeth of the new species from Grozon have been named *Grozonodon candau* (Cuny *et al.*, in press). Finally, Johns *et al.* (1997) have published a review of the Triassic Canadian shark teeth and dermal denticles which complete the present work.

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