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The histology of Middle Devonian chondrichthyan teeth from southern Victoria Land, Antarctica

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Abstract – The tooth histology of recently discovered Middle Devonian (Givetian) elasmobranchs *Antarctilamna prisca, Aztecodus harmsenae,* and *Portalodus bradshawae* has been investigated using fluorescence and scanning electron microscopy. The internal structures of the crowns are surprisingly different in these three Antarctic genera. Only *Portalodus* has an enameloid cap overlying orthodentine and a core of trabecular dentine. *Antarctilamna*'s crown is constructed of ortho- and trabecular dentine, whereas *Aztecodus* only shows pleromin.

A cladistic analysis based on the hard tissues reveals that *Antarctilamna* may be the sister group of the specialized and successful xenacanthid sharks. The relationships of other Palaeozoic elasmobranchs remain unresolved.

INTRODUCTION

Fossil fishes have long been known from the Transantarctic Mountains of southern Victoria Land (Figure 1). Fossil shark remains were first collected from a moraine at Granite Harbour, near the coast of McMurdo Sound, during the British Antarctic *Terra Nova* Expedition of 1910–13. Woodward (1921) reported fossil scales that he attributed to sharks, but these were later shown to be from agnathan thelodonts (Turner and Young 1992). White (1968) described the first definite shark specimen; a single tooth, which he described as a new form, *Mcmurdodus featherensis,* that he placed in a new family, the Mcmurdodontidae. This specimen came from Mt Feather, 18 km due east of the Lashly Range, Skelton Névé area (Figure 1). Young (1982) described *Antarctilamna prisca,* based on partially articulated remains which included teeth, scales and fin-spines. He also illustrated large diplodont teeth from Portal Mountain recorded by Ritchie (1972) as resembling those of *Xenacanthus* sp.

Over the summer season of 1991–1992 Long participated in a joint NZARP-ANARE expedition to the Cook Mountains and Skelton Névé regions, southern Victoria Land, collecting fossil fish remains from many new localities, as well as visiting some well-known sites. During this trip many new fossil shark teeth were collected. Long and Young (1995) described these teeth as belonging to three new genera and species, *Portalodus bradshawae, Aztecodus harmsenae* and *Anareodus statei.* These sharks are part of a diverse fossil fish fauna occurring in the Aztec Siltstone, that includes arthrodires (Ritchie 1975; Long 1995), antiarchs (Young 1988), acanthodians (Young 1989), rhipidistians (Young *et al.* 1992), lungfish (Woolfe *et al.* 1990; Young 1991), and an undescribed actinopterygian (Young 1991). The total now exceeds 40 species of macro- and

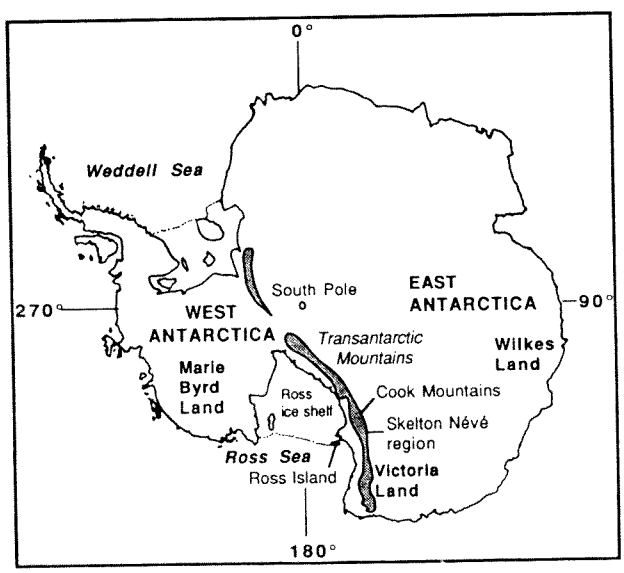

Figure 1 Map showing locality where material was collected. Specific localities and stratigraphy of sites are given in Long and Young (1995). The Lashley Ranges site where many of the specimens were collected, including the holotype of *Antarctilamna prisca,* is in the Skelton Névé region.

microvertebrates, making it the most diverse assemblage of fishes of Middle Devonian age in the Southern Hemisphere, and a foundation for biostratigraphic correlations in the East Gondwana Province (Young 1993; Turner 1993).The fauna is believed to range in age from Late Givetian through to possibly early Frasnian (Young 1993), although Turner (1997) has suggested it could be much older, ranging from earliest Eifelian to late Givetian. All three of the specimens studied in this paper are from horizons thought to be within the Givetian section of the Aztec Siltstone.

Research on the histological characteristics of Palaeozoic shark remains began with British Carboniferous material described by Agassiz (1837–44), followed by detailed reports by Owen only a few years later. The techniques of preparation have not changed very much since then, but the number of investigation methods has increased with the use of petrographic microscopes with polarized light, scanning electron microscopes, cathodoluminescence instrumentation and fluorescence microscopy. Gaps still exist in knowledge of the histology of many groups of Palaeozoic sharks which have not been investigated in as much detail as the phoebodontids were studied by Gross (1973), the xenacanthids by Hampe (1991), or the petalodontids by Zangerl *et al.* (1993).

The enameloid structure of sharks' teeth has been the focus of much study in the second half of this century. Recent shark teeth have been predominantly investigated with the transmission electron microscope (e.g. Sasso and Santos 1961; Kemp and Parr 1969; Garant 1970) or with the SEM (Reif 1973). However, not all sharks' teeth possess an enameloid layer. The xenacanthids developed none, and in this paper we describe another form lacking such a layer. Several 'primitive' sharks are known to lack enameloid, as does the early neoselachian *Anachronistes* (Duffin and Ward 1983).

The histological structure can be used for systematics as shown by Hampe (1991) for xenacanthids. The xenacanthids are intragenerically consistent in their histological characteristics. This has been well demonstrated in four species of *Triodus* from the SW-German Permo-Carboniferous Saar-Nahe Basin.

This paper presents the histological features of some primitive sharks of the Antarctic continent, and interprets the significance of the hard tissues of a number of Palaeozoic forms in a cladistic analysis.

MATERIALS AND METHODS

The specimens were collected *in situ* from outcrops of the Aztec Siltstone in Antarctica and then underwent manual preparation with fine chisels and needles to expose them from the matrix. In some cases whole specimens could be freed entirely from the rock (Long and Young 1995).

For the histological investigation we used both a fluorescence microscope and a SEM. Fluorescence microscopy can be used for transmitted light observations on one hand, or, for the topic of this work, reflected light for excitation of fluorescence radiation. Fluorescing substances will emit light of specific colour while the non-fluorescing material remains dark. If an object or specimen is irradiated by short-wave excitation light, filters select exactly those wavelengths which cause fluorescence from the light that comes from the source. All other wavelengths not contributing to the fluorescence in question are cut off by barrier filters. This method reveals a distinct image of the internal structure of teeth or other hard parts. Primarily, fluorescence microscopy is used in the fields of coal petrology and palynofacies (e.g. Clausing 1991).

The samples, mostly embedded in their original matrix, were sectioned in different directions and polished. The teeth were ground down slowly, investigated and photographed at each level to simulate tomography. Some of the prepared surfaces were etched and/or stained with 2M HCl, tetracycline, or toluidine blue.

The studies were carried out with a special research microscope (Orthoplan/Leitz) with a reflected light fluorescence illuminator with filterblocks and a camera system attached. A halogen lamp and a high-pressure mercury vapour lamp were used as the light sources. Whereas the halogen lamp provided the violet and blue light excitation (range 420–490 nm), the mercury vapour lamp was employed for the ultraviolet fluorescence (340–380 nm).

For the supporting SEM investigations a Cambridge Stereoscan 250 MK 2 was used.

The PAUP program, version 3.1.1., Smithsonian Institution, 1993, for Apple Macintosh computer was used for the cladistic analysis.

Teeth referred to in this paper are held in the following institutions, designated by the following abbreviations: AM, Australian Museum, Sydney; CPC, Australian Geological Survey Organisation, Canberra; WAM, Western Australian Museum, Perth.

Terminology

There is confusion in the terminology of certain tooth tissues, which often depends upon the investigator's opinions or educational bias (i.e. zoological or histological as opposed to mineralogical). Three important terms we use herein are defined below.

Orthodentine = circumpulpously developed dentine characterized by distinct growth lines

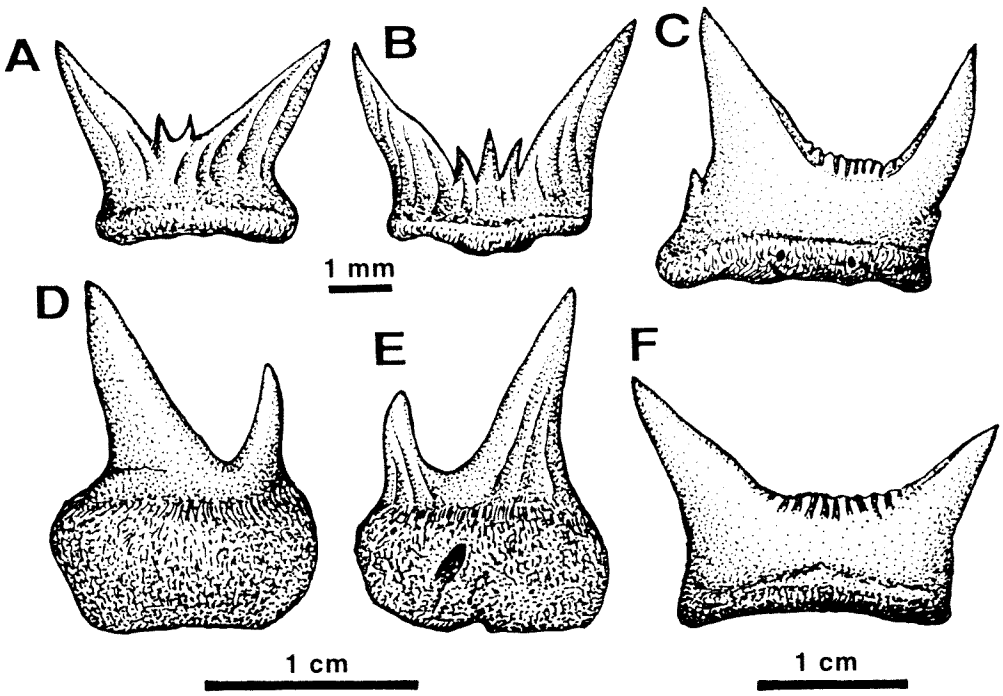

Figure 2 A, B, typical teeth of *Antarctilamna prisca* in labial view (A, CPC 21187, from the holotype, partially reconstructed from a damaged tooth; B, WAM 92.3.68). D, labial view and E, lingual view of one tooth of *Portalodus bradshawae* (AM F54330). C, F, labial views of two teeth of *Aztecodus harmsenae* (C, WAM 92.3.58, F, W.A.M. 92.3.59; both reconstructed from partially damaged specimens).

(Owen's lines) parallel to the tooth surface (see Francillon-Vieillot *et al.* 1990; Hampe 1991).

Pallial dentine = initially developed dentine zone of less density (for a discussion on the use of this term see Rieppel 1981). Pallial dentine develops during the initial phase of dentinogenesis when the basal membrane thickens and the odontoblasts go through their terminal differentiation (Schroeder 1992).

Pleromin (synonymous with 'pleromic hard tissue') = hypermineralized dentine matrix (in the sense of Ørvig 1976). Pleromin is a term originally introduced for scales of psammosteid heterostracans (Tarlo 1964).

Tissue terminology is further considered in the Discussion.

HISTOLOGICAL DESCRIPTIONS

Antarctilamna prisca Young, 1982

The teeth of *Antarctilamna prisca* (Figures 2A,B; 3) have two lateral cusps and up to three small median cuspules. In the last case, the central one is the most prominent. Vertical cristae are commonly present on the oval cross-sectioned cusps of this genus; they have wavy outlines and tend to spiral slightly towards the tip of the cusps (Young 1982). The base is somewhat extended lingually, without showing a button on the upper side. The bottom side is regularly depressed lacking a basal tubercle, too. The surface of the base bears many miniature pores.

The base of the specimen (WAM 94.2.5) shows the usual development of trabecular dentine, a vascularized matrix grown intrapulpously (Figure 3F,G). Distinctly formed denteons can be distinguished, that are defined by concentric dentine depositions around lacunae or ducts (Figure 3E). The small dark spots in the periphery of the base (Figure 3E) represent 'Tomes granular layer'. This is an area of hypomineralized dentine with numerous interglobular spaces (Schroeder 1992: 111). One larger pulp canal seems to proceed through the base.

The cusps on the crown are distinguished by the development of a mantle of orthodentine, whereas the centre is composed of trabecular structure (Figure 3A). The orthodentine fills up to half the diameter of the cusps and increases in thickness towards the apex. In *Antarctilamna* no evidence for enameloid could be found. The dentine tubules which run perpendicular to the growth lines, reach the outermost layer (Figure 3A,B). Only the cristae-bearing zones seem to show a differentiation of the outermost layer, in this case pallial dentine (Figure 3C,D), distinguished by its fluorescent colour changes.

Portalodus bradshawae Long and Young, 1995

Following the diagnosis of Long and Young (1995), *Portalodus bradshawae* (Figures 2D,E; 4) has robust diplodont teeth with cusps of unequal size that are oval in cross-section and show cutting

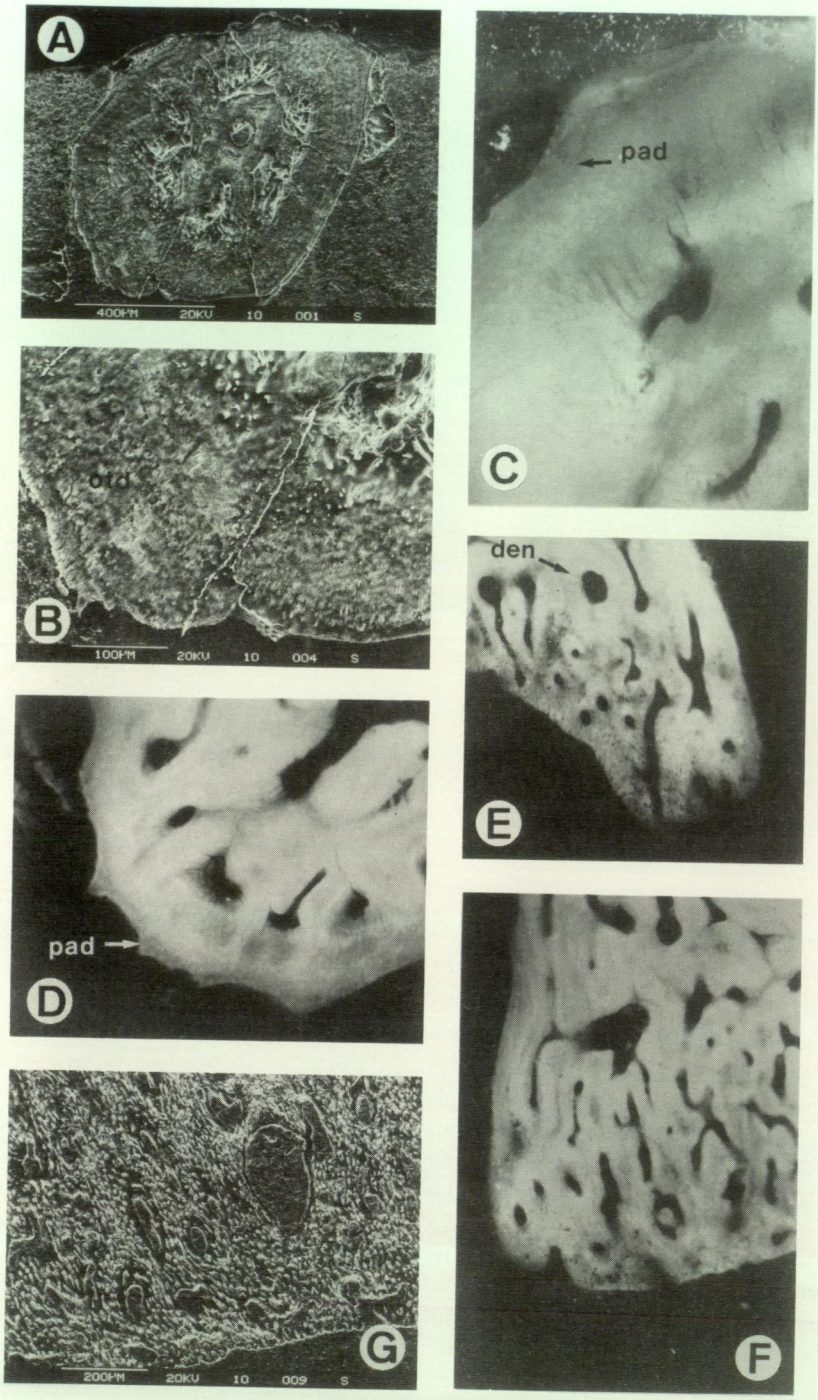

Figure 3 Histology of *Antarctilamna prisca* (WAM 94.2.5) from Gorgon's Head, lowermost fish horizon, Cook Mountains (Woolfe *et al.* 1990; Long and Young 1995). A, horizontal section through a lateral cusp showing inner core of trabecular dentine and circumpulpously developed orthodentine. The light fibres are dentine tubules; SEM photo, etched with 2 N HCl. B, magnification of the lower part of (A) with a dentine tubule protruding through the outermost layer. C, cross-section through a cusp with peripheral zone of hypomineralized pallial dentine (cristae-bearing zone); Nh, t = 3.73 sec, 95x. D, tangential section from base of a lateral cusp, trabecular dentine with a thin layer of orthodentine and the cut vertical cristae on the surface (pallial dentine, remains darker under fluorescence excitation); Bh, t = 10:08 min, 62x. E, horizontal section through base, labial part, composed of trabecular dentine with denteons and a granulous zone related to Tomes' granular layer in the outer part; Bh, t = 6:34 min, 38x. F, horizontal section through base, lingual part, trabecular dentine; Bh, t = 7:07 min, 38x. G, SEM photo of trabecular dentine of the base, etched with 2 N HCl. The rounded to oval fields are secondarily (diagenetically) filled lacunae. **Abbreviations** (all figures). B – blue light excitation, range 420–490 nm; den – denteon; det – dentine tubule; ena – enameloid; h – source of light: halogen lamp; lcr – longitudinal crack; N – standard illumination; otd – orthodentine; pad – pallial dentine; ple – pleromin; q – source of light: mercury lamp, t – exposure time; trd – trabecular dentine; Uv – ultraviolet excitation, range 340–380 nm; x – magnification.

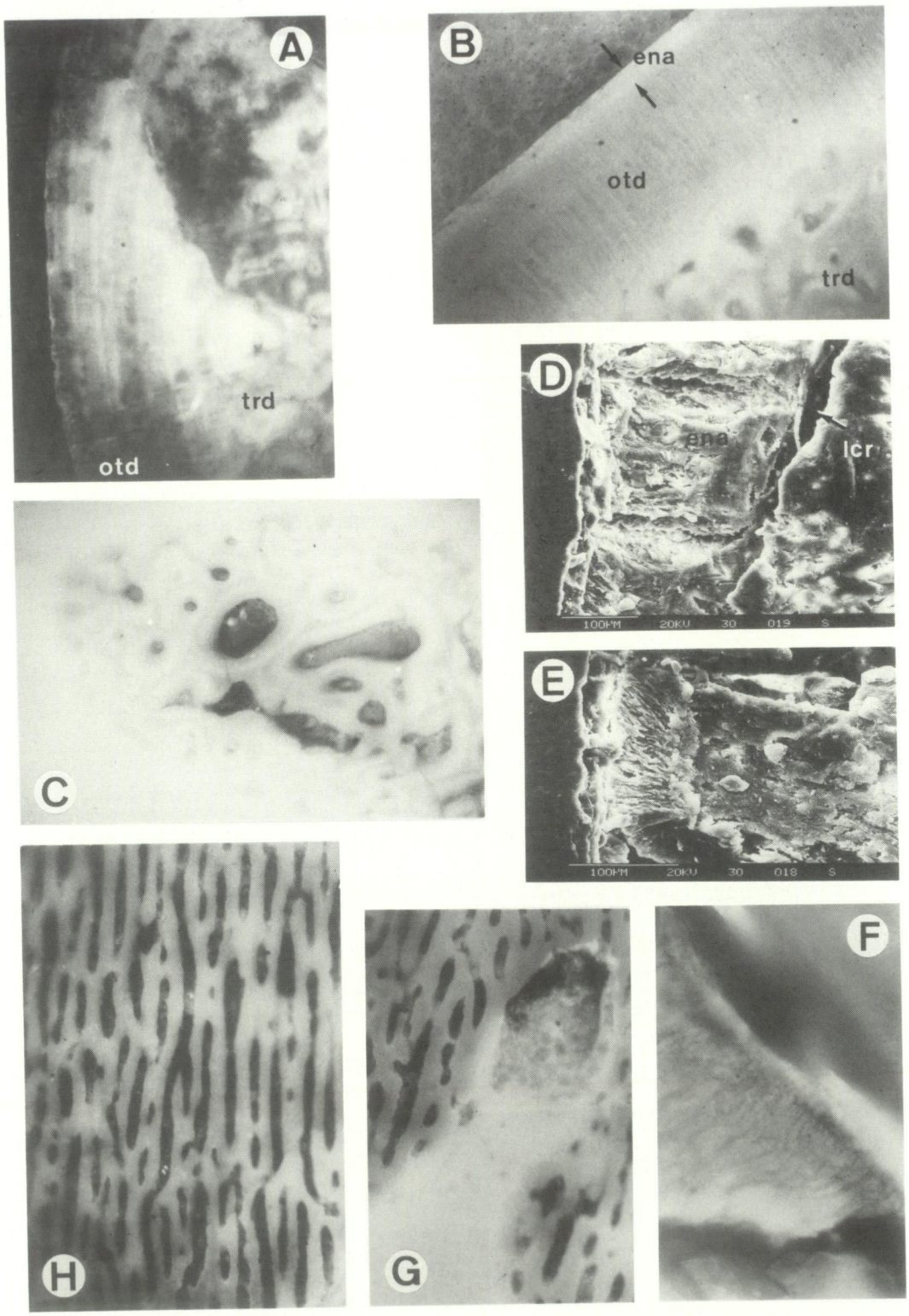

Figure 4 Histology of *Portalodus bradshawae* (WAM 92.3.64) from Mt Ritchie, middle horizon 'M' of Long and Young (1995). A, vertical section through a cusp showing orthodentine with typical parallel growth lines (Owen's lines) surrounding a core of trabecular dentine, treated with tetracycline; Uvq, t = 4:00 min, 53x. B, horizontal section through a cusp with peripheral orthodentine zone exhibiting parallel dental tubules; Bh, t = 47.12 sec, 67x. C, horizontal section through cusp with vascular matrix in the centre; Bh, t = 20.25 sec, 42x. D, SEM picture of the peripheral zone of a cusp showing enameloid separated by a longitudinal crack from the orthodentine, horizontal section, treated with tetracycline. E, parallel-fibred enameloid (after Reif 1973) in the outermost area, horizontal section, SEM, treated with tetracycline. F, ramifications of dentine tubules in the peripheral part of a cusp, horizontal section, treated with toluidine blue; Bh, t = 2:58 min, 210x. G, one of the two larger nutrient canals in the base, vertical section; Bh, t = 1:12 min, 42x. H, vertical section through the base with mesio-distally 'compressed' trabecular dentine; Bh, t = 2:56 min, 42x. For abbreviations see Figure 3 caption.

edges along mesial and marginal edges. The lingual sides of the cusps sometimes show very weak striations, whereas the labial side appears completely smooth. The base is large and undifferentiated, lacking tubercles, but it has a large foramen on the lingual margin. In some examples a notch is present on the lingual side directly below the foramen.

Histologically, major parts of the teeth of *Portalodus bradshawae* are constructed of trabecular dentine. It is of typical sponge-like character, and looks as if the trabecular dentine is mesio-distally compressed in that the cavities seem to be stretched, being greater in height than in width in a vertical section of the base (Figure 4H). It gives the appearance of strongly parallel arrangement of the cavities. Two larger canals run through the base more or less labio-lingually directed, probably below the two cusps of the crown (Figure 4G).

With the transition from base into crown, the lumina within the trabecular dentine become wider in the cusps than they are within the compressed formation of the base. The centre of the crown is filled with trabecular dentine, covered by a relatively thin zone of orthodentine. The cross-section of a tooth's tip shows the 'cell structured' trabecular dentine with larger, irregularly formed lumina in the centre of the cusp (Figure 4C).

The circumpulpously developed orthodentine shows its typical parallel organized growth lines (Figure 4A): passing through these, perpendicular to the growth lines, are closely parallel very fine dentine tubules (Figure 4B) that become ramified close to the tooth's surface (Figure 4F).

Enameloid, which shows differences in mineralization from the orthodentine, forms an extremely thin outer layer (Figure 4B). After colouring the vertical section with tetracyclinehydrochloride a secondary effect took place in that the dentine cracked. The sample subsequently shows fissures and cracks in different directions. The outer layer, here interpreted as enameloid, is separated from the other orthodentine tissue by longitudinal cracks (parallel

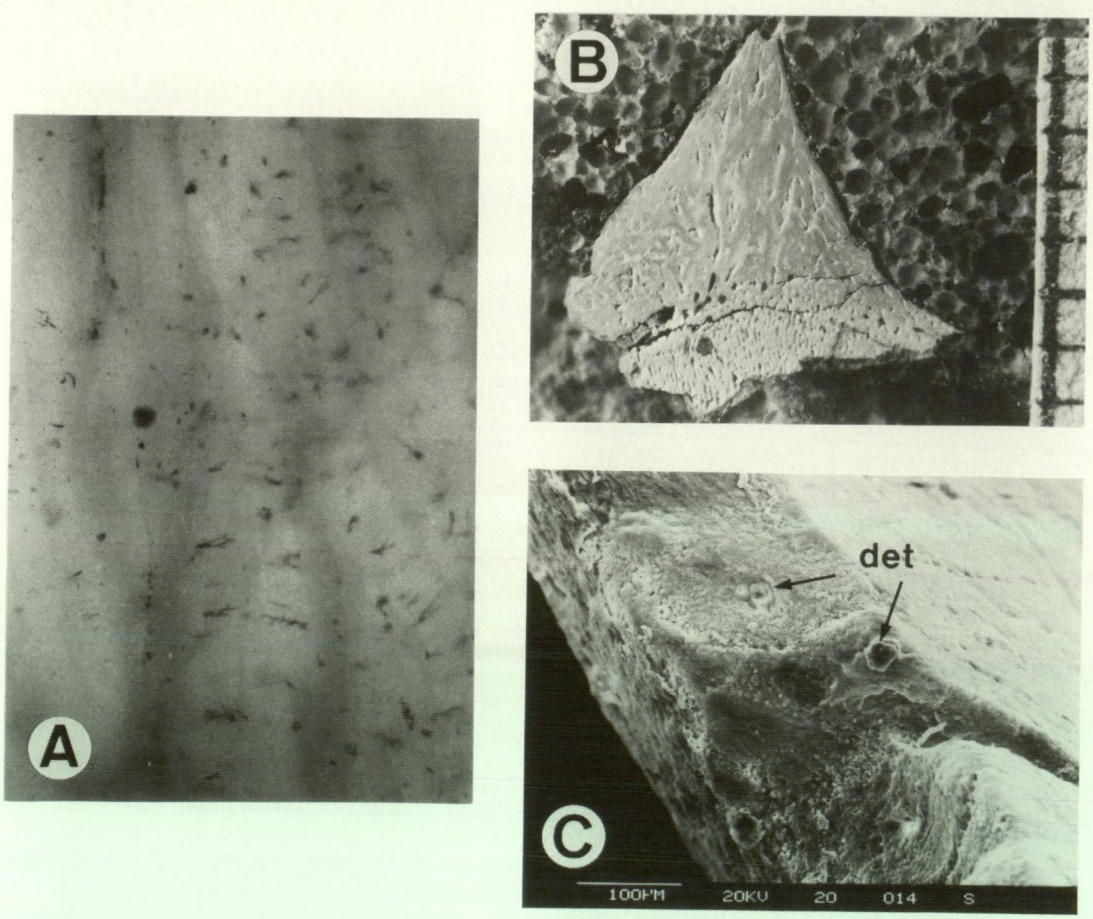

Figure 5 Histology of *Aztecodus harmsenae* (WAM 92.3.69) from 'fish hotel level B', Cook Mountains (Long and Young 1995). A, vertical section through a cusp with dense pleromin, dentine tubules arranged perpendicular to the surface; Bh, t = 1:12, 83x. B, vertical section of an incomplete tooth with polished surface showing pleromin in the cusp (above) and trabecular dentine, of lower density, in the base (below). One of the larger pulp canals can be distinguished in the base below the cusp. C, SEM photo of a crown fragment with dentine tubules coming out of the pleromin matrix, etched with 2 N HCl. For abbreviations see Figure 3 caption.

to the tooth surface, Figure 4D) whereas the inner orthodentine reveals diagonally and perpendicularly arranged cracks. The SEM also reveals a different kind of mineralization of the enameloid: a fibrous structure, shown in Figure 4E. The fibres of this outermost layer can be compared with the radial 'parallel-fibred enamel' of Reif (1973). Preuschoft *et al.* (1974) regarded parallel-fibred enameloid as indicating tensile stress resistance in fangs and cutting teeth. The structure of the mesial and marginal edges seen in *Portalodus* may indicate a predatory mode of feeding.

***Aztecodus harmsenae* Long and Young, 1995**

The teeth of *Aztecodus harmsenae* (Figures 2C,F; 5) are characterized by very low bases which are broader than the heights of the cusps (Long and Young 1995). The two principal lateral cusps are mostly of unequal size with a compressed cross-section becoming rounded towards the base. Between these widely separated main cusps there is a saw-blade shaped distinctly crenulated crest. Small accessory cusplets can be developed mesially or distally adjacent to the main cusps. The surfaces of *Aztecodus* teeth are smooth, with lateral cutting edges developed.

The flat base has a more or less mesio-distally broadened rectangular outline. Two large nutrient foramina can be observed on the labial side. The bottom side is undifferentiated and shows only slightly labio-lingually directed 'stripes' (ridges).

The histological architecture in *Aztecodus* is comparatively simple. The whole crown is composed of a dense material structured with scattered narrow spaces (Figure 5B). The dense tissue is comparable with pleromin (cf. Ørvig 1976). No orthodentine occurs in the crown area. The minor vascularized pleromin of the crown seems to be stable, strong and resistant enough against mechanical influences (biting processes). No isolated pulp canal is developed. Dentine tubules can be observed in vertical section, perpendicularly oriented to the surface and in regular intervals (Figure 5A,C). The base, separated from the crown by a relatively sharp border, consists of trabecular dentine with a large number of very delicate pores (Figure 5B). Within the base, below each cusp, there is one larger labio-lingually directed nutrient canal.

DISCUSSION

The investigations show surprisingly different histological structures in the teeth of the three Antarctic fossil sharks. The results are compared with the teeth of other Palaeozoic sharks in Table 1.

Enameloid is one of the tissues that has been the subject of much discussion. The most important problem in the histology of Palaeozoic sharks, is how to distinguish enameloid beyond doubt. Recent sharks have this outer zone well developed and therefore easy to identify, although it is sometimes comparatively thin (Bendix-Almgreen 1983). However, the enameloid is only weakly developed in ancient sharks as Reif (1973) described, for example, in *Cladodus*. The xenacanthids can be characterized by lack of enameloid (Hampe 1991, 1995; Hampe and Heidtke 1997) and further investigations have revealed that apparently other fossil sharks had also lost enameloid.

Garant (1970) pointed out the continuing controversy about the process of enameloid histogenesis, which is still not clearly understood. The mineral component of enameloid is regular hydroxyfluorapatite which differs from that of

Table 1 Tissues composing the crowns and bases of the teeth of Palaeozoic sharks, including the main histological characteristics of the specimens discussed in this paper. ena = enameloid; otd = orthodentine; ple = pleromin; trd = trabecular dentine.

Genus	Current Systematics	Crown	Base
Aztecodus	Ordo et Familia indet.	ple	trd
Portalodus	Ordo et Familia indet.	ena + otd + trd	trd
Ctenacanthus	Ctenacanthiformes: Ctenacanthidae	ena + otd + trd	trd
Leonodus	Ctenacanthiformes: Familia incertae sedis	ena + otd + trd	trd
Phoebodus	Ordo indet.: Phoebodontidae	otd + trd	trd
Antarctilamna	Ordo indet.: ?Phoebodontidae	otd + trd	trd
Symmorium	Symmoriida: Symmoriidae	ena + otd + trd	trd
Stethacanthus	Symmoriida: Stethacanthidae	ena + otd + trd	trd
Diplodoselache	Xenacanthida: Diplodoselachidae	otd + trd	trd
Orthacanthus	Xenacanthida: Orthacanthidae	otd	trd
Xenacanthus	Xenacanthida: Xenacanthidae	otd	trd
Plicatodus	Xenacanthida: Xenacanthidae	otd	otd
Triodus	Xenacanthida: Xenacanthidae	otd	otd
Hagenoselache	Xenacanthida: Familia incertae sedis	otd	otd

dentine only in its structure. Peyer (1963) noted that the optic attributes of enameloid in fishes do not conform with those of enamel in mammals or reptiles. It is not resolved whether the germ layer responsible for the production of enameloid is ectoderm or mesenchyme. Tooth development always takes place at the boundary between ectoderm (epidermis) and mesoderm (dermis), separated by the epidermal basal or basement membrane.

At the beginning of its formation, enameloid is a gel-like substance (Shellis 1978) which later mineralizes through loss of most of the collagen from the matrix (for additional information about the chemical mechanisms of apatite formation, see Newesely 1970). The vast majority of researchers consider elasmobranch enameloid as mesenchymal in origin (e.g., Schmidt 1958; Kent 1987), in contrast to true enamel synthethized by the basal layer of the ectodermal epidermis, as occurs in mammals. Gängler and Metzler (1989) described the enameloid in sharks as a specially-developed tissue containing ectodermal substances and mesodermal fibres. Reif (1978a) used different structures of enameloid as a taxonomic criterion for use in the identification of sharks. Brief descriptions and conclusions from a study of the histogenesis of elasmobranch teeth were presented by Kerr (1955), Ørvig (1967), and Peyer (1968) amongst others.

As noted in the Materials and Methods section, there is confusion in the terminology of some tooth tissues. The term 'trabecular dentine' was first introduced by Röse (1897). Ørvig (1951) united varieties of dentine under the common designation 'osteodentine', rejecting terms like trabecular dentine and vascular dentine which he considered inadequate terms for different reasons. Typically, there is no visible structural difference between osteo- and trabecular dentine, although the trabecular framework may be thin or even absent (e.g., *Diodon* tooth plates [Euteleostei: Tetradontiformes]) or very thin (e.g., *Myliobatis* teeth [Batoidea]). Ørvig argued that the cylindrical deposition around vascular tubules in osteodentine resembles primary bone material. He assumed that the bony trabecles were histogenetically formed first and later dentine was integrated into the bony framework. Peyer (1968) showed for *Prionace glauca* that early stages of formation do not reveal any bone. It remains uncertain if the 'bony' structure found in Palaeozoic sharks can be histologically termed 'bone'. Peyer did not accept a sequence of odontoblasts producing an outer coat of orthodentine, succeeded by others differentiated to osteoblasts for the development of intervascular matrix, again followed by odontoblasts in a third step which deposited circumvascular layers of dentine (see also Zangerl *et al.* 1993: 5). For these reasons, the term trabecular dentine should be used for shark teeth characterized by intrapulpously-developed dentine which contains canals and ducts and short dentine tubules (with typical concentric arrangement in the denteons).

The histology of the teeth of *Antarctilamna* seems close to that in *Phoebodus* and the basal xenacanthid *Diplodoselache*. Gross (1973) described *Phoebodus politus* as having trabecular dentine within the base, orthodentine in the crown and a durodentine-like tissue as the outermost thin layer. After additional investigations on further, newly discovered, *Phoebodus* teeth, it seems more likely that they have no enameloid. So, it is not yet clear if phoebodontid elasmobranchs always have, or lack, enameloid. In recent research on *Diplodoselache* material, the senior author also observed a lack of enameloid, contrary to Dick (1981) who described *Diplodoselache* teeth as having 'an extremely fine enameloid layer coating a quite thick layer of orthodentine'. What Dick described as enameloid is usually named 'terminal dentine'. It belongs to the basal membrane which separates the mesenchyme from the ectodermal tissue, is calcified, and covers the dentine (see Schmidt 1958).

In histological structure the teeth of *Portalodus* have affinities with *Ctenacanthus costellatus* (Moy-Thomas 1936: text-figure 2). The teeth of this shark possess cusps that are seen in vertical section to be filled with trabecular dentine ('osteodentine' of Moy-Thomas) surrounded by a layer of orthodentine. They have a clearly distinguishable enameloid outermost layer. Moy-Thomas mentioned that this structure resembles essentially that in Recent sharks, such as *Lamna*, and in hybodonts (but it must be noted that many hybodont teeth have cusps primarily composed of orthodentine; J.G. Maisey, pers. comm.). The same structure has been described in *Stethacanthus* sp. (Lund 1985) with an outer enameloid layer, orthodentine within the cusps, and a thin core of trabecular dentine extending into the whole of the tooth's base. Mader (1986) described a relatively thick shiny 'durodentine' layer (= enameloid) which covers the cusps of *Leonodus carlsi*. The rest of the tooth in this genus is constructed like those of *Ctenacanthus* and *Stethacanthus*. The inner morphology of the cusps has a bundle of canals that show a lot of fusion between each other. This looks like simple trabecular dentine and not regular orthodentine, which Mader erroneously referred to in his paper. In *Symmorium reniforme* the teeth consist of trabecular dentine, in the base as well as in the crown (Mertiniene 1995: figure 2). The trabecular dentine of the cusps is overlain by a relatively thin 'pallial dentine' (= orthodentine in this case), and the cusps are covered by enameloid.

The inner structure of *Aztecodus* teeth is comparable to pleromin. This peculiar tissue is

seldom observed in other elasmobranchs (e.g., Reif 1973: figure 4 for *Ptychodus decurrens*; Turonian age). By definition, pleromin contains only a few dentine tubules and has a content like 'massive spongiosa', as Gross (1930, 1935) termed it. Beside its hypermineralization, continuous growth is another property of pleromin. Although unusual for teeth forming pointed cusps, this could indicate durophagous feeding by *Aztecodus*.

The internal tooth structure of the xenacanthids, to which some of these Antarctic forms were compared by Young (1982), is totally different from all of the newly investigated specimens. (For detailed descriptions of xenacanthids see Hampe 1991, 1995; Hampe and Heidtke 1997.) In xenacanthid teeth the internal structure of the cusps is constructed exclusively of orthodentine. In addition, some taxa have bases also composed of orthodentine (*Triodus*, *Plicatodus* and *Hagenoselache*; see Table 1).

PHYLOGENETIC ANALYSIS

Fourteen genera of Palaeozoic sharks, including the three Antarctic genera studied in this paper, were used to construct a cladogram (Figure 6), based on their clearly distinguishable hard parts: teeth (including tooth histology), spines and scales (Table 2). The selection of characters is limited to these dermal structures because only isolated hard parts are known from many genera. However, the following analysis is only one model to describe the relationships between the sharks discussed herein. In his analysis of shark interrelationships, using skeletal features, (Maisey 1984: 365) came to essentially the same conclusions about the xenacanthids, although he included *Antarctilamna* within the group (this is discussed further, below).

In the cladogram, *Ctenacanthus* is used for outgroup comparison (characteristics after Moy-Thomas 1936; Maisey 1975; Zidek 1977; Derycke 1992).

At the base of the cladogram is a polytomy of *Ctenacanthus*, and the symmoriids *Symmorium* (Mertiniene 1995; Ivanov 1996) and *Stethacanthus* (Lund 1974; Zangerl 1984; Williams 1985; Zidek 1993). *Leonodus* (characters from Mader 1986; Wang 1993) forms the sister group of all following genera. It has in common with these the development of bicuspid teeth [1a]. *Leonodus* itself is characterized by two autapomorphies, the lack of nutrient foramina on the upper side of the base [7] and the laterally constricted base with peanut-shaped outline in basal view [10], although we note that a similar outline, but with labio-lingual constriction of the base, is also seen in some symmoriids (e.g., Long 1990: figure 7K).

The next node is defined by the occurrence of nutrient foramina on the labial side of the base [6] and suggests that *Portalodus* (Long and Young 1995) is the sister group of *Aztecodus*, the phoebodonts and xenacanthids. The last three groups are characterized by the absence of enameloid [14]. *Aztecodus* (Young 1982; Long and Young 1995) has two autapomorphic features: the development of a crenulated occlusal cutting ridge between the lateral cusps [3] and the hypermineralized tooth structure called pleromin [11]. The results of this analysis indicate that *Aztecodus* is the sister taxon of *Phoebodus*, *Antarctilamna* and all xenacanthids. *Phoebodus* (Gross 1973; Ginter 1990, 1995; Long 1990; Ginter and Ivanov 1992, 1995) is united with *Antarctilamna* by the reversal [1aR] which shows the presence of multicuspid teeth, a characteristic that is also found in *Ctenacanthus* and the symmoriids. *Phoebodus* has as an autapomorphy a half-moon-shaped labial margin on the bottom of the base [9b] instead of a prominent basal tubercle. *Antarctilamna* (Young 1982; Long and Young 1995) and the 'crown-group' of xenacanthids are united by one synapomorphy, the always shorter median cusp [2].

The xenacanthid sharks (*Diplodoselache*, *Hagenoselache*, *Orthacanthus*, *Xenacanthus*, *Triodus*, and *Plicatodus*) can clearly be classified by the synapomorphy of their development of tricuspid teeth [1b], which represents another example of reduction of multicuspidity. The crown (cusps) consists histologically of orthodentine [12]. As a reversal [6R] no labially-positioned nutrient foramina exist on the labial side of the base in all xenacanthids. The single well-defined coronal button on the upper side of the base [8] is considered here as a homoplasy which also occurs in *Phoebodus*. The labially-positioned, prominently-developed basal tubercle on the bottom side of the base [9a] is also seen in *Leonodus*. The xenacanthids share with *Stethacanthus* the character of a usually smooth surface of the dorsal spine [17]. *Diplodoselache* (Dick 1981) represents the sister group of the other xenacanthids, represented by *Orthacanthus* (Fritsch 1889; Schneider 1985, 1988; Hampe 1988a, 1991) and its sister group the Family Xenacanthidae. *Orthacanthus* has one autapomorphy, cusps with laterally serrated cutting edges [4b]. A synapomorphy of all Xenacanthidae in which *Xenacanthus* (Fritsch 1895; Hampe 1988b, 1991, 1994; Schneider and Zajíc 1994) is the sister group of *Hagenoselache*, *Triodus* and *Plicatodus*, is the cranial dorsal spine [15]. This feature can also be present in some species of the genus *Orthacanthus* (Soler-Gijón 1997). A second synapomorphy is the dorso-ventral compression of the dorsal spine with laterally arranged denticles [16], instead of the oval or rounded cross-section in *Orthacanthus*, which shows a double row of posteriorly positioned denticles. *Hagenoselache* (Hampe and Heidtke 1997), *Triodus* (Hampe 1989, 1991, 1993), and *Plicatodus* (Hampe 1995) cannot yet be grouped

dichotomously until new information extends this analysis. They share one synapomorphy: their tooth bases consist of orthodentine like the crowns [13]. The position of *Hagenoselache* in this cladogram is different from that presented in Hampe and Heidtke (1997). In that publication, *Hagenoselache* is placed between *Diplodoselache* and *Orthacanthus* because of its more primitive skeletal elements. Such characters are excluded from our analysis, because the skeleton is either unknown or poorly known in some of the elasmobranchs that we included in this study (see above).

Homoplasies are suggested between *Diplodoselache*, *Xenacanthus* and *Portalodus*, including smooth lateral cutting edges on the cusps [4a]; as well as between *Antarctilamna* and *Plicatodus* in having vertical cristae of a wavy design [5]. The development of monocuspid scales of 'non-growing' type [19], is seen in the xenacanthids *Orthacanthus* and *Triodus*, and in *Stethacanthus* (here in combination with blunt and strongly ornamented scales). However, there is a general lack of information from the fossil record about this last character. The spine-'brush' complex [18] is autapomorphic to *Stethacanthus*.

Antarctilamna is not considered to be a xenacanthid. The bases of its teeth lack the coronal button and the basal tubercle. Furthermore, the variable number of median cuspules, and the strongly ornamented dorsal spine, typical for phalacanthous sharks, is strikingly different from those of xenacanthids. The known cartilage remains (Young 1982; Long and Young 1995) of *Antarctilamna prisca* are different from xenacanthids in that the palatoquadrate has a very low height on the quadrate region and a distinctly shortened palatine region. The only affinity is suggested by the generally elongated otic region of the braincase (which was figured restored in an upside-down position in Young 1982), but other features like the weakly developed preorbital, postorbital, and otic processes do not conform with neurocrania of xenacanthids (Schaeffer 1981; Schwind 1991). We consider the arbitrary combination of the skeleton of *Diplodoselache* with integrated known elements of *Antarctilamna* (such as the dorsal spine) in Janvier's (1996: figure 4.34) manual of early vertebrates to be incorrect. The known remains of *Antarctilamna* appear to belong to a different kind of elasmobranch, possibly a primitive phoebodontid. *Diplodoselache* possesses a different kind of spine which is small, with fewer striations, a rounded cross-section and a double row of denticles on the posterior surface.

The strict consensus tells us that there are still a lot of questions about Palaeozoic sharks that cannot

Table 2 Characters used to construct the cladogram (Figure 6).

[1] Teeth bicuspid (a), or tricuspid (b) – plesiomorphous: teeth multicuspid.
[2] Median cusp always shorter than laterals – plesiomorphous: median cusp sometimes of equal height but mostly distinctly longer, 'cladodont' design.
[3] Development of a crenulated cutting ridge between the lateral cusps – plesiomorphous: presence of median cusp/cusplets.
[4] Cusps with laterally developed cutting edges (a), which can show lamnid serration (b) – plesiomorphous: no serration of edges.
[5] Vertical cristae of wavy design – plesiomorphous: cristae straight or lacking.
[6] Nutrient foramina occur on the labial side of the base – plesiomorphous: no labially positioned nutrient foramina.
[7] Lack of nutrient foramina on the upper side of the base – plesiomorphous: nutrient foramina present on the upper side of the base.
[8] Upper side of base with one well-defined coronal button – plesiomorphous: no distinctly developed coronal button.
[9] Bottom side of base with a labially-positioned prominently-developed basal tubercle (a), or an only half-moon shaped labial margin (b) – plesiomorphous: no basal tubercle.
[10] Base laterally constricted with peanut-shaped outline in bottom view – plesiomorphous: more or less rounded base without constriction.
[11] Teeth constructed of pleromin – plesiomorphous: teeth constructed of regular ortho- and/or trabecular dentine.
[12] Crown of tooth (cusps) consists of orthodentine – plesiomorphous: crown consists predominantly of trabecular dentine.
[13] Base of tooth consists of orthodentine – plesiomorphous: base consists of trabecular dentine.
[14] Absence of enameloid from tooth – plesiomorphous: enameloid present.
[15] Dorsal spine articulates with the neurocranium – plesiomorphous: no 'cranial' spine developed.
[16] Dorsal spine dorso-ventrally compressed having laterally arranged denticles – plesiomorphous: rounded, laterally 'ovalized' cross-section and often equipped with two rows of denticles on the posterior surface.
[17] Dorsal spine with usually smooth surface – plesiomorphous: surface with strong longitudinal ridges.
[18] Dorsal spine forming a spine-'brush' complex – plesiomorphous: no brush developed.
[19] Development of monocuspid scales of the 'non-growing' type, after Reif (1978b, 1979) – plesiomorphous: scales multicuspid and/or shovel-shaped with strong ornamentation.

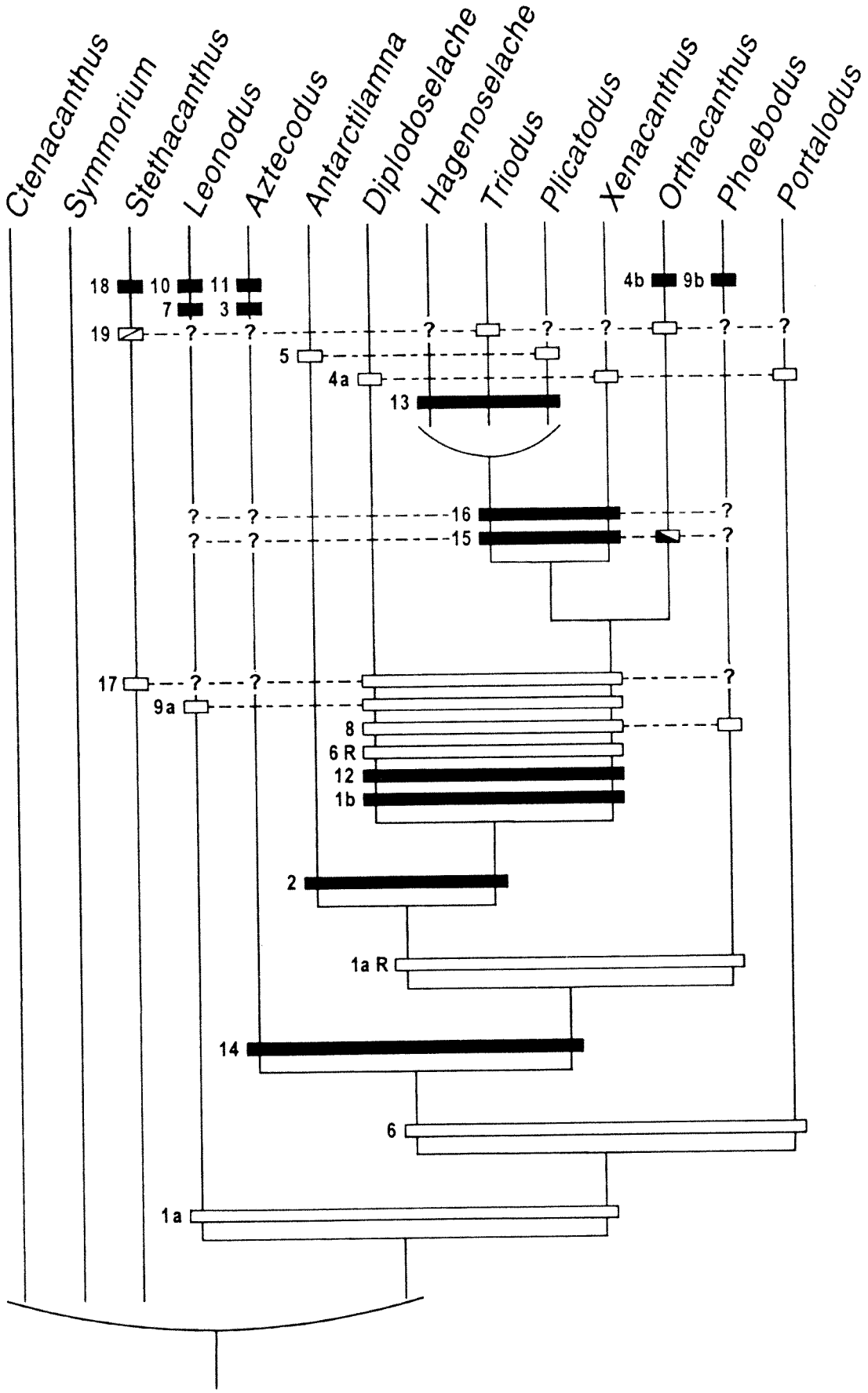

Figure 6 Cladogram of Palaeozoic elasmobranch genera based upon only their hard parts (teeth, characters 1–10; tooth histology, 11–14; spines, 15–18; scales, character 19; see Table 2), using *Ctenacanthus* for outgroup comparison.

be answered because of lack of information due to poor preservation of fossil remains. Only a few articulated specimens are known. Plenty of taxa are only known from teeth, scales, or spine fragments, which makes it difficult to integrate them into a satisfactory system.

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REFERENCES

Agassiz, L. (1837–44). *Recherches sur les Poissons fossiles. 3. Contenant l'Histoire de l'Ordre des Placoïdes:* 1–422, Petitpierre, Neuchâtel, Switzerland.

Bendix-Almgreen, S.E. (1983). *Carcharodon megalodon* from the Miocene of Denmark, with comments on elasmobranch tooth enameloid: coronoin. *Bulletin of the Geological Society of Denmark* **32**: 1–32.

Clausing, A. (1991). Zur Anwendung der Fluoreszenzmikroskopie bei der Untersuchung von Sedimenten, mit Beispielen aus dem saarpfälzischen Rotliegend (Unter-Perm; SW-Deutschland). *Mainzer geowissenschaftliche Mitteilungen* **20**: 131–142.

Derycke, C. (1992). Microrestes de sélachiens et autres vertébrés du Dévonien supérieur du Maroc. *Bulletin du Muséum nationale d'Histoire naturelle, 4e série, Section C*, **14**: 15–61.

Dick, J.R.F. (1981). *Diplodoselache woodi* gen. et sp. nov., an early Carboniferous shark from the Midland Valley of Scotland. *Transactions of the Royal Society of Edinburgh, Earth Sciences* **72**: 99–113.

Duffin, C.J. and Ward, D.J. (1983). Neoselachian sharks' teeth from the Lower Carboniferous of Britain and the Lower Permian of the U.S.A. *Palaeontology* **26**: 93–110.

Francillon-Vieillot, H., Buffrénil, V. de, Castanet, J., Géraudie, J., Meunier, F.J., Sire, J.Y., Zylberberg, L. and de Ricqlès, A. (1990). Microstructure and mineralization of vertebrate skeletal tissues. *In* Carter, J.G. (ed.), *Skeletal biomineralization: patterns, processes and evolutionary trends*, **1**: 471–530, Van Nostrand Reinhold, New York, N.Y., U.S.A.

Fritsch, A. (1889). *Fauna der Gaskohle und der Kalksteine der Permformation Böhmens* **2**: 1– 114, Rivnác, Prague, Czech Republic.

Fritsch, A. (1895). *Fauna der Gaskohle und der Kalksteine der Permformation Böhmens* **3**: 1–132, Rivnác, Prague, Czech Republic.

Gängler, P. and Metzler, E. (1989). Die periodontale und endodontale Differenzierung der Ontogenese – Der phylogenetische Weg zum Thekodont, Teil III. *Freiberger Forschungs-Hefte* **C436**: 70–92.

Garant, P.R. (1970). An electron microscopic study of the crystal-matrix relationship in the teeth of the dogfish *Squalus acanthias* L. *Journal of Ultrastructure Research* **30**: 441–449.

Ginter, M. (1990). Late Fammenian shark teeth from the Holy Cross Mts, Central Poland. *Acta Geologica Polonica* **40**: 69–81.

Ginter, M. (1995). Ichthyoliths and Late Devonian events in Poland and Germany. *Ichthyolith Issues, special publication* **1**: 23–30.

Ginter, M. and Ivanov, A. (1992). Devonian phoebodont shark teeth. *Acta Palaeontologica Polonica* **37**: 55–75.

Ginter, M. and Ivanov, A. (1995). Middle/Late Devonian phoebodont-based ichthyolith zonation. *In* Lelièvre, H., Wenz, S., Blieck, A. and Cloutier, R. (eds), *Premiers vertébrés et vertébrés inférieurs. Géobios*, Mémoire Spécial 19: 351–355.

Gross, W. (1930). Die Fische des mittleren Old Red Süd-Livlands. *Geologische und Paläontologische Abhandlungen, Neue Folge* **18**: 121–156.

Gross, W. (1935). Histologische Studien am Aussenskelett fossiler Agnathen und Fische. *Palaeontographica* **A83**: 1–60.

Gross, W. (1973). Kleinschuppen, Flossenstacheln und Zähne von Fischen aus europäischen und nordamerikanischen Bonebeds des Devons. *Palaeontographica* **A142**: 51–155.

Hampe, O. (1988a). Über die Bezahnung des *Orthacanthus* (Chondrichthyes: Xenacanthida; Oberkarbon-Unterperm). *Paläontologische Zeitschrift* **62**: 285–296.

Hampe, O. (1988b). Über die Bezahnung des *Xenacanthus* (Chondrichthyes: Xenacanthida; Unterperm, SW-Deutschland). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* **1988**: 743–756.

Hampe, O. (1989). Revision der *Triodus*-Arten (Chondrichthyes: Xenacanthida) aus dem saarpfälzischen Rotliegenden (Oberkarbon-Perm, SW-Deutschland) aufgrund ihrer Bezahnung. *Paläontologische Zeitschrift* **63**: 79–101.

Hampe, O. (1991). Histological investigations on fossil teeth of the shark-order Xenacanthida (Chondrichthyes: Elasmobranchii) as revealed by fluorescence microscopy. *Leica Scientific and Technical Information* **10**: 17–27.

Hampe, O. (1993). Variation of xenacanthid teeth in the Permo-Carboniferous deposits of the Saar-Nahe Basin (SW-Germany). *In* Heidtke, U.H.J. (comp.), *New research on Permo-Carboniferous faunas*: 37–51, POLLICHIA-Buch **29**, Bad Dürkheim, Germany.

Hampe, O. (1994). Neue Erkenntnisse zur permokarbonischen Xenacanthiden-Fauna (Chondrichthyes: Elasmobranchii) und deren Verbreitung im südwestdeutschen Saar-Nahe-Becken. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **192**: 53–87.

Hampe, O. (1995). *Plicatodus jordani* n.g., n.sp., a new xenacanthid shark from the Lower Permian of Europe (Saar-Nahe Basin, Germany). *In* Arsenault, M., Lelièvre, H. and Janvier, P. (eds), *Studies on early vertebrates. Bulletin du Muséum nationale d'Histoire naturelle, 4e série, Section C*, **17**: 209–226.

Hampe, O. and Heidtke, U.H.J. (1997). *Hagenoselache sippeli* n. gen. n. sp., ein früher xenacanthider Elasmobranchier aus dem Oberkarbon (Namurium B) von Hagen-Vorhalle (NW Sauerland/ Deutschland). *Geologie und Paläontologie in Westfalen* **47**: 5–42.

Ivanov. A. (1996). The Early Carboniferous chondrichthyans of the South Urals, Russia. *In* Strogen, P., Somerville, I.D. and Jones, G.L. (eds), *Recent advances in Lower Carboniferous geology. Geological Society, Special Publication* **107**: 417–425.

Janvier, P. (1996). Early vertebrates. *Oxford Monographs in Geology and Geophysics* **33**: 1–393.

Kemp, N.E. and Park, J.H. (1969). Fine structure of enamel and collagen in the crown of mineralizing teeth of the shark *Carcharhinus menisorrah*. *Anatomical Record* **163**: 210.

Kent, G.C. (1987). *Comparative anatomy of the vertebrates*: 1–681, W.C. Brown Publishers, Dubuque, Iowa, U.S.A.

Kerr, T. (1955). Development and structure of the teeth in the dog fish, *Squalus acanthias* L. and *Scyliorhynus caniculus* (L.). *Proceedings of the Zoological Society of London* **125**: 95–114.

Long, J.A. (1990). Late Devonian chondrichthyans and other microvertebrate remains from northern Thailand. *Journal of Vertebrate Paleontology* **10**: 59–71.

Long, J.A. (1995). A new groenlandaspidid arthrodire (Pisces; Placodermi) from the Middle Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *Records of the Western Australian Museum* **17**: 35–41.

Long, J.A. and Young, G.C. (1995). Sharks from the Middle-Late Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *Records of the Western Australian Museum* **17**: 287–308.

Lund, R. (1974). *Stethacanthus altonensis* (Elasmobranchii) from the Bear Gulch Limestone of Montana. *Annals of the Carnegie Museum* **45**: 161–178.

Lund, R. (1985). Stethacanthid elasmobranch remains from the Bear Gulch Limestone (Namurian E2b) of Montana. *American Museum Novitates* No. 2828: 1–24.

Mader, H. (1986). Schuppen und Zähne von Acanthodiern und Elasmobranchiern aus dem Unter-Devon Spaniens (Pisces). *Göttinger Arbeiten zur Geologie und Paläontologie* **28**: 1–59.

Maisey, J.G. (1975). The interrelationships of phalacanthous selachians. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* **1975**: 553–567.

Maisey, J.G. (1984). Chondrichthyan phylogeny: a look at the evidence. *Journal of Vertebrate Paleontology* **4**: 359–371.

Mertiniene, R. (1995). The teeth of *Symmorium reniforme* Cope from the Upper Carboniferous of the Moscow area (Russia). *Géobios*, Mémoire Spécial 19: 147–150.

Moy-Thomas, J.A. (1936). The structure and affinities of the fossil elasmobranch fishes from the Lower Carboniferous rocks of Glencartholm, Eskdale. *Proceedings of the Zoological Society of London* **3**: 761–788.

Newesely, H. (1970). Die mineralogisch-geochemische und die biogene Kristallisation des Apatits. *Biomineralisation: Forschungsberichte* **2**: 38–47.

Ørvig, T. (1951). Histologic studies of placoderms and fossil elasmobranchs. I. The endoskeleton, with remarks on the hard tissues of lower vertebrates in general. *Arkivs Zoologie* **2**: 321–454.

Ørvig, T. (1967). Phylogeny of tooth tissues: evolution of some calcified tissues in early vertebrates. *In* Miles, A.E.W. (ed.), *Structural and chemical organization of teeth*: 45–110, Academic Press, New York, N.Y., U.S.A.

Ørvig, T. (1976). Palaeohistological notes. 3. The interpretation of pleromin (pleromic hard tissue) in the dermal skeleton of psammosteid heterostracans. *Zoologica Scripta* **5**: 35–47.

Peyer, B. (1963). *Die Zähne*: 1–102, Springer, Berlin, Germany.

Peyer, B. (1968). *Comparative odontology*: 1–347, University of Illinois Press, Chicago, Ill., U.S.A.

Preuschoft, H., Reif, W.-E. and Müller, W.H. (1974). Funktionsanpassungen von Haifisch-Zahnen in Form und Struktur. *Zeitschrift fur Anatomie und Entwicklungsgeschichte* **143**: 315–344.

Reif, W.-E. (1973). Morphologie und Ultrastruktur des Hai-"Schmelzes". *Zoologica Scripta* **2**: 231–250.

Reif, W.-E. (1978a). Tooth enameloid as a taxonomic criterion 2. Is *"Dalatias" barnstonensis* Sykes, 1971 (Triassic, England) a squalomorphic shark? *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* **1978**: 42–58.

Reif, W.-E. (1978b). Types of morphogenesis of the dermal skeleton in fossil sharks. *Paläontologische Zeitschrift* **52**: 110–128.

Reif, W.-E. (1979). Protective and hydrodynamic function of the dermal skeleton of elasmobranchs. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **157**: 133–141.

Rieppel, O. (1981). The hybodontiform sharks from the Middle Triassic of Mte. San Giorgio, Switzerland. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **161**: 324–353.

Ritchie, A. (1972). Appendix. Devonian fish. *In* McKelvey, B.C., Webb, P.N., Gorton, M.P. and Kohn, B.P., Stratigraphy of the Beacon Supergroup between the Olympus and Boomerang Ranges, Victoria Land. *In* Adie, R.J. (ed.), *Antarctic Geology and Geophysics*: 345–352, Universitetsforlaget, Oslo, Norway.

Ritchie, A. (1975). *Groenlandaspis* in Antarctica, Australia and Europe. *Nature* **254**: 569–573.

Röse, C. (1897). Ueber die verschiedenen Abänderungen der Hartgewebe bei niederen Wirbeltieren. *Anatomischer Anzeiger* **14**: 21–69.

Sasso, W. da S. and Santos, H. de S. (1961). Electron microscopy of enamel and dentine of teeth of

Odontaspis (Selachii). *Journal of Dental Research* **40**: 49–57.

Schaeffer, B. (1981). The xenacanth shark neurocranium, with comments on elasmobranch monophyly. *Bulletin of the American Museum of Natural History* **169**: 1–66.

Schmidt, W.J. (1958). Faserung und Durodentin-Metaplasie bei Fischzähnen. *Anatomischer Anzeiger* **105**: 349–360.

Schneider, J. (1985). Elasmobranchier-Zahntypen (Pisces, Chondrichthyes) und ihre stratigraphische Verbreitung im Karbon und Perm der Saale-Senke (DDR). *Freiberger Forschungs-Hefte* **C400**: 90–100.

Schneider, J. (1988). Grundlagen der Morphogenie, Taxonomie und Biostratigraphie isolierter Xenacanthodier-Zähne (Elasmobranchii). *Freiberger Forschungs-Hefte* **C419**: 71–80.

Schneider, J.W. and Zajíc, J. (1994). Xenacanthiden (Pisces, Chondrichthyes) des mitteleuropäischen Oberkarbon und Perm — Revision der Originale zu Goldfuss 1847, Beyrich 1848, Kner 1867 und Fritsch 1879–1890. *Freiberger Forschungs-Hefte* **C452**: 101–151.

Schroeder, H.E. (1992). *Orale Strukturbiologie. Entwicklungsgeschichte, Struktur und Funktion normaler Hart- und Weichgewebe der Mundhöhle und des Kiefergelenks*: 1–421, Thieme, Stuttgart, Germany.

Schwind, C. (1991). *Zur Organisation und zur Phylogenie der beiden Gattungen* Triodus *und* Xenacanthus. Unpublished Ph.D. thesis: 1–201, University of Mainz, Germany.

Shellis, R.P. (1978). The role of the inner dental epithelium in the formation of the teeth in fish. *In* Butler, P.M. and Joysey, K.A. (eds), *Development, function and evolution of teeth*: 31–42. Academic Press, London, U.K.

Soler-Gijón, R. (1997). *Orthacanthus meridionalis*, a new xenacanth shark (Elasmobranchii) from the Upper Carboniferous of the Puertollano basin, Spain. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **204**: 141–169.

Tarlo, L.B.H. (1964). Psammosteiformes (Agnatha) — a review with descriptions of new material from the Lower Devonian of Poland. I. General part. *Palaeontologica Polonica* **13**: 1–135.

Turner, S. (1993). Palaeozoic microvertebrate biostratigraphy of eastern Gondwana. *In* Long, J.A. (ed.), *Palaeozoic vertebrate biostratigraphy and biogeography*: 174–207, Belhaven Press, London, U.K.

Turner, S. (1997). Sequence of Devonian thelodont scale assemblages in East Gondwana. *In* Klapper, G., Murphy, M.A. and Talent, J.A. (eds.), *Paleozoic sequence stratigraphy, biostratigraphy and biogeography: studies in honour of J. Granville ("Jess") Johnson*. Geological Society of America, Special Paper **321**: 295–315.

Turner, S. and Young, G.C. (1992). Thelodont scales from the Middle-Late Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *Antarctic Science* **4**: 89–105.

Wang R. (1993). Taxonomie, Palökologie und Biostratigraphie der Mikroichthyolithen aus dem Unterdevon Keltiberiens, Spanien. *Courier Forschungsinstitut Senckenberg* **161**: 1–205.

White, E.I. (1968). Devonian fishes of the Mawson-Mulock area, Victoria Land, Antarctica. *Trans-Antarctic Expedition 1955–1958. Scientific Reports, Geology* **16**: 1–26.

Williams, M.E. (1985). The "cladodont level" sharks of the Pennsylvanian Black Shales of Central North America. *Palaeontographica* **A190**: 83–158.

Woodward, A.S. (1921). Fish remains from the Upper Old Red Sandstone of Granite Harbour, Antarctica. British Antarctic ('Terra Nova') Expedition, 1910. *Natural History Report (Geology)* **1**: 51–62.

Woolfe, K.J., Long J.A., Bradshaw M., Harmsen, F. and Kirkbride, M. (1990). Discovery of fish bearing Aztec Siltstone (Devonian) in the Cook Mountains, Antarctica. *New Zealand Journal of Geology and Geophysics* **33**: 511–514.

Young, G.C. (1982). Devonian sharks from south-eastern Australia and Antarctica. *Palaeontology* **25**: 817–843.

Young G.C. (1988). Antiarchs (placoderm fishes) from the Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *Palaeontographica* **A202**: 1–125.

Young, G.C. (1989). New occurrences of culmacanthid acanthodians (Pisces, Devonian) from Antarctica and southeastern Australia. *Proceedings of the Linnean Society of New South Wales* **111**: 11–24.

Young, G.C. (1991). Fossil fishes from Antarctica. *In* Tingey, R.J. (ed.), *The Geology of Antarctica*: 538–567, Oxford University Press, Oxford, U.K.

Young, G.C. (1993). Middle Palaeozoic macrovertebrate biostratigraphy of Eastern Gondwana. *In* Long, J.A. (ed.), *Palaeozoic vertebrate biostratigraphy and biogeography*: 208–251, Belhaven Press, London, U.K.

Young, G.C., Long, J.A. and Ritchie, A. (1992). Crossopterygian fishes from the Devonian of Antarctica: systematics, relationships and biogeographic significance. *Records of the Australian Museum* Supplement No. 14: 1–77.

Zangerl, R. (1984). On the microscopic anatomy and possible function of the spine-"brush" complex of *Stethacanthus* (Elasmobranchii: Symmoriida). *Journal of Vertebrate Paleontology* **4**: 372–378.

Zangerl, R., Winter, H.F. and Hansen, M.C. (1993). Comparative microscopic dental anatomy in the Petalodontida (Chondrichthyes, Elasmobranchii). *Fieldiana Geology* **26**: 1–43.

Zidek, J. (1977). Oklahoma paleoichthyology addendum to Part V. *Oklahoma Geology Notes* **37**: 151–156.

Zidek, J. (1993). A large stethacanthid shark (Elasmobranchii: Symmoriida) from the Mississippian of Oklahoma. *Oklahoma Geology Notes* **53**: 4–15.

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