

GILLES CUNY & MICHAEL J. BENTON

## EARLY RADIATION OF THE NEOSELACHIAN SHARKS IN WESTERN EUROPE

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**ABSTRACT** - The Palaeozoic history of neoselachian sharks is barely known, and the first unequivocal member of this clade is recognized from the Lower Triassic. At the end of the Triassic, neoselachians show a dramatic radiation in Western Europe, where they are represented by seven genera. In the same area, we notice also the appearance of four genera of sharks of uncertain affinities, but showing some convergences with the neoselachians. So far, there is no evidence for such a radiation in other parts of the world, although this could be due to a sampling bias. We suggest that the Rhaetian transgression, which created an extensive shallow epicontinental sea over most of Western Europe, has favoured the diversification of the Neoselachii by providing a suitable environment.

**KEYWORDS:** SHARKS, NEOSELACHII, RADIATION, TRIASSIC, WESTERN EUROPE.

**RÉSUMÉ** - L'histoire des néosélaciens durant le Paléozoïque est pratiquement inconnue, et le premier représentant de ce clade qui puisse être reconnu avec certitude n'apparaît pas avant le Trias inférieur. A la fin du Trias cependant, les néosélaciens montrent une spectaculaire radiation adaptative avec pas moins de sept genres répertoriés en Europe de l'Ouest. Dans la même zone géographique, on note également l'apparition de quatre autres genres d'é-lasmobranches aux affinités encore mystérieuses mais montrant d'indéniables convergences avec les néosélaciens. Jusqu'à présent, aucun indice d'une radiation adaptative similaire n'a été noté ailleurs dans le monde, bien que cela puisse être lié à un artefact dans l'échantillonnage des fossiles. Nous proposons que la transgression rhétienne, installant une mer épicontinentale très peu profonde sur la plus grande partie de l'Europe de l'Ouest, a favorisé cette radiation en fournissant un environnement favorisant le développement des néosélaciens.

**MOTS-CLÉ:** REQUINS, NEOSELACHII, RADIATION, TRIAS, EUROPE DE L'OUEST.

### INTRODUCTION

The Neoselachii, modern sharks and rays, is a well characterized clade, with a range of features that relate to a more adaptable feeding system and capabilities of faster swimming than seen in earlier sharks (Maisey 1986; Gaudin 1991). The study of the early radiation of this clade is, however, made difficult by the lack of reasonably complete fossils, as the cartilaginous elements of their skeletons are rarely preserved. On the other hand, they produce hundreds of teeth during a lifetime, and these highly mineralized elements represent most of the fossil record of this group. 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). 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). On the basis of this character, the relationships of isolated Triassic shark teeth may be better

understood, and recent studies have demonstrated that neoselachian sharks were more common in the Upper Triassic than usually thought and that they show a wide range of adaptation.

**Abbreviations used in the text:** BRSMG: Bristol City Museum, Geology Collection; GPIT: Institut für Paläontologie und historische Geologie der Universität Tübingen; SMNS: Staatliches Museum für Naturkunde in Stuttgart.

### ORIGIN AND EARLY STAGES IN THE EVOLUTION OF THE NEOSELACHIAN SHARKS

The origin and the early stages in the evolution of neoselachian sharks are still controversial, because of a poor Palaeozoic fossil record. It is now well established that they are the sister-group of the hybodontoids (Young 1982; Maisey 1984a,b; Gaudin 1991; De Carvalho 1996), although there are still some disagreements about the position of some primitive genera (*Onychoselache*, *Tristychius* and *Hopleacanthus*, compare Gaudin 1991 & Maisey 1984a, 1989 for example). The oldest known Hybodontoid is from the Late Devonian (*Lissodus*, Derycke et al. 1995). The Neoselachii should therefore have appeared before this time. However, the

Palaeozoic genera described so far as belonging to the Neoselachii (*Mcmurdodus*, *Cooleyella* and *Hopleacanthus*; Turner & Young 1987; Duffin et al. 1996; Schaumberg 1982) need further studies (*Hopleacanthus* and *Mcmurdodus*) or are unlikely to be true Neoselachii (*Cooleyella* = *Anachronistes*) (Thies & Reif 1985; Turner & Young 1987; Gaudin 1991; Cappetta et al. 1993; Cuny 1998). The situation is currently unclear.

### NEOSELACHIAN SHARKS OF THE EARLY AND MIDDLE TRIASSIC

The earliest unequivocal neoselachian tooth, displaying a SLE and a PFE, is known from the Lower Triassic of Turkey (Thies 1982) and was attributed to the genus *?Palaeospinax* EGERTON, 1872. However, the diagnosis of the *Synechodontiformes*, including the *Palaeospinacidae*, includes the possession of a peculiar vascularization termed pseudo-polyaulacorhize (Cappetta 1987, 1992; Thies 1993; Duffin & Ward 1993), while the overall morphology of the crown among *Palaeospinacidae* appears primitive, quite similar to that seen among *Hybodontidae* (cusps rather blunt and moderately compressed labio-lingually, with lateral cusplets not well separated from the main cusp, crown often heavily ornamented). 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 & Ward 1993; Thies 1993), and if the Turkish specimen does belong to a *palaeospinacid*, it should therefore be attributed to the genus *Synechodus*. Quite similar teeth have also been reported recently from the Middle Triassic of Nevada (USA) as *?Palaeospinax* sp. by Rieppel et al. (1996). The roots of these teeth are also 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*. The exact relationships of the Turkish and Nevada teeth among the neoselachians cannot be assessed at present, although if they do not belong to the *Synechodontiformes*, they should be closely related to them.

Recently Johns et al. (1997) described four species of *Synechodus* (*S. multinodosus*, *S. volaticus*, *S. sp. 1*, *S. sp. 2*) from British Columbia (Canada), ranging in age from the Ladinian to the Carnian. These specimens represent the first unquestioned *Palaeospinacidae* (*Synechodontiformes*). The phylogenetic position of the *Palaeospinacidae* [*Synechodus* (*Palaeospinax*) + *Paraorthacodus*] remains, however, 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. Nevertheless, during the Early and Middle Triassic, and up to the Carnian, the neoselachian sharks were represented only by *Synechodontiformes*, or by forms closely related.

### NEOSELACHIAN SHARKS OF THE LATE TRIASSIC

Until recently, six species from the latest Triassic (Norian + Rhaetian) were attributed to the Neoselachii, all restricted to Europe: *Nemacanthus monilifer*, *Hueneichthys costatus*, *Reifia minuta*, *Vallisia coppi* DUFFIN, 1982; *Synechodus rhaeticus* (DUFFIN, 1982); and *Rhomphaiodon nicolensis* DUFFIN, 1993. Recent studies, allying morphological and structural approaches, allowed the recognition of four new taxa: "*Hybodus*" *minor* (CUNY, 1998), *Pseudocetorhinus pickfordi* (DUFFIN, 1998a), *Synechodus incrementum* (JOHNS et al., 1997), and *Grozonodon candau* (CUNY et al., 1998). "*Polyacrodus*" *holwellensis* may also represent another neoselachian species, while the relationships of *Vallisia coppi* now appear unclear.

*Nemacanthus monilifer* is known solely from isolated fin spines, but is a common species in the Upper Triassic of Western Europe. 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*, but the characters used by this author seem to be primitive for the Neoselachii (Cuny 1998). The presence of an enamelled ornamentation would preclude *Nemacanthus* from belonging to the *Ctenacanthoidea* (Maisey 1982), but this would remain a primitive character for the Neoselachii. Whether *Nemacanthus* is a true neoselachian, or belongs to its sister-group, appears therefore impossible to prove on the basis of fin-spines alone. On the other hand, teeth of "*Hybodus*" *minor* are found in association with fin spines of *Nemacanthus monilifer* on an almost regular basis in Belgium (Duffin et al. 1983), France (Cuny 1995a), Germany (Schmidt 1928), Great Britain (Woodward 1891; Storrs 1994), and Luxemburg (Duffin 1993a; Delsate 1995; Godefroit et al. 1998). 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 in Thierry et al.

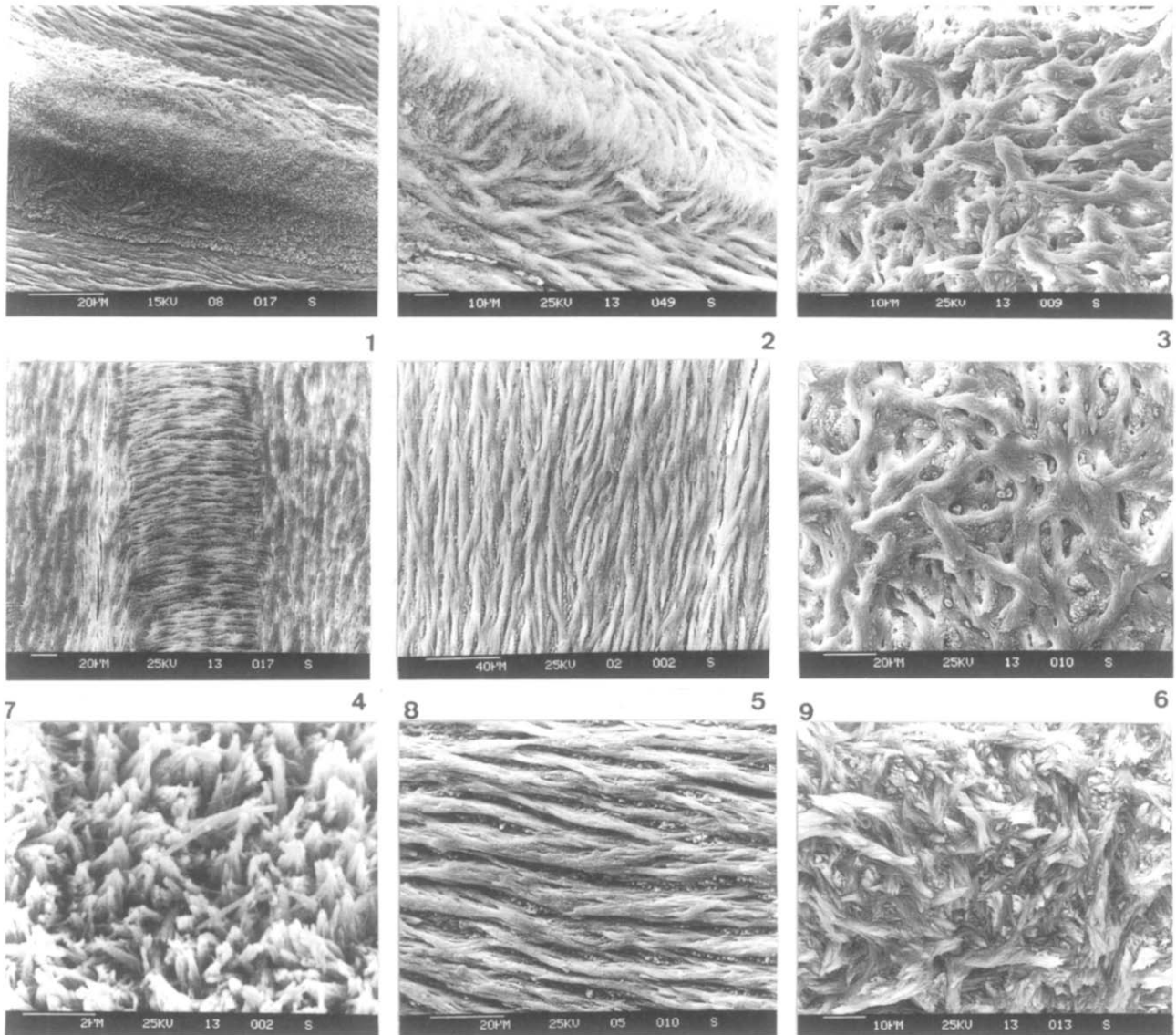


FIGURE 1 - 1-3. "*Hybodus*" *minor*: 1. Thick SLE at the level of a ridge ornamenting the surface of the crown, tooth from the Norian of Medernach (Great Duchy of Luxembourg) etched 20 s in 10% HCl. x 550. The SLE has disappeared from the other part of the crown, showing the underlying PFE. 2. Ridge at the surface of the crown of a tooth from the Rhaetian of Syren (Great Duchy of Luxembourg) etched 1 mn in 10% HCl, with the SLE removed, showing the change in orientation of the bundles of fibres of the PFE. x 500. 3. Inner TFE at the apex of a tooth from the Rhaetian of Brentry (Bristol, England) etched 16 mn 35 s in 10% HCl. x 400. 4. *Paraorthacodus eocenicus*, Eocene of Dormaal, Belgium. Tooth etched 5 mn 30 s in 10% HCl showing the change in orientation of the bundles of fibres of the PFE at the level of a ridge ornamenting the crown. x 200. 5-6: "*Hybodus*" *minor* (?) from Saint-Nicolas-de-Port (Lorraine, France). 5. PFE in a tooth etched 50 s in 10% HCl, x 275 and 6. TFE at the apex of a tooth etched 5 mn 50 s in 10% HCl, x 400. 7-9. *Pseudocetorhinus pickfordi*. 7. SLE of a tooth etched 10 s in 10% HCl. x 5500. 8. PFE in a tooth etched 40 s in 10% HCl, x 550 and 9. TFE at the apex of a tooth etched 5 mn 40 s in 10% HCl. x 600. 7 from the Rhaetian of Aust and 8-9 from the Rhaetian of Habay-la-Vieille, Belgium. All the photographs represent the surface of the teeth after etching. 1-3. "*Hybodus*" *minor*: 1. SLE épaissi au niveau d'une ride d'ornementation de la couronne d'une dent provenant du Norien de Medernach (grand-duché de Luxembourg) attaquée 20 s dans de l'HCl dilué à 10%. Le SLE a disparu sur les autres parties de la couronne, découvrant le PFE sous-jacent. 2. Ride d'ornementation à la surface d'une dent provenant du Rhétien de Syren (grand-duché de Luxembourg) attaquée 1 mn dans de l'HCl, et dont le SLE a été enlevé, montrant le changement d'orientation des faisceaux de fibres du PFE. x 500. 3. TFE interne à l'apex d'une dent provenant du Rhétien de Brentry (Bristol, Angleterre) attaquée 16 mn 35 s dans de l'HCl dilué à 10%. x 400. 4. *Paraorthacodus eocenicus*, Eocène de Dormaal, Belgique. Dent attaquée 5 mn 30 s dans de l'HCl dilué à 10% montrant le changement d'orientation des faisceaux de fibres du PFE au niveau d'une ride ornementant la couronne. x 200. 5-6. "*Hybodus*" *minor* (?) provenant de Saint-Nicolas-de-Port (Lorraine, France). 5. PFE dans une dent attaquée 50 s dans de l'HCl dilué à 10%, x 275, et 6: TFE à l'apex d'une dent attaquée 5 mn 50 s dans de l'HCl dilué à 10%. x 400. 7-9. *Pseudocetorhinus pickfordi*. 7. SLE d'une dent attaquée 10 s dans de l'HCl dilué à 10%. x 5500. 8. PFE dans une dent attaquée 40 s dans de l'HCl dilué à 10%, x 550, et 9. TFE à l'apex d'une dent attaquée 5 mn 40 s dans de l'HCl dilué à 10%. x 600. 7 provenant du Rhétien d'Aust et 8-9 provenant du Rhétien d'Habay-la-Vieille, Belgique. Toutes les photographies ont été prises en surface après attaque à l'acide.

1907; Priem 1908; Maisey 1977; Storrs 1994; Cuny 1995a). The main problem with this hypothesis, however, was 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. However, it has been demonstrated that the teeth of "*Hybodus*" *minor* show a triple-layered enameloid (Fig. 1.1-3), although with some peculiarities, and they must therefore belong to a neoselachian shark (Cuny 1998). The peculiarities of the enameloid of the teeth of "*Hybodus*" *minor* are located at the level of the ridges ornamenting the crown. The SLE is here thicker than in other parts of the crown (Fig. 1.1). 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. 1.2, Cuny 1998). 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 1995a), forming what Maisey (1975, 1977) called a lingual torus. The basal face of the root 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. 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 figs 10, 11, 12 provided by Duffin 1993a). It is probable that the pseudo-polyaulacorhize state of the *Synechodontiformes* arose from a "*Hybodus*" *minor*-like anaulacorhize state (Cuny 1998). Interestingly enough, a similar structure to that described in "*Hybodus*" *minor* has been found at the level of the ridges ornamenting the teeth of *Paraorthacodus eocenicus* from the Eocene of Dormaal (Belgium, fig. 1.4), and this feature may be an autapomorphy for the family Palaeospinacidae, although more work is required in order to demonstrate this. "*Hybodus*" *minor* appears therefore to be closely related to the Palaeospinacidae, but possesses a vascularisation of the root more primitive than in *Synechodus*. Interestingly, the fin-spines of *Nemacanthus monilifer* also appear more primitive than those of *Synechodus* (Maisey 1977). The teeth of "*H.*" *minor* have 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.

*Rhomphaiodon nicolensis* is known from hundreds of teeth from the French locality of Saint-Nicolas-de-Port and it may also be present in the Knollenmergel of Halberstadt, Germany (Duffin 1993b). This genus has also been cited at Varangéville, a locality a few kilometres east of Saint-Nicolas-de-Port, by Godefroit (1997). Morphologically, the teeth of *Rhomphaiodon nicolensis* are quite similar to those of "*Hybodus*" *minor* (Duffin 1993b). According to Duffin (1993b), the enameloid of the teeth of *Rhomphaiodon* possesses 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,f and Duffin 1993b, Pl. 4, fig. 2). One of us (GC) has studied the enameloid of one tooth from Saint-Nicolas-de-Port, and has found the remnants of a surface SLE, a central PFE (Fig. 1.5), and a typical TFE (Fig. 1.6) made of entangled bundles of fibres of apatite (Cuny 1998). This latter layer was only found in the upper third of the cusps. This strongly suggests that this tooth belongs in fact to "*Hybodus*" *minor*. Some other teeth from Saint-Nicolas-de-Port have been studied by one of our students, Owen Edwards, who has also discovered a structure similar to that described in "*Hybodus*" *minor* at the level of the ridges ornamenting the crown. On the other hand, no hint of the presence of a basal layer of haphazard single-crystallite enameloid like that illustrated by Duffin (1993b) has been found. These results may indicate that at least two different species of neoselachian sharks co-existed at Saint-Nicolas-de-Port, but more work is required to reach a firm conclusion.

A new genus recently found at Grozon (Eastern France), *Grozonodon candau* (Cuny et al. 1998) displays the same structure of the enameloid as in "*Hybodus*" *minor* and is probably closely related to this latter genus.

Teeth of *Pseudocetorhinus pickfordi* were found in the Rhaetian of Aust (England, pers. obs., Duffin pers. com.), Holwell (England; Duffin 1998a), Syren (Luxemburg, Godefroit et al. in press), Attert (Belgium; Duffin & Delsate 1993), Habay-la-Vieille (Belgium; Delsate & Lepage 1991), and Saint-Germain-les-Arlay (France; Cuny et al. 1994). The teeth of Habay-la-Vieille show a triple-layered enameloid, but it is quite different from that of the above-mentioned taxa. Firstly, the surface of the crown is mainly smooth and a peculiar structure associated with ridges does not appear. Secondly, the SLE may be unusually thick in some teeth (Fig. 1.7, Cuny 1998), a fact which certainly explains why Duffin (1998a) thought that the enameloid was mainly made of a SCE. But underneath, there are a PFE (Fig. 1.8) and a TFE (Fig. 1.9), although the

latter layer has been found in the upper third of the teeth only (Cuny 1998). As Duffin (1998a) considers *Pseudocetorhinus* to have been a filter-feeding shark, the meaning of a thick SLE is difficult to explain in supposedly useless teeth.

*Synechodus rhaeticus* was first named as *Palaeospinax rhaeticus* (Duffin 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). In 1993, Duffin & 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* and the teeth of this species were described by Duffin (1998b). Moreover, teeth of "*Palaeospinax rhaeticus*" have been cited in the Rhaetian of Habay-la-Vieille (Belgium) by Delsate & Lepage (1991) and teeth of this species were also found in the French Rhaetian of Lons-le-Saunier (Jura; Cuny et al. in prep.). The ultrastructure of the enameloid of some teeth from Habay-la-Vieille and Lons-le-Saunier have been studied by one of us (GC). Superficially, the enameloid is formed of thin, small, less than 1 mm in maximum length, crystallites of apatite. They are preferentially oriented perpendicular to the surface (Fig. 2.1). Underneath, in posterior teeth only, more or less parallel bundles of fibres are oriented parallel to the surface and perpendicular to the axis of the crown (Fig. 2.2). Near the contact of the enameloid with the dentine, these bundles appear to be more randomly oriented (Fig. 2.3). Some differences exist between this enameloid and that of typical neoselachians. The bundles of fibres are not very well individualized, comparing for example with the parallel-fibred enameloid (PFE) of the contemporary "*Hybodus*" *minor* or *Pseudocetorhinus pickfordi*, and the orientation of these fibres, perpendicular to the axis of the tooth, is unusual. Sections of anterior teeth of *S. rhaeticus*, showing a well developed main cusp, show that the enameloid is made up of poorly individualized bundles of fibres, most of them being perpendicular to the surface (Fig. 2.4). This is also a very unusual feature, not known in any neoselachian teeth studied so far, and this indicates also a change in the structure of the enameloid between anterior and posterolateral teeth. The main alteration of the typical triple-layered enameloid in extant non-batoid neoselachian sharks is linked to a durophagous diet, as exemplified by *Heterodontus* (Reif 1973), and the low profile of the posterolateral teeth of *Synechodus rhaeticus* is suggestive of an adaptation toward such a diet. The study of posterior teeth of *Heterodontus portusjacksoni* by Reif (1973) showed an enameloid

made of only two layers, an external SCE and an internal TFE. The PFE, resistant to tensile stresses (Preuschoft et al. 1974), is of little use in a crushing tooth and tends to disappear. The ultrastructure of the enameloid of the teeth of *S. rhaeticus* is, however, very different from that observed in *Heterodontus* where the TFE formed the main part of the enameloid. *Synechodus rhaeticus* may therefore represent a different kind of adaptation to a durophagous diet among neoselachian sharks. The poorly individualized bundles of fibres, perpendicular to the axis of the tooth in *Synechodus rhaeticus* may indicate the partial loss of the PFE which would have become subsequently a SCE layer, resistant to compressive stresses (Preuschoft et al. 1974). However, this does not explain the unusual orientation of the bundles. Another hypothesis would be that *Synechodus rhaeticus* is not a true neoselachian, but belongs to a specialized lineage of hybodontid sharks, which have convergently developed an enameloid similar to that of neoselachians and a pseudo-polyaulacorhize vascularization of the teeth. This would explain the poorly individualized bundles of fibres and their unusual orientation. Considering our current lack of knowledge about the variation of enameloid structure among neoselachians and hybodonts, this latter hypothesis cannot be ruled out. Moreover, a preliminary study of the enameloid of teeth of "*Polyacrodus*" *holwellensis* DUFFIN, 1998 from the Rhaetian of Habay-la-Vieille has revealed an enameloid similar to that of posterolateral teeth of *Synechodus rhaeticus*. The teeth of *Synechodus incrementum* from the Norian of British Columbia (Canada), described by Johns et al. (1997), show an enameloid ultrastructure also reminiscent of that of *S. rhaeticus*. 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, quite similar to what has been observed in the anterior teeth of *S. rhaeticus* from Lons-le-Saunier. As no illustrations of etched surfaces of the teeth were provided, it is not possible to assess whether *S. incrementum* shares with *S. rhaeticus* a layer of bundles of fibres parallel to the surface and 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 allied. Whether or not they should be assigned to the genus *Synechodus* is beyond the scope of this paper.

*Hueneichthys costatus* is known from a single tooth (GPIT 1510) from the Rhaetian 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

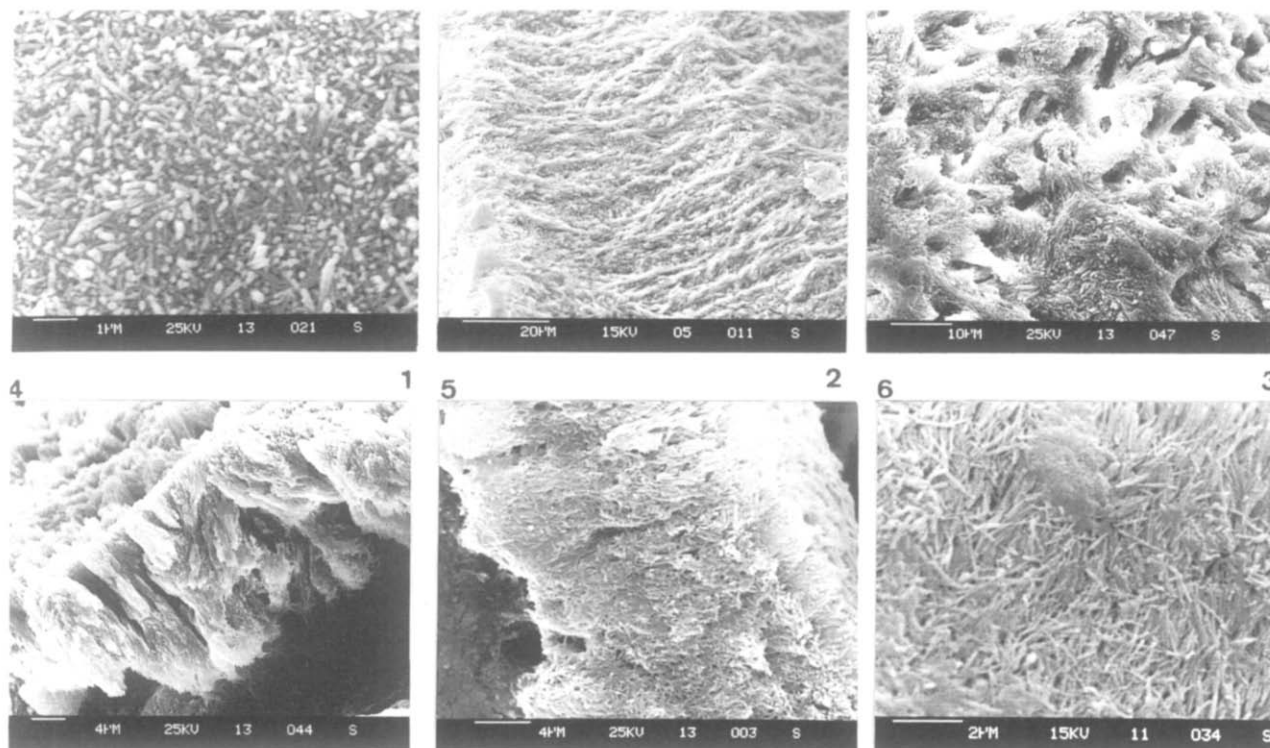


FIGURE 2 - 1-4. *Synechodus rhaeticus* from the Rhaetian of Lons-le-Saunier, Jura, France. 1. Surface of a postero-lateral tooth etched 1mn 5s in 10% HCl, showing the SLE. x 6000. 2. Surface of a postero-lateral tooth etched 2mn in 10% HCl, showing indistinct bundles of fibres perpendicular to the axis of the tooth. x 550. 3. Surface of a postero-lateral tooth etched 3mn 35s in 10% HCl, showing pseudobundles of fibres. x 800. 4. Transverse section of the enameloid of an anterior tooth etched 1mn 30s in 10% HCl, showing pseudobundles of crystallites perpendicular to the surface. x 1250. 5. *Vallisia coppi* (BRSMG Cc403) from the Rhaetian of Vallis Vale, Somerset, England. Tooth etched 5s in 10% HCl showing a section of the enameloid at the level of the broken main cusp. x 1875. 6. *Pseudodalatias barnstonensis*, Rhaetian of Habay-la-Vieille, Belgium, tooth etched 10s in 10% HCl. Ultrastructure of the enameloid showing single crystallites of apatites. x 4500. 1-4. *Synechodus rhaeticus*, Rhétien de Lons-le-Saunier, Jura, France. 1. SLE à la surface d'une dent postéro-latérale attaquée 1 mn 5 s dans de l'HCl dilué à 10%. x 6000. 2. Surface d'une dent postéro-latérale attaquée 2 mn dans de l'HCl dilué à 10%, montrant les faisceaux de fibres mal individualisés orientés perpendiculairement à l'axe de la dent. x 550. 3. Surface d'une dent postéro-latérale attaquée 3 mn 35 s dans de l'HCl dilué à 10%, montrant des faisceaux de fibres enchevêtrés. x 800. 4. Coupe transversale de l'émailloïde d'une dent antérieure attaquée 1 mn 30 s dans de l'HCl dilué à 10%, montrant des pseudofaisceaux de cristaux perpendiculaires à la surface. x 1250. 5. *Vallisia coppi* (BRSMG Cc403) provenant du Rhétien de Vallis Vale, Somerset, Angleterre. Dent attaquée 5 s dans de l'HCl dilué à 10% montrant une coupe de l'émailloïde au niveau de la cuspidie principale cassée. x 1875. 6. *Pseudodalatias barnstonensis*, Rhaetien d'Habay-la-Vieille, Belgique, dent attaquée 10s dans de l'HCl dilué à 10%. Ultrastructure du pseudo-émail montrant des cristaux simples. x 4500.

(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. According to Reif, the most important characteristic of this tooth is the presence of an additional layer of bundles of fibres in the PFE at the level of the ridges ornamenting the crown. The bundles of fibres of this extra layer were thought by Reif to run perpendicular to the axis of the crown, parallel to the surface. The bundles of fibres appear, however, more regular than the ones observed in posterolateral teeth of *Synechodus rhaeticus* with a similar orientation, and they strongly recall the structure seen at the level of the ridges in "*Hybodus*" *minor*, *Rhomphaiodon nicolensis*, *Grozonodon candau* and *Paraorthacodus eocenicus*. Unfortun-

ately, the detail of the structure in between each ridge is masked by numerous radial fibres in the figure provided by Reif (1977, fig. 4). It is nevertheless probable that there is no extra layer in the teeth of *Hueneichthys costatus*, but a change of orientation of the bundles of fibres located only at the level of the ridges.

*Reifia minuta* is known from five isolated, minute teeth (SMNS 50.200 to 50.204) from 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 bundles of fibres (Duffin 1980, fig. 3e,f). 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) 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, rather than galean, affinities. 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 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 within the Squalea or the Galea.

#### LATE TRIASSIC SHARKS OF PROBLEMATIC AFFINITIES

Four species from the Upper Triassic of North-Western Europe have problematic affinities: *Vallisia coppi* DUFFIN, 1982; *Doratodus* cf. *tricuspidatus* SCHMID, 1861; *Pseudodalatias barnstonensis* (SYKES, 1971); and *Raineria osswaldi* CAPPETTA, 1987.

*Vallisia coppi* is a genus known from a few isolated teeth from the Rhaetian of England and Belgium which has been attributed to the Neoselachii (Duffin 1982b; Duffin et al. 1983). The crown morphology of this genus is however unique among neoselachians, and its superficial resemblances to Orectolobiformes and Heterodontiformes seem to be the result of convergence (Duffin 1982b; Cappetta 1987). Duffin (1982b, 1983) suggested that *Vallisia* was a batoid, based mainly on the holaulacorhize root of the teeth. However, Duffin (1982b) stated that some teeth have a rhinobatoid-type vascularization (foramen set in the centre of the groove, Casier 1947), while others have a scyliorhinoid-type pattern (foramen set in the lingual part of the groove, Casier 1947). Casier (1947) suggested however that the rhinobatoid and scyliorhinoid vascularization patterns of the teeth arose independently. Moreover, at least two teeth show two medial canals, one of which is partially roofed (Duffin 1982b), a condition unknown in neoselachian sharks. A study of the ultrastructure of the enameloid of *Vallisia* teeth confirms that it is not a neoselachian. A broken tooth (BRSMG Cc403) shows an enameloid made of a single-crystallite enameloid (SCE, fig. 2.5). At the surface of the crown, the crystallites are oriented perpendicular to the axis of the crown, while deeper in the enameloid, they are randomly oriented. If the enameloid is similar to that

of the hybodonts, other features of the teeth are unknown among hybodonts: the tooth crown is strongly differentiated from the root and the crown/root junction is deeply incised around the whole root. The affinities of *Vallisia coppi* are therefore difficult to assess, but it is neither an hybodont, nor a neoselachian shark.

*Doratodus tricuspidatus* was originally described by Schmid (1861) from the Lower Keuper near Jena (Germany) but the type series of teeth seems 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 (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 Neoselachii, it does not seem to be a hybodont shark either. Moreover, the lip developed at the crown shoulder is a character also known in *Vallisia coppi* (Duffin 1982b), and the two genera may be closely related.

*Pseudodalatias barnstonensis* is a common species, reported in the Rhaetian of Great Britain (Westbury Formation, Sykes 1974; Storrs 1994), Belgium (Duffin et al. 1983; Duffin & Delsate 1993), and the French Jura (Cuny 1995a; Cuny et al. 1994). *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 Rhaetian of Lavigny (Jura, France) may also represent a lower tooth of *Pseudodalatias* (Cuny 1998, but see Duffin 1981). *Pseudodalatias barnstonensis* was first named as *Dalatias barnstonensis* by Sykes (1971) on the basis of isolated teeth. The dentition of this genus, with strongly dignathic heterodonty, indeed shows remarkable convergence with that of the extant *Dalatias* (Squalea: Dalatiiformes: Dalatiidae). However, Reif (1978a) showed later 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 (Fig. 2.6), 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 ortho-

dentine. The rest of the crown and the whole root are formed by atubular dentine, a very rare condition among advanced elasmobranchs (Reif, 1978c). Reif (1978a) very tentatively attributed this family to the Hybodontidae, but there are no convincing arguments to do so (Cappetta, 1987). The affinities of this genus therefore remain poorly understood (Duffin 1981; Cappetta 1987; Storrs 1994; Cuny 1995c). As is the case for *Doratodus* and *Vallisia*, the teeth of *Pseudodolalotias* show, in their overall shape, many similarities with those of neoselachians, but the structure of the teeth appears very different, which strongly suggests convergence.

*Raineria osswaldi* is known only by an almost complete rostrum from the Rhaetian of Austria. 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 & 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). Finally, placoid scales are present in all Neoselachii but also in pre-Rhaetian Hybodontidae according to Reif (1978b). Cappetta (1987) stated that "It is not impossible that the rostrum of *Raineria* belongs to the selachian of doubtful affinities.... *Pseudodolalotias* Reif." and so he considers it as a possible hybodont. There is however no direct evidence of the association of *Raineria* and *Pseudodolalotias*, as the latter was never recorded in the Rhaetian 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*, but it is unlikely to belong to the Hybodontiformes.

### SHARK RADIATION DURING THE UPPER TRIASSIC

From the Carnian to the end of the Rhaetian, marine faunas were strongly modified (Johnson & Simms 1989; Smith 1990; Benton 1991; Gilliland 1992). Among the actinopterygians, we note the appearance of the Teleostei and the explosive radiation of the Neopterygii (Dapediidae, Semionotidae, Macrosemiidae, Pycnodontiformes, Caturidae) (Gardiner 1993; Patterson 1993; Tintori 1996). Among the elasmobranchs, the Upper Triassic

(Norian + Rhaetian) of Western Europe has yielded at least seven different neoselachian species (see above). Some of these (*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. 3). Four species of doubtful affinities have also been recorded in the same area: *Vallisia coppi*, *Doratodus tricuspoidatus*, *Pseudodolalotias barnstonensis*, and *Raineria osswaldi*. The Hybodontidae remain, however, the commoner component of the shark fauna in that area, but with a lower diversity at generic level, being represented by only five genera (*Hybodus*, *Lissodus*, *Palaeobates*, *Polyacrodus*, and *Acrodus*, Delsate 1997; Duffin 1985, 1993b, 1998b; Schmidt 1928). *Acrodus* and *Palaeobates* possess a specialized grinding dentition indicating that they fed mainly upon prey possessing protective shells, while *Lissodus*, by far the most abundant genus, possesses a less specialized dentition, of crushing type, indicating more opportunistic feeding behaviour (Cappetta 1986). Hybodonts with dentition of a clutching or tearing type (*Hybodus* and *Polyacrodus*) are rather rare in Western Europe, and they may be quite large, such as *Hybodus cloacinus* (Storrs 1994). Thus, no hybodont sharks show any peculiar ability to catch small, agile fishes like the first teleosteans. On the contrary most neoselachian sharks described above are of small size, probably within one metre in total length, and show clutching dentition. They appear therefore better adapted to prey upon this new kind of potential prey. In the latest Triassic, more specialized neoselachians appear, with *Synechodus rhaeticus* which possesses a clutching-grinding type of dentition, showing adaptations towards a durophagous diet, and *Pseudocetorhinus pickfordi* which, according to Duffin (1998a), was probably a filter-feeding shark. According to their abundance in the Upper Triassic, these two sharks seem to have been successful, but it remains unexplained why, if *Pseudocetorhinus* is indeed a filter-feeder, filter-feeding sharks disappear at the end of the Triassic, to reappear only in the Eocene (Cappetta 1987).

*Hueneichthys costatus*, *Rhomphaiodon nicolensis*, "*Hybodus*" *minor*, and *Grozonodon candau* may represent the most primitive lineage among neoselachian sharks and may be closely allied to the *Synechodontiformes*, with which they shared a similar crown morphology and also possibly the presence of perpendicular bundles of fibres in the PFE at the level of the ridges ornamenting the crown. But they did not possess pseudo-polyaulacorrhize vascularization of the root (although this cannot be ascertained in *Hueneichthys costatus*). The phylogenetic positions of *Reifia minuta* and *Synechodus rhaeticus* are unclear, and they may prove



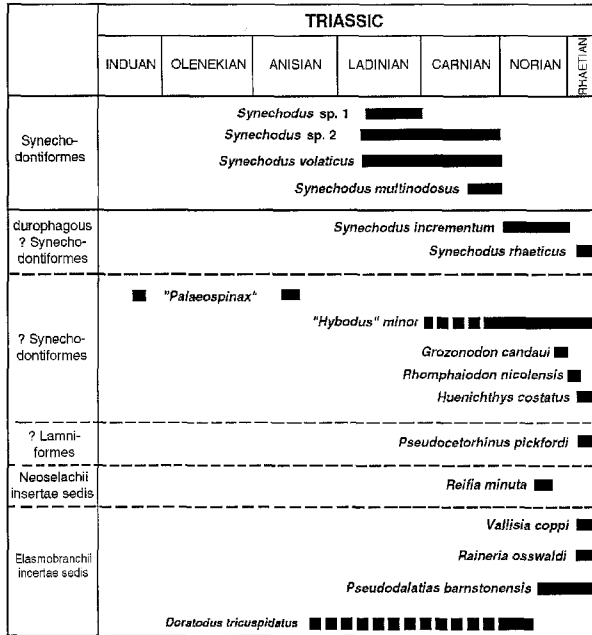


FIGURE 3 - Stratigraphic distribution of Triassic neoselachian sharks and of several sharks of unclear relationships (see text for details). Répartition stratigraphique des néosélaciens et des requins de relations de parenté non résolues du Trias (voir le texte pour les détails).

to be unrelated to the other Upper Triassic sharks, representing then two different lineages which seem to have disappeared at the end of the Triassic. According to Duffin (1998a), *Pseudocetorhinus pickfordi* may represent the first known lamniform and the first filter-feeding shark. The radiation of the neoselachian sharks in Western Europe appears then to be genuine in terms of number of lineages and adaptation to various diets. However, this radiation includes almost none of the extant orders of neoselachians, which did not appear before the Lower Jurassic (Thies & Reif 1985).

At the Triassic/Jurassic boundary, important sea-level changes occurred (Hallam 1981, 1997) which strongly affected Western Europe, as this is the only part of the world away from the Pacific margins and Tethys where the basal Jurassic is fully developed as marine deposits (Hallam 1990). After the Rhaetian, northern and central Europe was covered by extensive shallow epicontinental seas of a type which does not exist today, characterized by extremely low slopes over large areas, facies belts of vast extent, few sediment gravity flows and extensive storm influences (Hallam 1997). As noted by Courel (1973), the Rhaetian transgression progressed over a remarkably even area, explaining the creation of these unusual epicontinental seas. Nowadays, 50% of neoselachian species occur in shelf waters (Camhi et al. 1998), and the Rhaetian seas would therefore have been very suitable envi-

ronments for their ancestors. The neoselachian radiation in Western Europe may therefore be explained by the appearance of a suitable environment and of a new type of prey, the teleosteans. This could also explain the appearance at that time of some ephemeral sidebranch shark lineages (*Vallisia*, *Doratodus*, *Pseudodalatias*, *Rainieria*), showing some convergences with the neoselachians. It is interesting to note that *Pseudodalatias* is the first known shark to develop a cutting-clutching dentition, which indicates it was preying upon rather large, soft prey (Cappetta 1986). These ephemeral shark lineages were however, quickly replaced by neoselachians in the Lower Jurassic.

Changes in selachian faunas at the Carnian/Norian boundary are not restricted to Europe, as shown by the study of dermal denticles in Canada (Johns 1996). However, in the deeper marine Canadian environment, the diversity of neoselachian sharks is much lower than in Europe. They are represented only by *Synechodus* and maybe another genus, as *S. incrementum* appears to be quite peculiar. In the more terrestrial environment of the South West United States, the shark fauna appears much more conservative, dominated by hybodonts and the last xenacanth, and with no neoselachians at all (Huber et al. 1993). In the present state of our knowledge, the neoselachian radiation appears therefore to be restricted to the Western Europe area.

## CONCLUSION

The neoselachian shark lineage probably appeared somewhere in the Palaeozoic, but until the Triassic, their history is unknown. At the end of the Triassic, they show, however, a dramatic radiation, mostly in Western Europe, which may have been favoured by the Rhaetian transgression. The Rhaetian transgression had a major effect over Western Europe where a large epicontinental sea existed and was responsible for a local faunal turn-over in terrestrial faunas at the end of the Triassic (Cuny 1995c). Nothing similar has been observed outside Europe so far (Hallam 1990). It offered shallow-water conditions favouring the radiation of new marine lineages, including the neoselachian sharks, but also other sharks of unclear affinities. The data available outside Europe, admittedly rather less complete, indicate that in deeper marine or in more terrestrial environments, the changes in shark faunas are far less spectacular.

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**G. CUNY & M.J. BENTON**

Department of Earth Sciences  
University of Bristol  
Wills Memorial Building, Queens Road  
UK, Bristol, BS8 1RJ