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

Oliver Hampe1 and John A. Long2

1 Museum für Naturkunde, Zentralinstitut der Humboldt-Universität zu Berlin, Institut für Paläontologie, Invalidenstraße 43, D-10115 Berlin, Germany; email: oliver.hampe@rz.hu-berlin.de
2 Western Australian Museum, Francis Street, Perth, WA 6000

Abstract - The tooth histology of recently discovered Middle Devonian (Givetian) elasmobranchs Antarctilamna prisca, Aztecodus harmsenae, and Portalodus bradshauae 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 overlaying orthodentine and a core of trabecular dentine. Antarctilamna’s crown is constructed of ortho- and trabecular dentine, whereas Aztecodus only shows pterom. 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, Memurodus feathersonis, that he placed in a new family, the Memurodomontidae. 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 bradshauae, 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), antararchs (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. Sass 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 Perm-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.

**Abbreviations**

Histology of Devonian sharks' teeth

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).

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 dentine canes 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 (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.
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 – pleommin; q – source of light: mercury lamp, t – exposure time; trd – trabecular dentine; Uv – ultraviolet excitation, range 340–380 nm; x – magnification.
Histology of Devonian sharks' teeth

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 circumpulsously 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

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**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 plerom, dentine tubules arranged perpendicular to the surface; Bh, t = 1:12, 83x. B, vertical section of an incomplete tooth with polished surface showing plerom 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 plerom 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

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<th>Table 1</th>
<th>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.</th>
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<td>Hagenoselachus</td>
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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 yet 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 synthesized by the basal layer of the ectodermal epidermis, as occurs in mammals. Gäggler 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 structure 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 depression 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 Priacanthus 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 Leomodus 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 Ptychodorus 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, Derrycke 1992).

At the base of the cladogram is a polytomy of Ctenacanthus, and the symmoriids Symmorius (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 [la]. 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 multicusp 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 1888b, 1991, 1994; Schneider and Zajic 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).

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


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