The shark fauna from the Middle Triassic (Anisian) of North-Western Nevada

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The shark fauna from the Anisian of Nevada is dominated by durophagous hybodontiforms but also shows an important neoselachian component. Two new species of hybodontiform sharks, *Acrodus cuneocostatus* and *Polyacrodus bucheri*, are described in addition to a new neoselachian taxon: *Mucrovenator minimus*. The enameloid of the teeth of *Acrodus* and *Polyacrodus* comprises two layers, an outer compact layer and an inner bundled layer. For the typical three-layered enameloid of neoselachian teeth, we propose to replace the terms parallel-fibred enameloid and tangled-fibred enameloid by the more appropriate parallel-bundled and tangled-bundled enameloid.

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ADDITIONAL KEY WORDS: Elasmobranchii – Hybodontoidea – Neoselachii – tooth – enameloid – ultrastructure.

INTRODUCTION

Rieppel, Kindlimann & Bucher (1996) described fish microremains from the lower part of the Fossil Hill Member of the Favret Formation (Star Peak Group, Anisian, Nevada) on the west slope of the Augusta Mountains (Figs 1, 2). The fauna was found to comprise three types of hybodontiform dermal denticles, eight shark taxa (seven hybodontiforms, *Acrodus spitzbergensis*, *Acrodus* cf. *A. vermicularis* [sic], *Acrodus* cf. *A. oreodontus*, *Palaeobates* cf. *P. shastensis*, *Polyacrodus* sp. (A), *Polyacrodus* sp. (B) and *Polyacrodus tregoi*, and a ?neoselachian, *?Palaeospinax* sp.) based on isolated teeth, five actinopterygian taxa based on jaw fragments, isolated teeth or scales, and a single toothplate fragment of *Ceratodus*, a lungfish. Since then, more material from the same locality has been collected, which allows a better understanding of the shark fauna. To complement gross morphological study, enameloid ultrastructure of the teeth has been investigated using scanning electron microscopy (SEM). These studies confirm the presence of neoselachian sharks in the Middle Triassic of North America. The terminology used to describe the teeth in the present paper follows Johnson (1981) and Rees (1998).

MATERIAL AND METHODS

In order to study the ultrastructure of the enameloid of isolated teeth, the method used by most authors, i.e. a short etching in highly concentrated HCl (Reif, 1973, 1977, 1978; Duffin, 1980, 1993; Maisey, 1987), has been improved. The teeth were etched in 10% HCl for between 5 s and 1 min according to the size of the tooth and the type of structure studied (for instance, the single crystallite enameloid of hybodonts is less acid resistant than the parallel bundled enameloid of neoselachian sharks). The treatment was repeated until the enameloid was almost completely removed. In between each treatment, photographs of the revealed surface of the enameloid were taken with a Cambridge Stereoscan 250MK3 scanning electron microscope, using an acceleration voltage of 25 kV. This allowed identification of differences in arrangement between the inner and outer parts of the enameloid, or between the apex and the base of the crown. To relate surface appearance of the enameloid to its microstructure, broken teeth were used for preference. This allowed comparison of the natural section of the tooth with the surface appearance of the enameloid. Although this method requires the destruction of some teeth, it permits a thorough understanding of the ultrastructure of the enameloid and of its variations.

One tooth of *Acrodus spitzbergensis*, two teeth of

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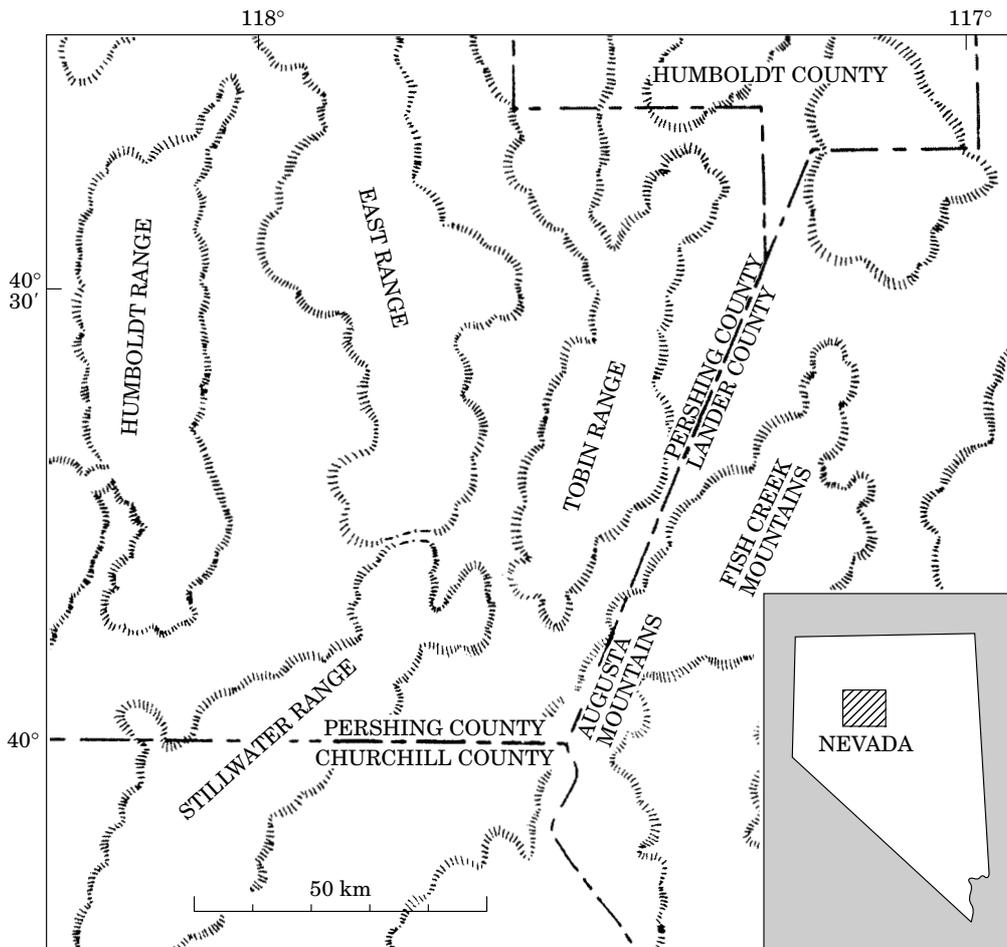
Figure 1. Locality map with arrow pointing to the fossiliferous area. From Sander, Rieppel & Bucher (1997) with the permission of the *Journal of Vertebrate Paleontology.*
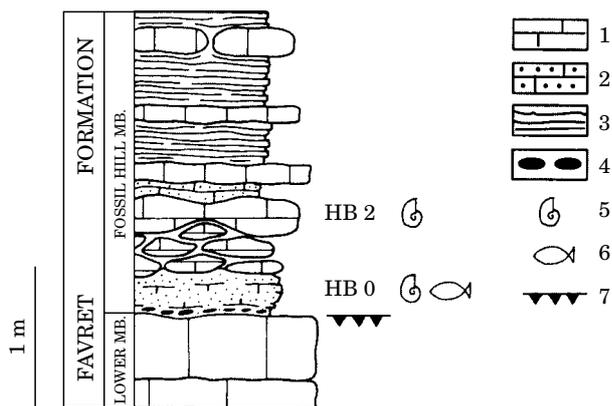
Figure 2. Stratigraphic context of the fossiliferous layer: 1, limestone; 2, litharenites; 3, silty shales; 4, black limestone pebbles; 5, ammonoids; 6, fish remains; 7, ferruginous hardground. From Rieppel *et al.* (1996).

Acrodus cuneocostatus sp. nov., one tooth of *Polyacrodus bucheri* sp. nov., three teeth of *Polyacrodus tregoi* and three teeth of *Mucrovenator minimus* gen.

nov., sp. nov. have been studied by the method described above. All the fossils described in this article are housed in the Field Museum of Natural History, Chicago (FMNH).

SYSTEMATIC PALAEONTOLOGY

CHONDRICHTHYES HUXLEY, 1880
ELASMOBRANCHII BONAPARTE, 1838
HYBODONTOIDEA ZANGERL, 1981
ACRODONTIDAE CASIER, 1959
GENUS *ACRODUS* AGASSIZ, 1837
ACRODUS SPITZBERGENSIS HULKE, 1873
(Figs 3A–C, 4A–D)

Material

Seven incomplete teeth (FMNH PF 14950–56), one of which has been acid etched to study its enameloid ultrastructure (FMNH PF 14950), plus one complete ?antero-lateral tooth (FMNH PF 15143).

Description

The incomplete teeth are similar to those described by Rieppel *et al.* (1996) and are mainly characterized by a double longitudinal crest (Fig. 3A).

The only complete tooth (FMNH PF 15124) is poorly preserved and the detail of the crown ornamentation is unclear. The tooth is 4.1 mm long and 1.2 mm wide at the level of the main cusp. In occlusal view, the extremities of the crown narrow slightly distally and mesially. The tooth shows a single longitudinal crest from which perpendicular ridges originate. Whether or not these ridges attain the base of the crown is difficult to determine as it is quite worn (Fig. 3B). However, they appear to be longer than those ornamenting the teeth of *Acrodus cuneocostatus* sp. nov. (Fig. 3F). In lingual view, the crown appears slightly convex and asymmetric, the main cusp being slightly displaced towards the ?mesial end of the tooth (Fig. 3C). This tooth is similar to the specimen P.99e (Museum of Evolution, University of Uppsala) from the Lower Triassic of Spitzbergen described by Stensiö (1921: pl. 2, fig. 6) and is therefore cautiously considered to be an antero-lateral tooth of *Acrodus spitzbergensis*.

The roots of the teeth recovered are badly preserved. However, one tooth shows a labial row of small foramina just under the junction of crown and root.

Enameloid ultrastructure

The average thickness of the enameloid of the tooth studied is 110 µm, reaching 150 µm at the level of the longitudinal crest. It is composed of two layers (Fig. 4A), each representing half the total thickness of the enameloid across most of the crown. In both layers, the enameloid is a single crystallite enameloid (SCE), composed of rod-like crystallites of apatite which are never longer than 1 µm (Figs 4B, C). In the inner layer, the crystallites are aggregated in bundles. These bundles show an orientation perpendicular to the contact zone with the dentine, but may sometimes cross over each other. Each bundle is between 4 and 9 µm in diameter. At the level of the longitudinal crest, the inner layer is much thicker than in other parts of the crown, representing most of the enameloid, and, in its upper part, the bundles of crystallites show a woven structure (Fig. 4D). The outer layer shows more tightly packed crystallites, and there are no discernible bundles (Fig. 4B). In general, the apatite crystallites are orientated perpendicular to the surface, although there is substantial variation (Fig. 4B).

ACRODUS CUNEOCOSTATUS SP. NOV.
(Figs 3D–G, 4E, F)

Material

Holotype: 1 complete tooth (FMNH PF 14957, figs 3D–F). Paratypes: 27 more or less fragmentary teeth (FMNH PF 14294, 14958–64, 15124–42), two of which have been acid etched to study their enameloid ultrastructure (FMNH PF 14958–59).

Etymology

From *cuneus*, wedge (Latin), and *costatus*, with ribs (Latin), referring to the typical aspect of the ornamentation on the basal part of the crown of this species.

Type locality

Favret Canyon, Pershing County, North-Western Nevada.

Type stratum

Lower part of the Fossil Hill Member, Favret Formation, Star Peak Group, Anisian (Middle Triassic).

Diagnosis

Chevron-shaped ornamentation on the basal part of the crown; well-developed, irregular longitudinal crest; upper part of the crown ornamented by short ridges originating from the longitudinal crest, with a radiating pattern on the main cusp, perpendicular to the longitudinal crest distally and mesially to the main cusp; flattened crown; well-developed lingual furrow separating the crown from the root; large, randomly distributed foramina scattered all over the root.

Description

The holotype is 4.3 mm long mesio-distally and its maximum labio-lingual width is 1.8 mm. In occlusal view, the labial face is convex while the lingual face is almost straight, but shows an irregular, crenulated margin (Fig. 3F). The main cusp is very weakly developed, and situated in the centre of the crown. As a consequence, the tooth appears rather flat.

The crown of all teeth shows a well-developed longitudinal crest which is lingually offset from the crown midline. It has a quite irregular course in occlusal view and appears irregularly crenulated in labial and lingual view (Fig. 3E). The crowns of the teeth are ornamented by two different sets of ridges, the 'upper' and the 'lower' ones. The 'upper' ridges originate from the longitudinal crest. On the main cusp, they show a radiating pattern and most of them reach the 'lower' ornamentation. Mesially and distally to the main cusp, they are more or less perpendicular to the longitudinal crest and parallel to each other. Their length is variable, but most of them are short and they do not extend to the 'lower' ornamentation. The 'lower' ridges originate from the shoulder of the crown, and show a bifurcating pattern, forming a chevron-shaped ornamentation (Fig 3D, E).
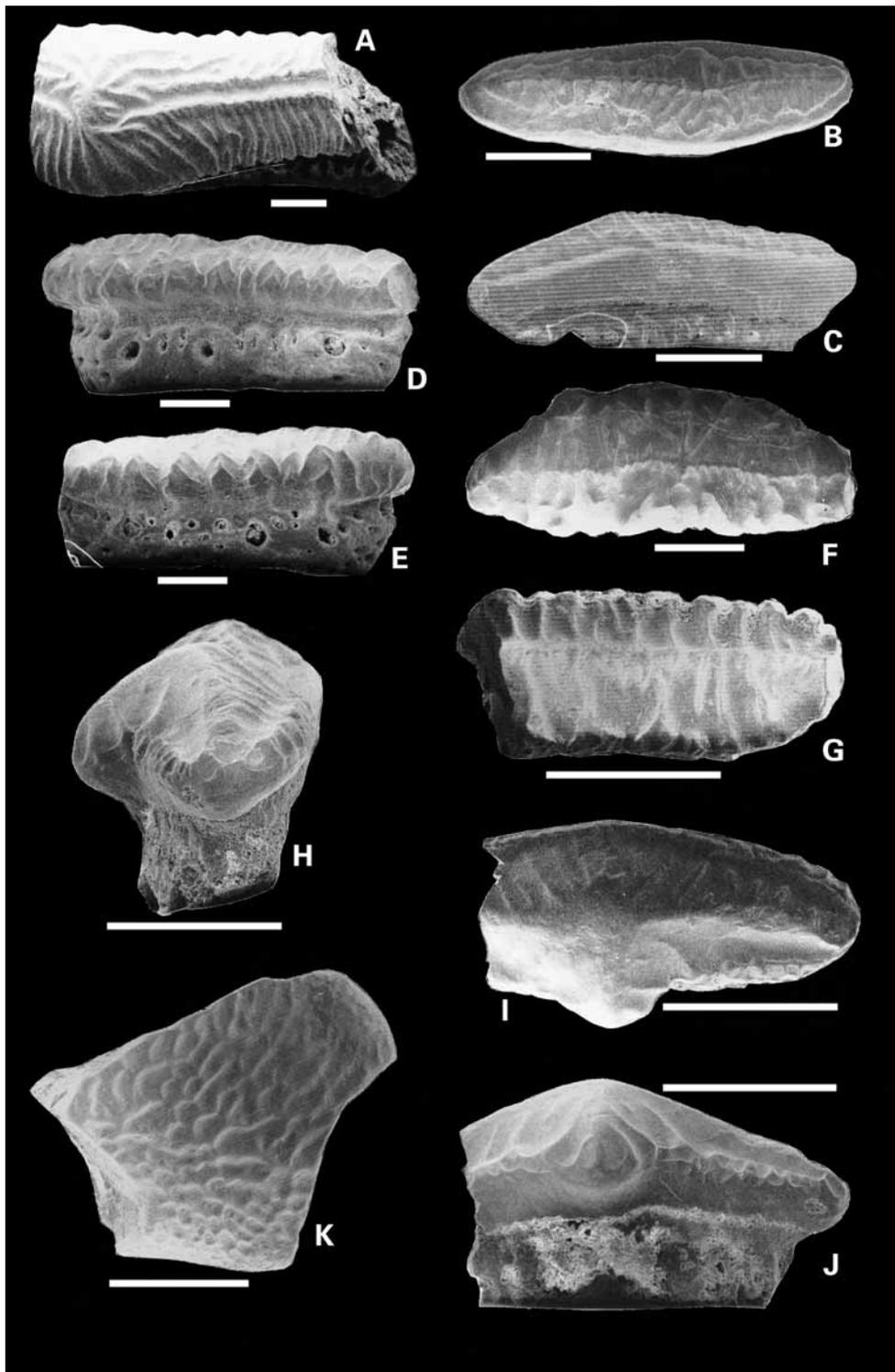
Figure 3. A–C, *Acrodus spitzbergensis*. A, tooth (FMNH PF 14951) in apical view; B, ?antero-lateral tooth (FMNH PF 15143) in apical view; C, ?antero-lateral tooth (FMNH PF 15143) in lingual view. D–G, ***Acrodus cuneocostatus* sp. nov.** D, holotype in lingual view; E, holotype in labial view; F, holotype in apical view; G, ?posterior tooth (FMNH PF 14960) in apical view. H–J, ***Polyacrodus bucheri* sp. nov.** H, holotype in ?mesial or ?distal view; I, holotype in apical view; J, holotype in lingual view. K, *Palaeobates* sp., apical view of a fragmentary tooth (FMNH PF 14965) showing a pitted ornamentation. All scale bars = 1 mm.
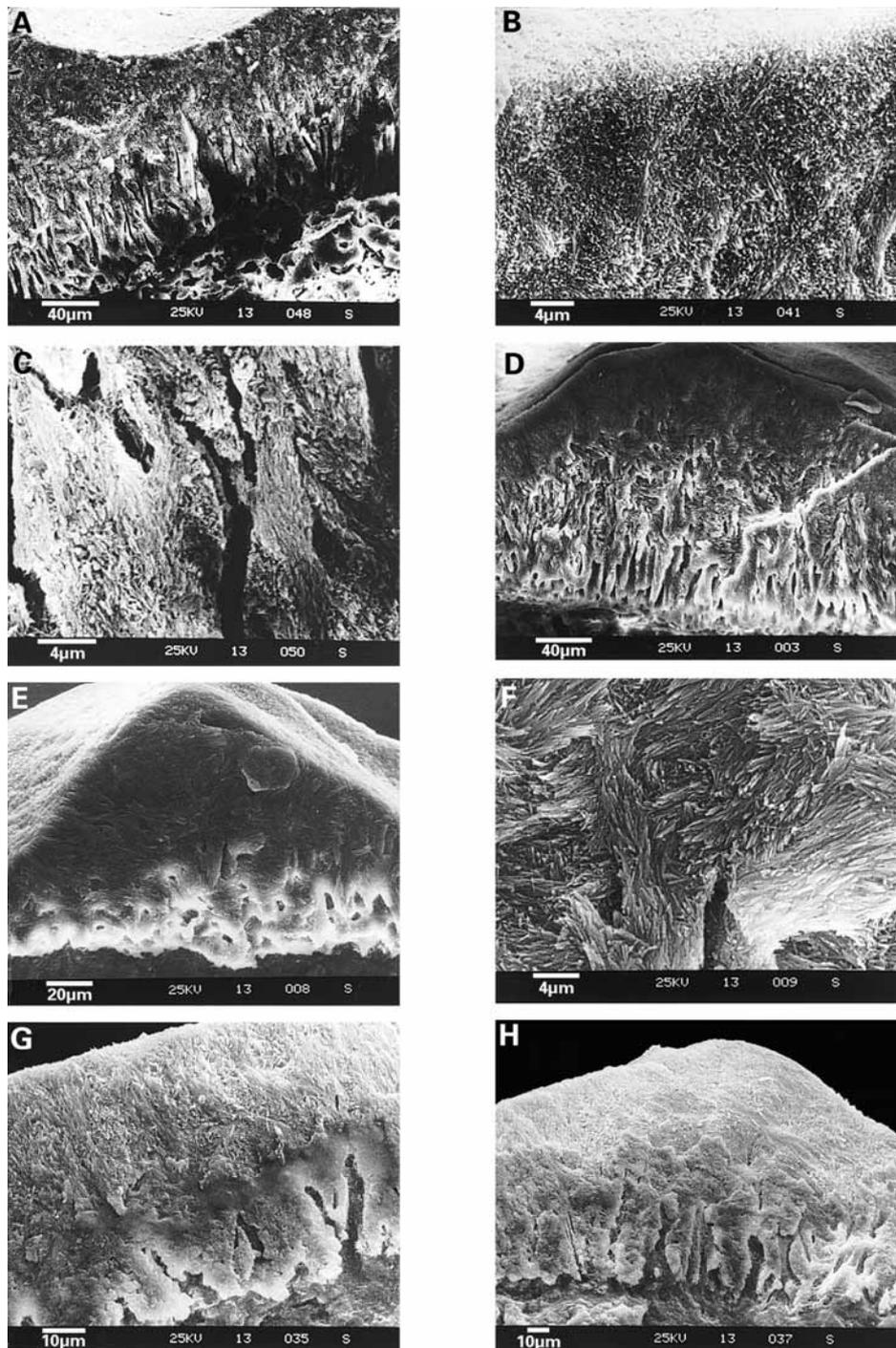
Figure 4. A–D, *Acrodus spitzbergensis*. A, transverse section of the enameloid of a tooth (FMNH PF 14950) etched 5 s in 10% HCl; B, detail of the outer layer of the enameloid in a transverse section of the same tooth etched 65 s in 10% HCl; C, detail of the inner bundled layer of the enameloid in a tranverse section of the same tooth etched 5 s in 10% HCl; D, transverse section of the enameloid at the level of the longitudinal crest showing the woven appearance of the inner layer of the enameloid. Same tooth etched 65 s in 10% HCl. E, F, ***Acrodus cuneocostatus* sp. nov.** E, transverse section of the enameloid at the level of the longitudinal crest. FMNH PF 14958 etched 95 s in 10% HCl; F, detail of the structure of the enameloid in the transverse section of the longitudinal crest. FMNH PF 14958 etched 95 s in 10% HCl. G, H, ***Polyacrodus bucheri* sp. nov.** G, transverse section of the enameloid of FMNH PF 14970 etched 35 s in 10% HCl; H, transverse section of the enameloid at the level of the longitudinal crest. FMNH PF 14970 etched 35 s in 10% HCl.

They do not reach the longitudinal crest. On the mesial and distal extremities of some teeth, these ridges are very well developed, and in occlusal view, the labial and lingual margins of the crown appear crenulated (Fig. 3G). The lingual and labial shoulders of the crown are convex.

There is a well-developed furrow separating the crown from the root on the lingual side of the teeth. On the labial side, this furrow may also be well developed, but is sometimes absent, as is seen in the holotype. The root projects slightly lingually. The basal face is flat. The lingual, labial, distal and mesial surfaces of the root show foramina of various size which are randomly distributed (Figs 3D, E). There is no row of specialized foramina *sensu* Johnson (1981). The depth of the root is usually 120% of the height of the crown.

Enameloid ultrastructure

The average thickness of the enameloid of the teeth studied is 60 µm, reaching 130 µm at the longitudinal crest. It is composed of two layers of SCE, similar to those observed in the teeth of *Acrodus spitzbergensis*. However, the inner layer is more reduced than in the latter species and is barely visible on the lower part of the lingual and labial faces of the crown. At the level of the longitudinal crest, it is also reduced and most of the enameloid is made of a compact tissue, the crystallites of which are not aggregated into bundles and show no preferential orientation (Fig. 4E, F). The crystallites are rod shaped and may attain 2 µm in total length. The enameloid ultrastructure of *A. cuneocostatus* is therefore basically the same as in *A. spitzbergensis* but appears more compact.

Discussion

The irregular longitudinal crest, the radiating pattern of the ridges ornamenting the main cusp and the ridges originating from the longitudinal crest without reaching the shoulder of the crown are all features reminiscent of *Acrodus vermiformis* Stensiö, 1921, mistakenly spelt *A. vermicularis* in Rieppel *et al.*, 1996. However, the ornamentation of the teeth from Nevada is sparser than in known teeth of *Acrodus vermiformis* (see Stensiö, 1921: pl. 2, figs 20 and 21). Indeed, most Triassic *Acrodus* species (*A. gaillardoti* Agassiz in Geinitz, 1837, *A. spitzbergensis* Hulke, 1873, *A. scaber* Stensiö, 1921, *A. oppenheimeri* Stensiö, 1921, *A. microdus* Winkler, 1880, *A. alexandrae* Wemple, 1906, *A. oreodontus* Wemple, 1906, *A. wemplae* Jordan, 1907, *A. lateralis* Agassiz, 1837) show a denser ornamentation (Winkler, 1880; Woodward, 1889; Wemple, 1906; Jordan, 1907; Stensiö, 1921; Rieppel, 1981; Cappetta, 1987) than *A. cuneocostatus*. Only the teeth of ?*Acrodus* sp. described from the Upper Triassic of

British Columbia by Johns, Barnes & Orchard (1997) have a similarly sparse ornamentation.

Another peculiarity of the teeth described above is the presence of the chevron-shaped ornamentation at the base of the crown (Fig. 3D, E; Rieppel *et al.*, 1996: fig. 2g) which is not present in *Acrodus vermiformis* (Stensiö, 1921: pl. 2, figs 20, 21). The crenulated aspect of the extremities of the teeth in occlusal view is found in *A. vermiformis* (Stensiö, 1921) and *A. alexandrae* (Wemple, 1906). However, *A. alexandrae* shows no radiating pattern of the ridges ornamenting the main cusp and it has a faint longitudinal crest (Wemple, 1906), different from the teeth from Nevada.

The teeth described above thus appear different from all currently known *Acrodus* species from the Triassic and hence justify the erection of a new species. However, it should be emphasized that the genus *Acrodus* is defined on rather weak grounds, mostly on the basis of tooth histology and the crushing function of the teeth (Rieppel, 1981). A revision of the genus in the near future may demonstrate that the species *A. cuneocostatus* belongs to a genus other than *Acrodus*.

Teeth of ?*Acrodus* from the Baldonnel Formation (Upper Carnian) of British Columbia (Johns *et al.*, 1997: pl. 1, figs 14–16) and *Acrodus lateralis*, from the Middle Triassic of Monte San Giorgio (Switzerland; Rieppel, 1981: figs 11D,E) show the same basic organization of the enameloid as *Acrodus* teeth from Nevada. The teeth of the Canadian ?*Acrodus* show an arrangement very reminiscent of *A. spitzbergensis* while *A. cuneocostatus* shows the most compact enameloid. The teeth of *A. lateralis* have the least compact enameloid. The basic two-layered structure seen in all these *Acrodus* teeth agrees well with the observations made by Poole (1967) in modern elasmobranch teeth in that the outer layer of the enameloid, i.e. the compact layer in the teeth studied above, is more highly mineralized than the inner layer. However, very few teeth have been studied so far and it is therefore difficult to assess the variability of these structures among each species, or the effect of preservational bias. An interpretation of these structures in terms of phylogeny or adaptation towards a specific diet would therefore be premature.

POLYACRODONTIDAE GLÜCKMAN, 1964
GENUS *PALAEOBATES* MEYER, 1849
PALAEOBATES SP.
(Fig. 3K)

Material

Four fragmentary teeth (FMNH PF 14965–68).

Description

The crowns of these teeth are flat and heavily ornamented. There is a poorly developed longitudinal

crest from which originates a dense network of irregular ridges, reaching the base of the crown. These ridges anastomose densely on two of the specimens which results in a pitted appearance on the surface of the crown (Fig. 3K). One fragment shows the distal or mesial extremity of the tooth, which appears to be rather angular in occlusal view with a non-pitted ornamentation. None of the teeth preserve the root.

Discussion

Based on histological study, Rieppel *et al.* (1996) referred similar tooth fragments to *Palaeobates* cf. *P. shastensis* Bryant, 1914. However, the teeth described by Bryant (1914) lack a longitudinal crest which is present, although weakly developed, in the above-described specimens. The lack of such a longitudinal crest in the teeth described by Rieppel *et al.* (1996) appears to be the result of wear, and any close relationships of the teeth from Nevada with *P. shastensis* is difficult to demonstrate. The fragmentary nature of the fossils precludes a more precise determination than *Palaeobates* sp.

GENUS *POLYACRODUS* JAEKEL, 1889
***POLYACRODUS BUCHERI* SP. NOV.**
(Figs 3H–J, 4G, H, 5A–C)

Material

Holotype: one incomplete tooth (FMNH PF 14969, Figs 3H–J), Paratypes: FMNH PF 14286 and 14288 + 14 incomplete teeth (FMNH PF 14970–83), one of which has been acid etched to study the enameloid ultrastructure (FMNH PF 14970).

Etymology

In honour of Dr Hugo Bucher who discovered the fossiliferous site which yielded the fauna described here and who has done important work which greatly improved our understanding of the Middle Triassic of Nevada and its global correlation.

Type locality

Favret Canyon, Pershing County, North-Western Nevada.

Type stratum

Lower part of the Fossil Hill Member, Favret Formation, Star Peak Group, Anisian (Middle Triassic).

Diagnosis

Main cusp low, with a well-developed lingual peg overhanging the root and no labial peg; lingual peg ornamented by one main ascending ridge, from which up to two pairs of secondary ridges originate; no, or very weakly developed, accessory cusplets; crown sparsely ornamented; faint longitudinal crest; root with a labial sulcus and a labial row of small foramina below the crown–root junction.

Description

No complete tooth has been recovered so far, and the overall shape of these teeth is difficult to describe precisely. The holotype shows the main cusp and the ?mesial or ?distal extremity of the crown. The actual length of the fossil is 2.3 mm and the complete mesio-distal length of the tooth may be estimated to be 3.3 mm. The maximum labio-lingual width of the tooth is 1.2 mm. The main cusp is very low and bears a well developed lingual peg that overhangs the root (Figs 3H, I). One main ridge ascends to this peg, from which up to two pairs of secondary ridges may originate (Fig. 3J). There are no discernible lateral cusplets. The longitudinal crest is not well developed and may be slightly deflected towards the labial side of the tooth. Ridges ascending the crown reach the longitudinal crest on the lingual and labial side. These ridges have a radiating pattern on the main cusp but run parallel to each other and perpendicular to the longitudinal crest mesially and distally. In most, but not all, teeth there is a circumferential rim at the crown shoulder which is ornamented by small, frequently anastomosing ridges (Fig. 3H, J). The density of the ridges on the rim is greater than in the rest of the crown. The rim always dies out around the lingual peg. The lingual and labial shoulders of the crown are convex.

The root and the crown are separated by a furrow on the labial and lingual side. The root shows a labial sulcus and is slightly projected lingually. There is one row of small, specialized, foraminae in the upper part of the labial face of the root. Another series of foraminae is located in the upper part of the labial sulcus and there are large foraminae on the upper part of the lingual side of the root.

Enameloid ultrastructure

The average thickness of the enameloid in the tooth FMNH PF 14970 is 80 μm, reaching 150 μm at the level of the longitudinal crest. It is composed of two layers of SCE and hence appears to be similar to the teeth of *Acrodus* described above. The outer, compact layer is slightly thicker than the inner, bundled layer (Fig. 4G), except at the level of the longitudinal crest where it represents two-thirds of the total thickness (Fig. 4H). The compact layer shows alternating bands of longitudinally and radially orientated crystallites (Fig. 5A). However, at the surface of the enameloid, this arrangement of the crystallites is not so easily discerned and they appear to be principally oriented

perpendicular to the crown surface (Fig. 5B). In the longitudinal crest, the crystallites show no preferential orientation (Fig. 5C). The crystallites are rod shaped and may attain 3 μm in total length. The bundles of the lower layer are between 8 and 10 μm in diameter.

Discussion. In overall morphology, the teeth described above are very reminiscent of those of *Lissodus*, but the peg at the base of the main cusp is lingual rather than labial as demonstrated by the morphology of the root. There is no hybodont root projecting labially and with a lingual sulcus. The presence of a well-developed lingual peg is shared with *Polyacrodus contrarius* Johns *et al.*, 1997, from the Ladinian and Carnian of Canada. These two species also share an ornamented circumferential rim and therefore appear to be closely related. They differ, however, in the more elongate shape and stronger ornamentation of the Canadian species. Moreover, the teeth of the Canadian species possess lateral cusplets, albeit reduced ones. The teeth of *Polyacrodus* sp. B described by Rieppel *et al.* (1996) also show a well-developed lingual peg (mistakenly interpreted as a labial peg by these authors, see their fig. 3d–g). They differ from the teeth described above in the possession of a higher main cusp and the presence of very weakly developed lateral cusplets. They also share with the teeth of *Polyacrodus bucheri* short, anastomosed ridges ornamenting the shoulder of the crown (compare Fig. 3J with fig. 3d and f in Rieppel *et al.*, 1996). These two teeth are therefore attributed to *Polyacrodus bucheri* and probably represent anterior teeth of that species.

POLYACRODUS TREGOI RIEPPEL *ET AL.*, 1996
(Fig. 5D–F)

Material
Thirty-one teeth (FMNH PF 14984–15014), none complete, from which three have been acid etched to study their enameloid ultrastructure (FMNH PF 14984–86).

Description
These teeth, although all fragmentary, agree well with those of the species *Polyacrodus tregoi* Rieppel *et al.*, 1996. Their crowns possess a well-developed main cusp, flanked by up to four pairs of lateral cusplets. There is no labial or lingual peg. The crown is ornamented by well-separated, coarse ridges which often bifurcate basally as they reach the shoulder of the crown. There is a moderately developed longitudinal crest. The crown is separated from the root by well-developed labial and lingual grooves.

The root is quadrangular in outline and there is no labial sulcus. The root projects lingually and also slightly labially, being labio-lingually wider than the crown. The root shows randomly distributed foramina of various sizes. There is no row of specialized foramina *sensu* Johnson (1981).

Enameloid ultrastructure
The enameloid is usually 50 μm thick, with a compact outer part representing up to 60% of the total thickness (Fig. 5D). In the compact part of the enameloid, all the crystallites are oriented perpendicular to the surface (Fig. 5D, E). The inner part is a less dense, bundled SCE (Fig. 5D, F). The bundles average 2.5 μm in diameter. They are therefore thinner than in any of the above-mentioned hybodont species whose enameloid ultrastructure has been studied. As is usual among hybodonts, the crystallites of apatite are rod-shaped and may attain 3 μm in length.

HYBODONTIDAE OWEN, 1846
GENUS *HYBODUS* AGASSIZ, 1837
?HYBODUS SP.
(Figs 5G, 6A, B)

Material
Five teeth more or less damaged (FMNH PF 15015–19).

Description
The main cusp of the crown is well developed, quite high and inclined lingually. It is flanked by up to one pair of poorly differentiated lateral cusplets (Fig. 6A). However, as no tooth is complete, more than one pair of lateral cusplets may have been present. There is no lingual or labial peg, but some poorly developed labial nodes occur at the base of the main cusp. The crown is ornamented by fine, bifurcating ridges (Fig. 6B), ascending the crown from the shoulder up to the apex of the cusps. They are generally denser on the lingual side than on the labial one. There is a moderately developed longitudinal crest.

The crown is separated from the root by a furrow. The root projects lingually and shows a labial sulcus. There are small foramina distributed randomly across the whole labial and lingual surface of the root. There is a poorly defined row of specialized foramina above the labial sulcus and on the lingual side just under the crown–root junction. On the middle part of the lingual side, the foraminae tend to be larger than in other parts of the root (Fig. 6A).

As very few teeth have been recovered, none has been prepared for the study of the enameloid ultrastructure. However, a photograph of an unprepared transverse section of the enameloid (Fig. 5G) suggests the presence of an SCE very similar to that observed in the teeth of *Polyacrodus* and *Acrodus* described above.
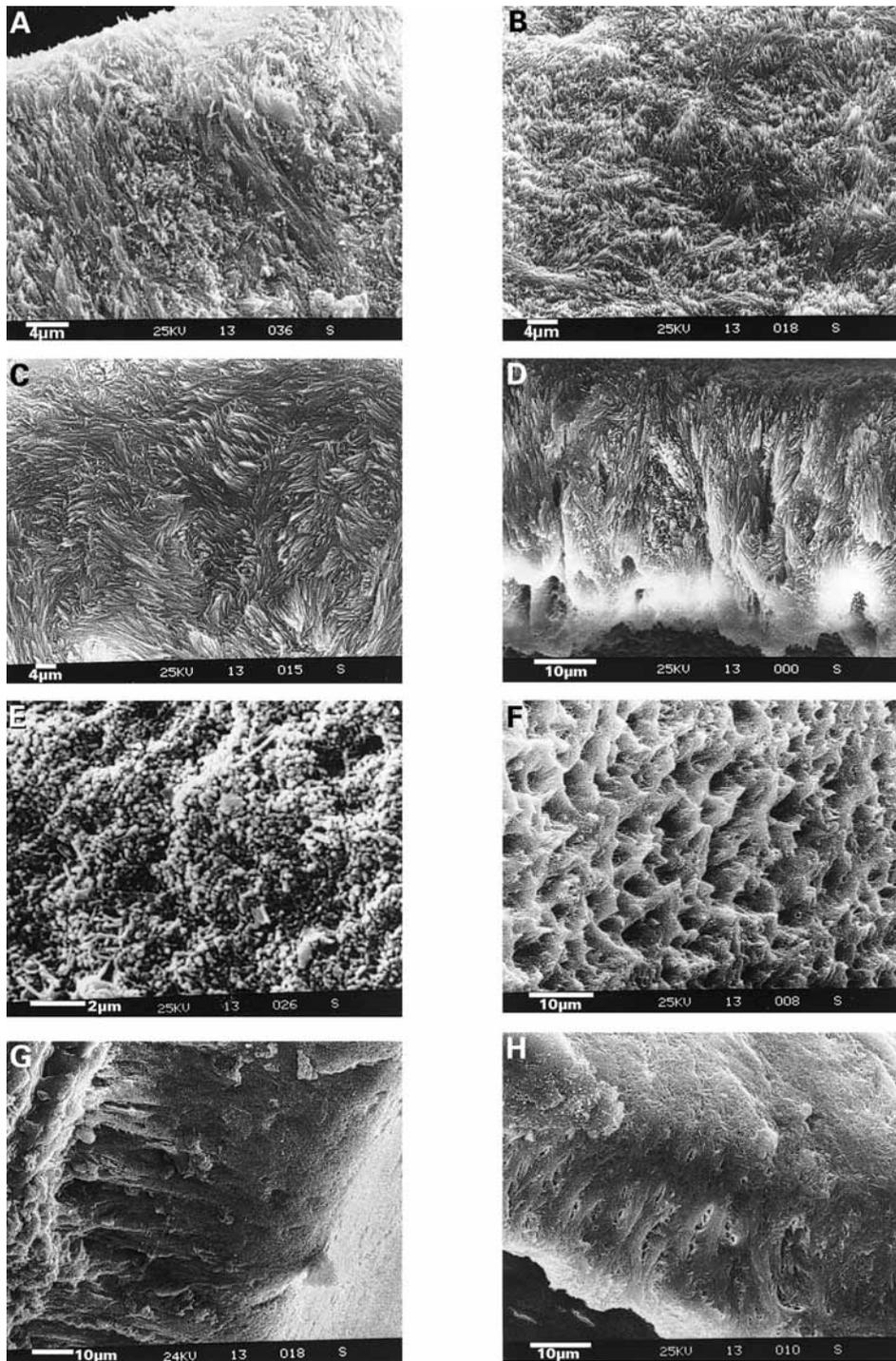
Figure 5. A–C, *Polyacrodus bucheri* **sp. nov.** A, detail of the outer layer of the enameloid FMNH PF 14970 etched 35 s in 10% HCl; B, surface view of the outer layer of the enameloid of the same tooth etched 95 s in 10% HCl; C, detail of the outer layer of the enameloid in a transverse section of the longitudinal crest. Same tooth etched 95 s in 10% HCl. D–F, *Polyacrodus tregoi*. D, longitudinal section of the enameloid of FMNH PF 14984 etched 35 s in 10% HCl; E, surface view of the outer enameloid of FMNH PF 14986 etched 35 s in 10% HCl; F, surface view of the inner enameloid of FMNH PF 14985 etched 155 s in 10% HCl. G, *?Hybodus* sp., transverse section of the enameloid of an unprepared tooth (FMNH PF 15015). The dentine is towards the left. H, *Mucrovenator minimus* **sp. nov.**, surface of a ridge ornamenting the surface of FMNH PF 15021 etched 95 s in 10% HCl. The ridge is covered by an SLE while near the base we can see bundles of crystallites set perpendicular to the axis of the ridge.
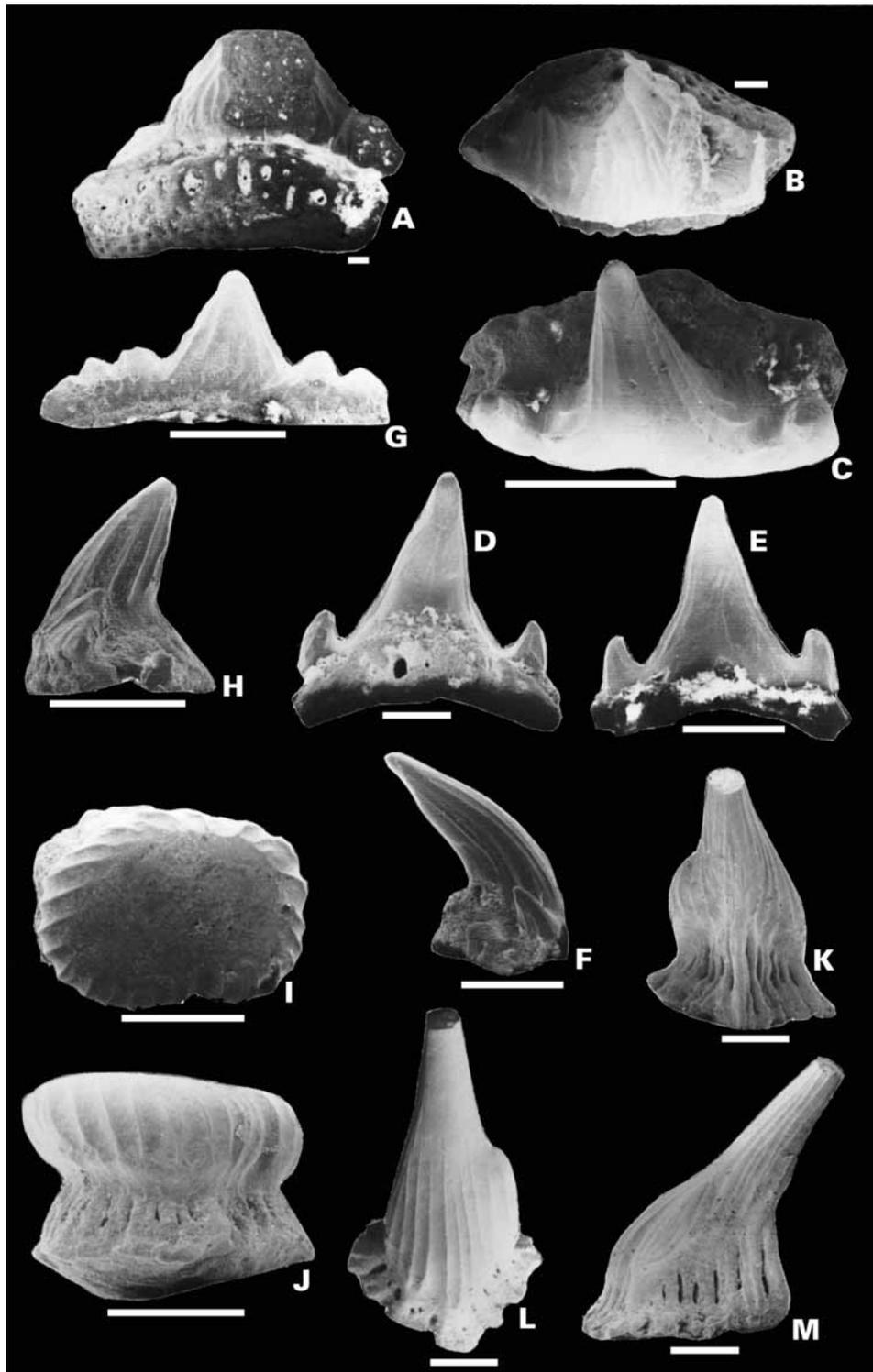
Figure 6. A, B, *?Hybodus* sp. A, tooth (FMNH PF 15015) in lingual view; B, tooth in apical view. C–H, ***Mucrovenator minimus* sp. nov.** C, holotype, an antero-lateral tooth, in apical view; D, holotype in lingual view; E. holotype in labial view; F, holotype in ?mesial or ?distal view; G, postero-lateral tooth (FMNH PF 15024) in lingual view; H, postero-lateral tooth (FMNH PF 15024) in ?mesial or ?distal view. I, J, *Complanicorona* aff. *C. rugosimargines* (FMNH PF 15119). I, dermal denticle in apical view; J, dermal denticle in lateral view. K–M, *Parvidiabolus* aff. *P. convexus* (FMNH PF 15042). K, dermal denticle in posterior view; L, dermal denticle in apical view; M, dermal denticle in lateral view. All scale bars = 500 μm.

Discussion

The teeth described above show insufficient diagnostic characters to allow identification at the species level. The general morphology of the crown, with a well-developed, slightly compressed labio-lingually oriented main cusp and a rather dense ornamentation, is more reminiscent of the genus *Hybodus* than *Polyacrodus*. Labial nodes, although rare in *Hybodus* teeth in general, are known in the following species: *H. hauffianus* Fraas, 1895, *H. delabechei* Charlesworth, 1839, *H. raricostatus* Agassiz, 1843, *H. obtusus* Agassiz, 1837 and *H. cloacinus* Quenstedt, 1858 (Duffin, 1997). However, in the absence of histological studies, it is not possible to corroborate the attribution of these teeth to the genus *Hybodus*.

NEOSELACHII COMPAGNO, 1977
SYNECHODONTIFORMES DUFFIN & WARD, 1993
FAMILY *INCERTAE SEDIS*
***MUCROVENATOR* GEN. NOV.**

Etymology

For *mucro*, sword in Latin, and *venator*, hunter in Latin, referring to the slender shape of the main cusp of the teeth and the fact that sharks are predators.

Diagnosis

Minute teeth, never exceeding 2.5 mm in height or width; well-developed sharp main cusp flanked by up to two pairs of well-separated lateral cusplets; ornamentation composed of parallel ridges ascending the crown up to its apex, more or less developed according to the position of the tooth in the jaws; no furrow separating the root from the crown; root very shallow and projecting lingually, with a mesio-distal depression on its basal surface showing the opening of a row of canals.

***MUCROVENATOR MINIMUS* SP. NOV.**
(Figs 5H, 6C–H, 7)

Material

Holotype: FMNH PF 15020. Paratypes: 21 teeth (FMNH PF 15021–41) + FMNH PF 14284, three of which have been acid etched to study their enameloid ultrastructure (FMNH PF 15021–23).

Etymology

For *minimus*, small in Latin, referring to the small size of the teeth.

Type locality

Favret Canyon, Pershing County, North-Western Nevada.

Type stratum

Lower part of the Fossil Hill Member, Favret Formation, Star Peak Group, Anisian (Middle Triassic).

Diagnosis

As for the genus *Mucrovenator* gen. nov. (monospecific genus).

Description

The teeth are minute, never exceeding 2.5 mm in height or mesio-distal length. They possess a well-developed and slender main cusp flanked by up to two pairs of pointed lateral cusplets (Fig. 6D, E). The main cusp is recurved lingually (Fig. 6F), sometimes showing a sigmoidal curvature, and in some teeth it may also be slightly angled distally. The maximal height of the first pair of lateral cusplets is half the height of the main cusp but they are generally much lower. The second pair of cusplets is always lower than the first pair (Fig. 6G).

The pattern of ornamentation of the crown is variable. Some teeth are almost smooth, showing only a few poorly developed ridges (Fig. 6D), while others show well-developed ridges on the labial and lingual sides of the main cusp and of the lateral cusplets (Fig. 6G). There are up to eight ridges on the labial and lingual faces of the main cusp, extending from the base of the crown to its apex. The better developed the lateral cusplets, the better developed are the ridges ornamenting the crown. The main cusp also possesses a moderately well-developed cutting edge distally and mesially. The cutting edges extend from the base of the cusp to its apex. Cutting edges are also present on the lateral cusplets. The latter are well separated from the main cusp, and the cutting edges die out between them. In occlusal view, the labial face of the teeth may be slightly convex or concave. There is no furrow separating the crown from the root.

The root is very shallow, projecting lingually and perpendicularly to the crown (Fig. 6C, H). In labial or lingual views, its base is concave. The labial face shows no canal opening. In basal view, when the root is well preserved, it shows a mesio-distally elongated depression on the labial half of the root, located just under the crown. Medial to this depression, there is a row of open canals. The lingual face of the root shows a more or less well-developed row of large canal openings near its base.

Enameloid ultrastructure

The enameloid is between 21 and 24 μm thick in the three teeth studied and appears to be made of at least two layers: a shiny-layered enameloid (SLE) and a
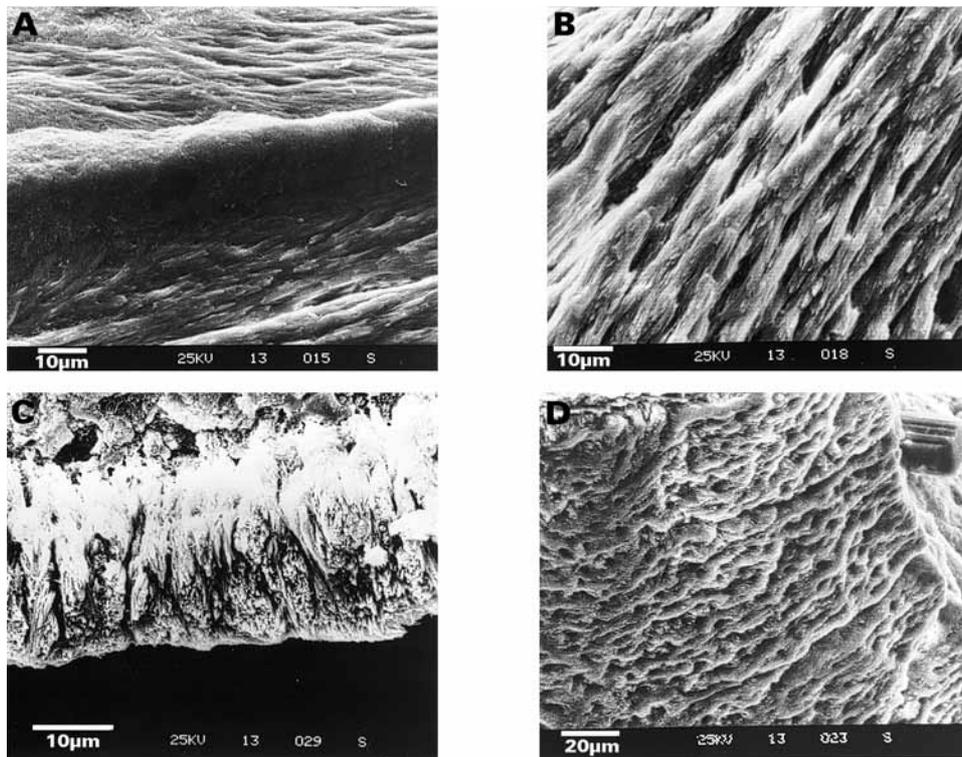
Figure 7. *Mucrovenator minimus* **sp. nov.** A, ridge ornamenting the surface of FMNH PF 15021 etched 35 s in 10% HCl. The SLE remains at the level of the ridge only; B, surface of the same tooth etched 65 s in 10% HCl showing the PBE; C, transverse section of the enameloid of FMNH PF 15022 etched 35 s in 10% HCl. Dentine is towards the upper part of the image; D, surface of the lower part of the crown of the same tooth etched 95 s in 10% HCl. Scale bar = 20 μm.

parallel-bundled enameloid (PBE). No tangled-bundled enameloid (TBE) has been found, but this might be due to the difficulty of correctly preparing such minute teeth. Note that the usual names of the three layers of the neoselachian enameloid (SLE, parallel-fibred enameloid and tangled-fibred enameloid) have been here replaced by SLE, PBE and TBE, as the two inner layers appear to be made of tightly packed bundles of crystallites of apatite, but which do not form true fibres.

The SLE is made up of minute crystallites, generally less than 0.1 μm in length, randomly orientated (Fig. 5H). The SLE is thicker at the level of the ridges than in any other part of the crown (Fig. 7A). Beneath the SLE, the enameloid is made of a PBE consisting of bundles of crystallites oriented parallel to the surface, to each other and to the axis of the cusps. They are 5–6 μm in diameter (Fig. 7B). At the level of the ridges ornamenting the crown, they show a change in orientation and become perpendicular to the axis of the cusps. Between these main bundles, there are well-developed thin radial bundles. In transverse section,

the enameloid is dominated by these radial bundles, and the main bundles parallel to the surface are difficult to spot (Fig. 7C). At the base of the crown, the PBE is so heavily dominated by the radial bundles that, even in surface view, the main bundles appear poorly defined (Fig. 7D).

Discussion

The presence of a PBE and the general morphology of the teeth of *Mucrovenator minimus* indicate neoselachian affinities. They appear to be close to the teeth of '*Hybodus*' *minor* from the upper Triassic of Europe. The teeth of these two species share a lingually projecting root with a basal median depression showing canal openings. Moreover, the ridges ornamenting the surface of the crown in these two taxa are made of a thick SLE with a PBE underneath showing a change in orientation of the crystallite bundles (Cuny, 1998; Cuny & Benton, 1999). However, the teeth of *M. minimus* are much more slender, with a less well-developed ornamentation and a more shallow root than
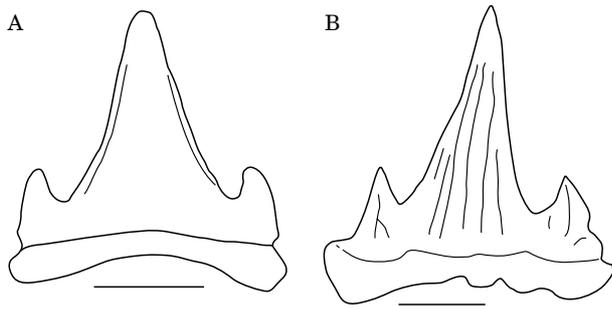
Figure 8. A, Outline of the labial view of the holotype of *Mucrovenator minimus*. B, Outline of the labial view of a parasymphyseal tooth of *Synechodus enniskilleni* Duffin & Ward, 1993, showing the corrugated labial base of the root. From Duffin & Ward, 1993. All scale bars = 500 μm.

those of '*Hybodus*' *minor*. The general morphology of the teeth of *M. minimus* is very similar to that of the anterior teeth of '*Palaeospinax*' *priscus* as illustrated by Maisey (1977). However, these teeth have been subsequently ascribed to *Synechodus enniskilleni* by Duffin and Ward (1993) who consider the genus *Palaeospinax* a *nomen dubium*. The reconstruction of these teeth given by these two latter authors differs significantly from Maisey's, mainly by the presence of a corrugated labial base of the root. This is diagnostic of the genus *Synechodus*, and the absence of this character in the teeth of *M. minimus* precludes the attribution of this species to *Synechodus* (Fig. 8). The slenderness of the teeth of *M. minimus* is also very reminiscent of the teeth of *Hybodus shastensis* described from the Middle Triassic of Nevada by Wemple (1906). These two species also share a root which is arched in labial or lingual view (Wemple, 1906: pl. 7, fig. 4). It is therefore possible that the teeth described by Wemple (1906) belong in fact to a neoselachian, but, in the absence of a study of the enameloid ultrastructure, this is very difficult to ascertain. On the contrary, the teeth of *Hybodus nevadensis* described from the same location by the same author appear to show a labial sulcus typical of a hybodont shark (Wemple, 1906: pl. 7, fig. 3). Teeth of *M. minimus* are also very similar to the teeth of '*Palaeospinax*' described from the Lower Triassic of Turkey by Thies (1982) which also possess a SLE and a PBE. They share a slender, high main cusp, and lateral cusplets well separated from the main cusp. However, because the root is lacking in the Turkish specimen (Thies, 1982), we cannot ascertain whether this tooth belongs to the same genus as those from Nevada.

Inside the Synechodontiformes, *M. minimus* is probably closer to the Palaeospinacidae (teeth with a moderately high central cusp, flanked by lateral cusplets and never flanked with low blades, basal root face arcuate to a variable degree, with deep open vascular

canals in the central depression, see Duffin & Ward, 1993) than to the Orthacodontidae, but its familial assignment is still problematic as it lacks the characteristic vascularization of the Palaeospinacidae (Duffin & Ward, 1993). It may be closely allied to '*H.*' *minor* and *Rhomphaiodon* Duffin, 1993, but this is only substantiated by the rather primitive vascularization of the root and does not justify the erection of a new family inside the Synechodontiformes.

The PBE is considered a synapomorphy of neoselachians (Reif, 1977; Thies, 1982; Maisey, 1984a,b, 1985; Thies & Reif, 1985; Gaudin, 1991), although this character is secondarily lost in batoids and in the posterior teeth of *Heterodontus* (Thies, 1982; Maisey, 1985) as a mechanical adaptation toward a durophagous diet (Preuschoft, Reif & Müller, 1974). So far, the oldest shark tooth showing a PBE is the tooth of '*Palaeospinax*' from the middle Scythian of Turkey described by Thies (1982). Next come the teeth of *Mucrovenator minimus*. When seen in section, the enameloid of *M. minimus* appears heavily dominated by radial bundles, and is then difficult to recognize as a PBE. The main orientation of the bundles forming the enameloid appears to be perpendicular to the contact surface with the dentine, which is very similar to that seen in the hybodontiform sharks (see above). This emphasizes the need, when looking for primitive neoselachian shark teeth, to study the enameloid both in section and in surface view. The absence of the TBE, although not demonstrated with certainty in the teeth of *M. minimus*, is probably not surprising as the TBE appears to be restricted to the terminal third of the cusps of many neoselachians (see Cuny, 1998; Cuny & Benton, 1999). It may, indeed, have appeared secondarily as a mechanical improvement to the teeth in the neoselachian lineage.

ELASMOBRANCHII *INCERTAE SEDIS*:
DERMAL DENTICLES

Many isolated dermal denticles have been recovered from the fossiliferous beds but their precise relationships are difficult to establish. Both neoselachian and hybodont shark teeth have been recovered in the site, and no dermal denticles of primitive Triassic neoselachians have been found so far in association with teeth. No attempt has therefore been made to refer these dermal denticles either to the hybodontiforms or to neoselachians. Here we follow the parataxonomy and terminology defined by Johns *et al.* (1997).

PARAGENUS *PARVIDIABOLUS* JOHNS *ET AL.*, 1997
PARVIDIABOLUS AFF. *P. ONVEXUS* JOHNS *ET AL.*, 1997
(Fig. 6K–M)

Material
Thirty-six dermal denticles (FMNH PF 15042–77).

Description

The crown of these dermal denticles is upright, slender and elongated. It is slightly recurved posteriad and its apex is rounded in cross-section (Fig. 6L). There are two wings flanking the base of the crown laterally (Fig. 6K), which are sometimes developed as a pair of accessory cusplets. The crown and the subcrown (ventral side of the crown, see Johns *et al.*, 1997: fig. 8) show a dense ornamentation of well-developed ridges, oriented parallel to each other. They reach the apex on the subcrown but not on the crown. The pedicle is anteriorly situated relative to the crown, fluted and shows a well-developed posterior buttress (Fig. 6M). The subpedicle (basal side of the pedicle, see Johns *et al.*, 1997: fig. 8) is rhomboid in outline, slightly concave and shows several canal openings, the central one being generally the largest.

Discussion

The presence of an anteriorly fluted pedicle with a concave subpedicle and the elongated, well ornamented crown is characteristic of the paragenus *Parvidiabolus* Johns *et al.*, 1997. The convex shape of the crown from side edge to side edge, the presence of lateral wings and the posterior buttress on the pedicle are more particularly reminiscent of *Parvidiabolus convexus* (Johns *et al.*, 1997: pl. 18, figs 4–7). However, the specimens from Nevada never show a multipetaloid subpedicle with a large central canal, but more material is needed to decide whether this warrants the erection of a new paraspecies. *Parvidiabolus convexus* is known from the Ladinian and Carnian of British Columbia.

PARAGENUS *LABASCICORONA* JOHNS *ET AL.*, 1997
LABASCICORONA SP.
(Fig. 9)

Material

Forty-one dermal denticles (FMNH PF 15078–15118).

Description

The crown of these dermal denticles is lanceolate in outline, wide, sometimes wider than long, with a single posterior apex. It is strongly recurved and ornamented by six or eight ridges oriented parallel to each other and reaching the apex of the crown (Fig. 9C). Most specimens show two well-developed furrows on the side of the mesial platform separating the crown into three distinct parts: a median platform with two to four ridges, flanked with two lateral wings, each with two ridges (Fig. 9A). The subcrown is ornamented by a single, well-developed, median ridge. The pedicle is very shallow and situated anteriorly in relation to

the crown (Fig. 9B). The surface of the subpedicle is rhomboid and convex, with a bulge. There is one central canal opening, with sometimes some accessory openings randomly distributed across the subpedicle.

Discussion

The lanceolate shape of the crown with a prominent furrow on each side of the mesial platform and the anterior pedicle with a rhomboid basal outline and a convex basal bulge are typical of the paragenus *Labascicorona* Johns *et al.*, 1997. Of the five species defined by these authors, three (*L. longifossae, L. nidifastigia, L. trifastigia*) usually have more than one posterior apex. The two remaining species, *L. alata* and *L. mediflexura,* have a more elongated crown, with less well-developed ridges, than the specimens from Nevada. However, as the specimens recovered so far do not show a good state of preservation, and as variation in the crown furrow development is difficult to evaluate, we prefer to leave the nomenclature open rather than erect a new paraspecies.

PARAGENUS *COMPLANICORONA* JOHNS *ET AL.*, 1997
COMPLANICORONA AFF. *C. RUGOSIMARGINES*
JOHNS *ET AL.*, 1997
(Fig. 6I, J)

Material

Five dermal denticles (FMNH PF 15119–23).

Description

The crown of these dermal denticles is flat, quadrangular to rounded in apical view (Fig. 6I). The central surface of the crown is smooth, while the shoulders are ornamented by short ridges. The pedicle is central in relation to the crown, and its lateral sides are fluted (Fig. 6J). The crown overhangs the pedicle around all margins. The subpedicle is rhomboid in outline, with a central canal opening. Sometimes, there are accessory canal openings forming a circle around the central one.

Discussion

The smooth and flat crown overhanging a central pedicle is typical of the paragenus *Complanicorona* Johns *et al.*, 1997. The shape of the crown with ornamented shoulders is very similar to the condition seen in *C. rugosimargines*. However, the latter species possesses a subcrown halo which appears to be lacking in the specimens from Nevada. *C. rugosimargines* is known from the Ladinian through the upper Carnian in British Columbia (Johns *et al.*, 1997).
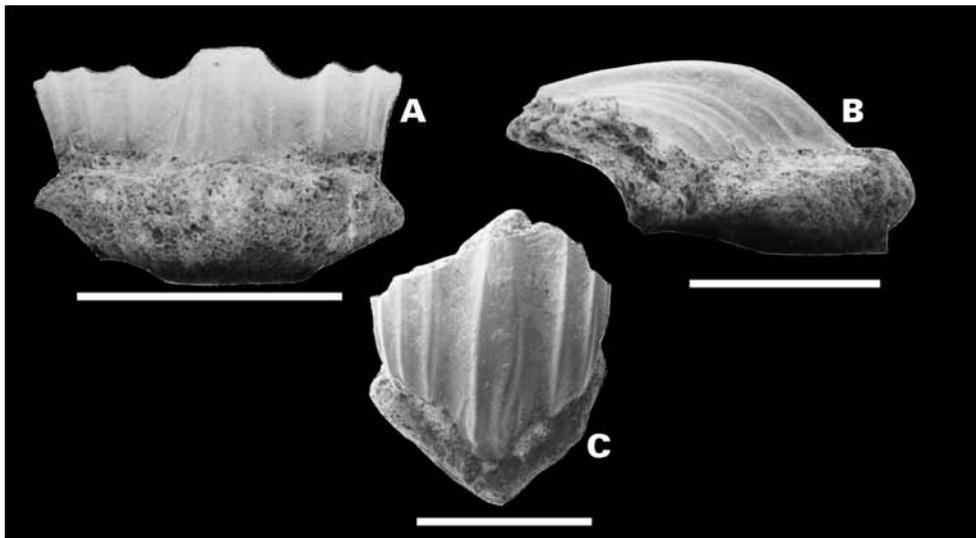
Figure 9. *Labascicorona* sp. (FMNH PF 15078). A, dermal denticle in anterior view; B, dermal denticle in lateral view; C, dermal denticle in apical view. All scale bars = 1 mm.

AFFINITY OF THE SHARK FAUNA FROM THE MIDDLE TRIASSIC OF NEVADA

When compared with the Lower Triassic of Spitzbergen, the Nevada shark fauna shares only the presence of *Acrodus spitzbergensis*. At a specific level, the rest of the hybodont fauna is quite different (Stensiö, 1921), which is in accordance with the difference in time between the two faunas. Based on the presence of *Nemacanthus*-like fin spines (Stensiö, 1921), neoselachian sharks were probably already present in Spitzbergen, but so far, their teeth have not been identified as such. On the other hand, the neoselachian teeth from Nevada are quite similar to those described from the Lower Triassic of Turkey (Thies, 1982).

When compared with other Middle Triassic shark faunas, the Nevada fauna appears rather different from the Monte San Giorgio fauna in Europe (Rieppel, 1981, 1982). There are no species in common and the genera *Asteracanthus* and *Acronemus* are absent in Nevada. The fauna recently described from the Middle Triassic of Saudi Arabia (Vickers-Rich *et al.*, 1999) appears also quite different from the one of Nevada as it lacks the genera *Polyacrodus* and *Palaeobates* while *Hybodus* is comparatively more abundant. However, the teeth described as *Acrodus* sp. are quite similar to those of *Acrodus cuneocostatus*, mainly because of the sparse ornamentation of their crown. The fauna from Nevada shares more similarities with the Ladinian fauna from British Columbia. *Polyacrodus contrarius* is very similar to *Polyacrodus bucheri*, as the two species share the presence of a well-developed lingual peg, a trait which is rare in hybodontiform teeth. *Synechodus* sp. 1 described by Johns *et al.* (1997) is also superficially similar to *Mucrovenator minimus*.

We also note, in the Carnian of British Columbia, the presence of the teeth of *?Acrodus* sp., similar to those of *Acrodus cuneocostatus*. Finally, the dermal denticles described in this article are also similar to those found in British Columbia, but few studies have taken into account the dermal denticles in faunas outside of Canada, making their significance difficult to assess. The shark fauna of Nevada therefore appears closely related to that of British Columbia. Since the faunas of British Columbia are younger than that of Nevada yet geographically close, the latter one could be a precursor of the former.

In all these Middle Triassic shark faunas, the hybodontiforms are largely dominant but appear mostly represented by durophagous forms, a feature also observed in the Upper Triassic of British Columbia and Europe (Johns *et al.*, 1997; Cuny & Benton, 1999). This would tend to demonstrate that, during the Triassic, hybodontiform sharks were mostly benthic animals, feeding on hard-shelled invertebrate prey, while large species, such as *Hybodus plicatilis*, represented probably the top predators of that time. Middle Triassic neoselachians have so far been found only in Nevada. Although they were already present in Early Triassic times (Thies, 1982), they were still rare in the Middle Triassic but they diversified and grew in abundance in the Late Triassic (Johns *et al.*, 1997; Cuny & Benton, 1999). In Nevada, they are represented only by small clutching teeth, indicating small opportunistic feeders. Rieppel *et al.* (1996) reconstructed the environment as a coastal setting, which is in accordance with the abundance of durophagous, benthic sharks. Early neoselachians were probably small, agile coastal predators hunting soft-bodied prey near the bottom of the sea.

CONCLUSION

The shark fauna from the Anisian of Nevada is reminiscent of the younger Ladinian and Carnian faunas of British Columbia. They share the presence of similar hybodontiforms, mainly durophagous species, and have a small neoselachian component. Neoselachian teeth are recognized on the basis of their enameloid ultrastructure as they show a PBE, while the ultrastructure of the enameloid of hybodont teeth is more homogenous. It consists of an SCE showing an outer compact layer and an inner bundled layer. In hybodontiforms, most of the crystallites of apatite forming the enameloid are oriented perpendicular to the surface, except at the level of the longitudinal crest, while, in neoselachian teeth, the PBE shows a change in the dominant orientation of the tissue which becomes parallel to the surface. However, neoselachians from the Triassic still show a very important component of the enameloid with a general bundle orientation perpendicular to the surface.

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