The histology and affinities of sinacanthid fishes: primitive gnathostomes from the Silurian of China

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On the basis of well preserved specimens from the Lower Silurian of the Tarim Basin, Xinjiang Uygur Autonomous Region and Shiqian County, Guizhou Province, People's Republic of China we describe in detail the histological structure of sinacanthid spines, the only known remains of a group of fishes common in Silurian strata from China. The sinacanthids have previously been assigned either to the acanthodians or to the chondrichthyans. The spine structure is composed of an outer layer of atubular dentine and an inner layer of globular calcified cartilage, and the nature and distribution of these tissues indicates that the spines were formed as a result of interaction between the endoskeleton and dermoskeleton. The tissue distribution and style of growth described herein places the sinacanthids crownwards of the placoderms, and possibly within the total group Chondrichthyes. However, before they can be firmly placed within a phylogenetic scheme, further evidence is required both on the general anatomy of sinacanthids and on the nature of chondrichthyan apomorphies.   © 2005 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2005, **144**, 379–386.

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INTRODUCTION

The sinacanthids are an enigmatic group of fishes represented in the fossil record by what are thought to be their fin spines. They are commonly part of Silurian shallow marine faunas from Tarim and South China. Little else is known about the group; this paucity of evidence has led to their assignment either to the acanthodians (P'an, 1959, 1964; Wang *et al*., 1980; Pan & Dineley, 1988; Zeng, 1988; Burrow, 2003), or the chondrichthyans (Gagnier *et al*., 1988; Zhu, 1998).

Additional records from Australia (Talent & Spencer-Jones, 1963; Turner, 1986; Burrow, 2003) and Bolivia (Gagnier *et al*., 1988) appear somewhat anomalous as they indicate, particularly in the case of the Bolivian record, isolated occurrences of the group outside of the East Proto-Tethyan and Proto-Tethyan realms (cf. He, 1994; Zhao, 1994). As reported here, the internal composition of sinacanthid spines is so distinctive that his-

tological examination of the Australian and Bolivian specimens will enable a firm acceptance or rejection of their assignment. The recent claims of possible sinacanthids in the Late Ordovician Harding Sandstone of Colorado by Blieck & Turner (2003) and Turner, Blieck & Nowlan (2004), based upon their interpretation of a single line drawing in Sansom, Smith & Smith (2001), are considered to be erroneous.

RECENT STUDIES OF SINACANTHID SPINES

Zhu (1998) provided a comprehensive review of previous research on the group, from their first description by P'an (1959). He erected the Family Sinacanthidae and assigned it to the Class Chondrichthyes and subclass Elasmobranchii. Zhu (1998) offered four lines of evidence to support the assignment of the sinacanthids to the chondrichthyans:

1. Fin spine ridges composed of trabecular dentine.
2. Fin spines from China and Australia lack an inserted base. Zhu (1998) suggested that the fin

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spine base in *Sinacanthus boliviensis* Gagnier *et al.*, 1988 represents a derived condition within the group.

3. Presence of numerous ornament ridges, 'always more than 15 per side' (Zhu, 1998: 160).
4. Their co-occurrence with 'numerous chondrichthyan scales . . . but no acanthodian scales' in the Tarim sections (Zhu, 1998: 161).

Of these, Zhu placed particular emphasis on what he considered to be trabecular dentine in sinacanthid spines: 'the tissue in the fin spine ridges is trabecular dentine and is the same as the tissue beneath the ridges. This pattern of hard tissue distribution is only found in the fin spines of some fossil chondrichthyans' (Zhu, 1998: 160).

We re-describe the histology of sinacanthid spines largely based upon well preserved material from the Tarim Basin, Xinjiang, People's Republic of China, and discuss their potential suprageneric classification based upon the histology and structure of the spines. It is important to emphasis here that the spines are the only demonstrably known remains of the group, and the widely accepted assumption that they represent fin spines (medial and/or lateral), although followed here, may prove erroneous in the light of future discoveries.

MATERIAL AND GEOLOGICAL SETTING

This report focuses on specimens of *Sinacanthus wuchangensis* P'an, 1959 from the Tataaiertage Formation around Kalpin and the Yimugantawu Formation, Bachu, both localities lying on the northern margin of the Tarim Basin, Xinjiang, People's Republic of China. Sinacanthids have been reported from these localities by Wang, Wang & Zhu (1996) and the specimens we report on herein are from the same shallow marine red sandstones as those on which Zhu (1998) based most of his histological observations. Additional information has been provided by fragmentary specimens referred to *Sinacanthus* sp. from micropalaeontological residues from the Xiushan Formation in Shiqian, Guizhou Province and described by Sansom, Aldridge & Smith (2000).

Although the Tataaiertage and Yimugantawu Formations have been cited as being Llandovery and Wenlock in age, respectively, we follow Wang *et al.* (1998) in considering both formations to largely represent Telychian, late Llandovery strata, notably at the levels which have yielded the *Sinacanthus* specimens described herein. This chronostratigraphy is supported by the presence of a similar ichthyolith microfauna in the Tataaiertage and Yimugantawu Formations and the Xiushan Formation. Shared microfaunal components include the mongolepid taxon *Shiqianolepis* Sansom *et al.*, 2000 and the

enigmatic *Rongolepis* Sansom *et al.*, 2000. The age of the Xiushan Formation in Shiqian has been dated as Telychian on the presence of the conodonts *Ctenognathodus? qiannanensis* and *Ozarkodina guizhouensis* (see Wang & Aldridge, 1996; Sansom *et al.*, 2000; Aldridge & Wang, 2002).

Figured specimens prefixed IVPP are deposited in the Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, whilst those with the prefix NIGP are deposited in the Nanjing Institute of Geology and Palaeontology.

HISTOLOGY OF SINACANTHID SPINES

The overall morphology of the sinacanthid spine when viewed in transverse-section is that of a flattened horseshoe with the apex of the spine orientated here dorsally for descriptive purposes (Fig. 1A, B). The anterior edge of the spine is closed, whilst the posterior margin is largely open or weakly mineralized (Fig. 2A). Based upon material from the Tarim Basin, it is clear that the sinacanthid spine is divided into two distinct layers:

1. An outer layer, equivalent to that part of the spine described by Zhu (1998) and Sansom *et al.* (2000), and which defines the external ornament and ridge and inter-ridge areas of the spine.
2. A previously unrecognized inner layer which lines the core of the spine and is commonly more extensively developed dorsally.

OUTER LAYER

The external ornament and ridges of the outer layer are composed of a highly globular tissue (Fig. 2A, B, E) which surrounds cavities underlying each external ridge. This tissue lacks any visible tubules or cell spaces, such as one would expect to find in trabecular dentine. Frequently, opaque diagenetic nonbiological minerals (such as haematite) infill the interglobular spaces giving an appearance resembling cell lacunae, but this is artefactual. Topologically, this tissue occupies a position within a fin spine that would be expected of a form of dentine, and Sansom *et al.* (2000) drew comparisons between this tissue type and globular atubular dentines such as lamellin (e.g. Karatajūtė-Talimaa *et al.*, 1990). The pulp cavities underlying each ridge show, much as one would expect from a growth surface of dentine, increasing restriction as the dentine thickens centripetally in presumably mature specimens (compare Fig. 2B and 2E).

The atubular dentine grades internally into a continuous sheet of lamellar tissue which lines the exterior of the spine core, closes off the cavities under each ridge and forms much of the inter-ridge area of the
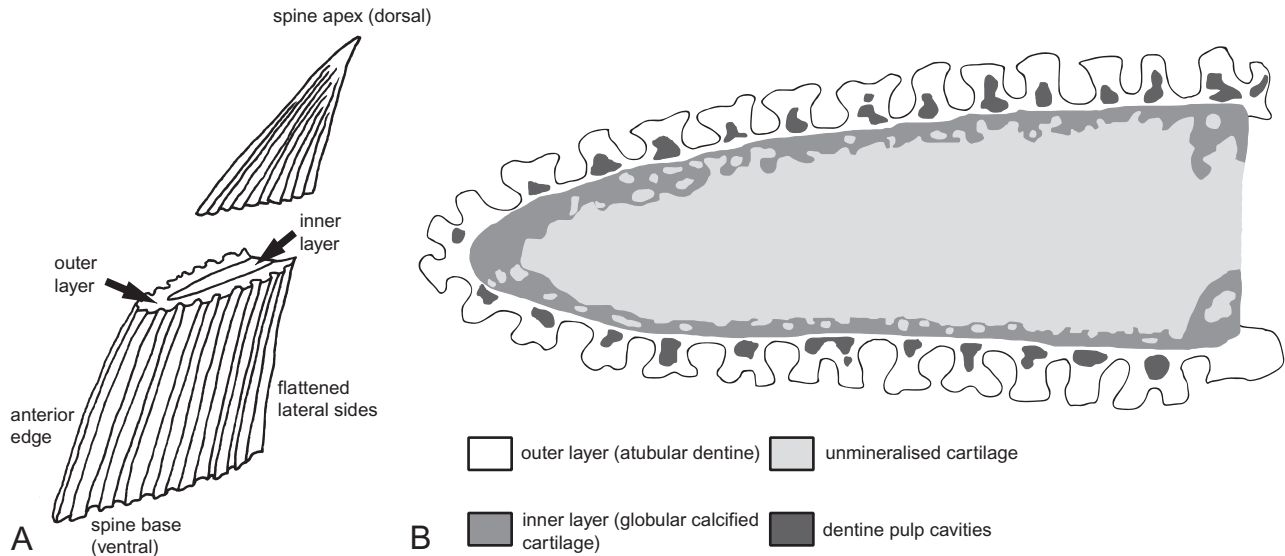
Figure 1. A, morphological terms used to describe sinacanthid spines; B, diagrammatic illustration of tissue distribution in a transverse section through a sinacanthid spine.

spine (Fig. 2B, C, E). Sansom *et al.* (2000) suggested that this tissue is a form of acellular lamellar dermal bone, but it could equally be a lamellar dentine, there is no obvious break between the atubular dentine of the ridges and this lamellar tissue.

INNER LAYER

The inner layer is separated from the acellular lamellar bone or dentine forming the bottom of the outer layer by a sharp junction (see Fig. 2B), and is formed entirely from globular calcified cartilage (Fig. 2C, F). Distribution of globular calcified cartilage within the core of the spine varies in extent from specimen to specimen, possibly dependent on the degree of permineralization of the specimen post mortem, but it is generally thickest close to the dorsal apex of the core. The globular calcified cartilage surrounds numerous peripheral vascular canals, and also encloses a large central cavity presumably occupied *in vivo* by unmineralized tissue (Fig. 2A).

TAXONOMIC POSITION OF SINACANTHIDS AND THE ACQUISITION OF CHONDRICHTHYAN SYNAPOMORPHIES

Placing the sinacanthids in any taxonomic scheme is made especially difficult by the very limited dataset with which to assess their relationship to other groups. In essence, the spine morphology and histology and the stratigraphical range are all that we know about the group.

The number of species and genera, we suspect, is vastly over-represented at present. Although there is considerable morphological variability in sinacanthid spine shape, little attempt has been made to view these in terms of 'multielement' taxonomy. Taxa such as *Neosinacanthus* and *Sinacanthus* are known to regularly co-occur which suggests that an individual sinacanthid may have borne a number of spine morphologies (see the numerous articulated taxa being described from the Devonian of the North-west Territories of Canada, e.g. *Kathemacanthus rosulentus* Gagnier & Wilson, 1998; as examples of gnathostomes bearing numerous spines of notably different morphology). An articulated specimen of *Doliodus problematicus* (Woodward, 1892), from the Early Devonian of Nova Scotia, indicates that at least one basal chondrichthyan possessed pectoral fin spines in addition to dorsal fin spines (Miller, Cloutier & Turner, 2003).

Of the four criteria used by Zhu (1998) to place the sinacanthids within the chondrichthyans, only the lack of an inserted base seems to withstand closer scrutiny. Trabecular dentine is not present in sinacanthid spines, although it is perhaps not surprising that Zhu would not have been familiar with atubular dentine. Only in recent years has the widespread occurrence of this tissue in mid-Palaeozoic taxa from China and Mongolia been realized (see, for example, Karatajūtė-Talimaa *et al.*, 1990; Karatajūtė-Talimaa & Novitskaya, 1992; Karatajūtė-Talimaa, 1995; Sansom *et al.*, 2000). The number of ridges clearly varies dramatically between species and genera – as an example, Zhu's (1998: text-fig. 2G) reconstruction of
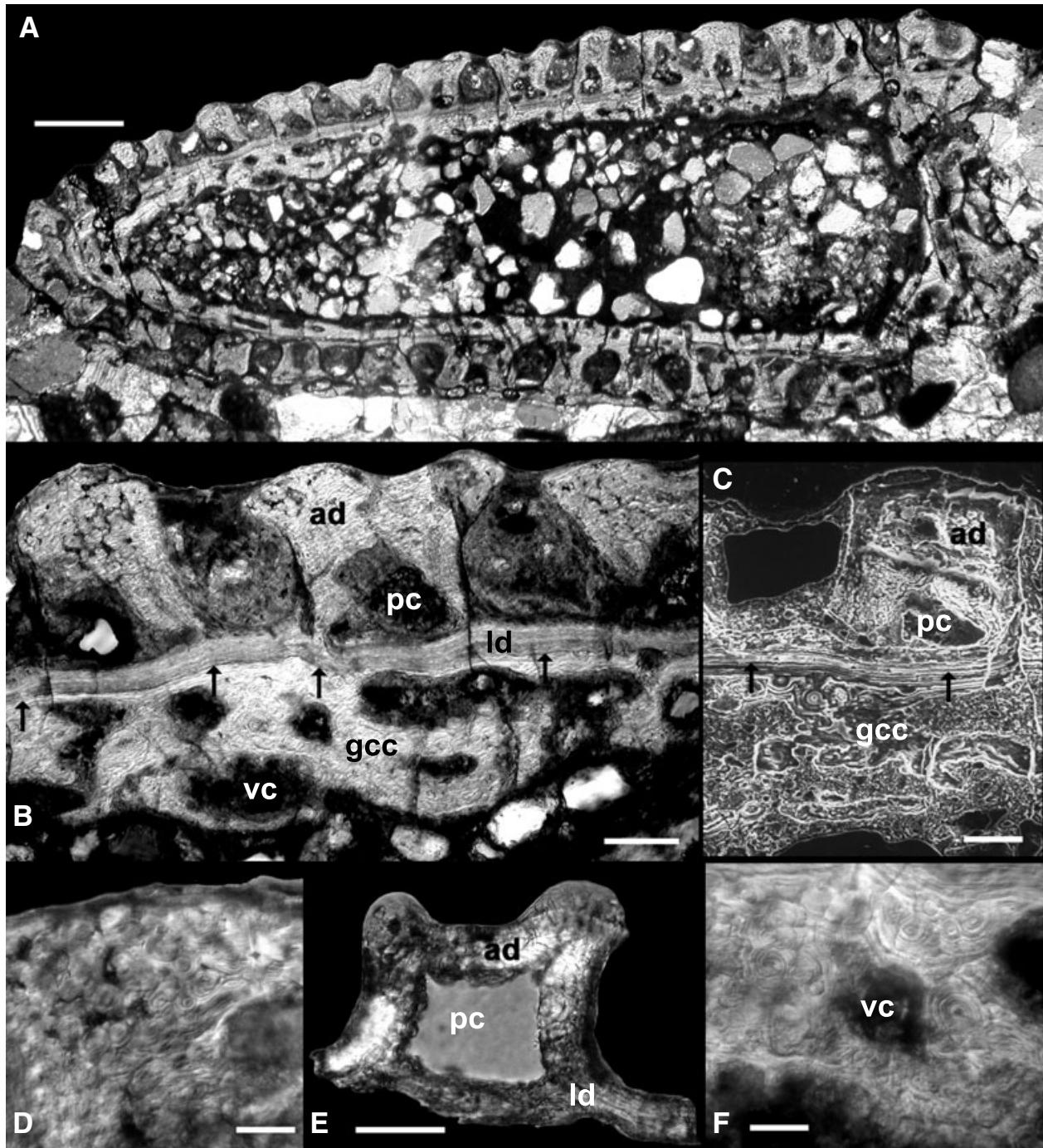
Figure 2. Histology of sinacanthid spines. A, montage of a single transverse section; B, detail showing clear boundary (arrowed) between the outer layer of atubular dentine and lamellar dentine and the inner layer of globular calcified cartilage, note also the pulp cavities beneath each ridge; C, scanning electron micrograph of HCl etched section through ridge and globular calcified cartilage showing boundary (arrowed) between the outer layer and the inner layer; D, detail of globular atubular dentine; E, cross section through presumed juvenile spine ridge showing open pulp cavity; F, globular calcified cartilage lining vascular canal. All transmitted light micrographs using Nomarski interference optics unless otherwise stated. A–D, F, *Sinacanthus wuchangensis* P'an (1959) from the Tataaiertage Formation, Lower Silurian, Kalpin, Xinjiang, IVPP.V14325; E, *Sinacanthus* sp. from the Xiushan Formation, Lower Silurian, Shiqian, Guizhou Province, NIGP 139378. *Abbreviations:* ad, atubular dentine; pc, pulp cavity; ld, lamellar dentine; gcc, globular calcified cartilage; vc, vascular canal. Scale bars: A = 500 µm; B, C, E = 100 µm; D, F = 50 µm.

the holotype of *Neoasiacanthus wanzhongensis* Wang, Xia and Chen has only ten ridges per side, and, as Zhu highlighted, acanthodian spines often have numerous lateral ridges. The scales most commonly encountered with sinacanthid spines in the Tarim sections are referable to the mongolepids, an enigmatic group that have been suggested to represent part of the total group Chondrichthyes (Sansom *et al.*, 2000), although we make no further comment on the affinities of mongolepids here. With the detailed description of the histology of sinacanthid spines presented above, it is now possible to have a revised discussion of their possible relationships.

Spines that form a single structural unit, such as those in sinacanthids, are most typically encountered within the chondrichthyans, acanthodians and basal osteichthyans (Janvier, 1996), and they are only documented from taxa that lie crownward of the placoderms. The spines of ptyctodont placoderms, for example, are composed of a number of individual scutes (Long, 1997), whilst other placoderms, such as the petalichthyids (Gross, 1961), possess spines that are clearly modified plates of their dermal armour. In osteichthyans, the median fin spine described by Zhu, Yu & Janvier (1999) from the sarcopterygian-like *Psarolepis* is clearly a single unit, whilst Otto (1993) described spines from *Lophosteus*, although the phylogenetic position of this enigmatic taxon is still problematic. However, in gross structure, sinacanthid spines are most similar in morphology to both chondrichthyans and acanthodians, but the detailed histological composition suggests a closer relationship to the former rather than the latter.

The spines of acanthodians are multilayered structures and show considerable variety in histological character. Spine ornament in acanthodians is formed from sculpted tubular dentine, overlying a middle layer of trabecular dentine or cellular bone, with a lamellar layer of either dentine or cellular bone surrounding the central cavity. The central cavity itself commonly lacks any mineralized tissues, but in mature specimens it can be filled with bone or dentine (Denison, 1979).

Chondrichthyan spines are simple structures and exhibit centrifugal growth away from a pulp cavity. There are a variety of dentines encountered, commonly with clear incremental layers close to the pulp cavity, with the development of osteonal or trabecular dentine forming the bulk of the spine structure and a superficial ornament developed from dentinal tubercles. Progressive intrapulpal deposition of the dentine leads to the complete enclosure of the pulp cavity towards the spine apex (see Maisey, 1977, 1978, 1979, 1981, 1982; Soler-Gijón, 1999 for discussions on chondrichthyan spine histology and growth).

Sinacanthid spines lack any sign of multiple growth generations typically encountered in acanthodian spines. They also lack trabecular dentine; the presence of trabecular dentine was considered characteristic of chondrichthyan spines by Zhu (1998). Atubular dentine has been encountered in a number of taxa, including conodonts (Sansom, 1996) and mongolepids (Karatajūtė-Talimaa, 1995; Sansom *et al.*, 2000). The distribution of dentine types has often been used to aid taxonomic assignment, but this appears to be a somewhat simplistic view given the range of dentine types encountered in primitive vertebrates (Smith & Sansom, 2000).

The topological relationship between the outer layer of dentine and the inner layer of globular calcified cartilage indicates that sinacanthid spines are formed from dermal and endoskeletal cell populations, respectively, similar in fashion to the development of chondrichthyan fin spines. In squalids and heterodontids, the development of the dorsal fin spine proceeds with the development of a dermal papilla and the production of mineralized dentine and enameloid sheathing a rod of cartilage projecting from the anterior of the basal cartilage of the fin (Maisey, 1979). This pattern of growth, with mineralized dentine surrounding a core of cartilage, is directly analogous to that which can be postulated for sinacanthid spines, although there is no positive evidence that sinacanthid spines are associated with fins and hence the basal cartilage of a fin.

Additionally, the presence of globular calcified cartilage in the spine core requires explanation if sinacanthids are to be placed within the chondrichthyans. Prismatic cartilage, rather than globular calcified cartilage, is considered to be a synapomorphy of crown group chondrichthyans. However, globular calcified cartilage is encountered in stethacanthids (Coates *et al.*, 1998) and xenacanthids (Ørvig, 1951). In stethacanthids, the globular calcified cartilage occurs in the baseplate, keel and rods of the spine-brush complex, and is largely surrounded by perichondral bone. The distribution of globular calcified cartilage in xenacanthids is more widespread within the endoskeleton (Ørvig, 1951). Coates *et al.* (1998) and Coates & Sequeira (2001a) considered that the presence of globular calcified cartilage in both stethacanthids and xenacanthids represented the retention of a plesiomorphic character for the total group Gnathostomata. This was based on the presence of globular calcified cartilage in *Eriptychius* (Denison, 1967), osteostracans (Janvier, 1996), galeaspids (Zhu & Janvier, 1998) and placoderms (Denison, 1978).

The overall structure, growth pattern and histological composition of sinacanthid spines favours an assignment close to the chondrichthyan node, be they as a highly derived component of the gnathostome

stem-group (crownward of the placoderms), plesiomorphic chondrichthyans or, more tentatively, as basal members of the chondrichthyan crown-group (Fig. 3). A more precise positioning of the sinacanthids is hindered, given the limited available evidence and the lack of clearly identifiable synapomorphies with which to identify the base of the chondrichthyan clade. As previously mentioned, prismatic calcified cartilage is widely accepted as a crown group chondrichthyan synapomorphy (e.g. Coates & Sequeira, 1998; Maisey, 2001), but globular calcified cartilage is present in parts of the skeleton of at least two crown-group taxa (Ørvig, 1951; Coates *et al.*, 1998). Ørvig (1951) suggested that globular calcified cartilage and prismatic cartilage were closely related, and he proposed that prismatic cartilage is a derivative of globular calcified cartilage. Given the persistence of globular calcified cartilage within parts of the skeleton of some crown-group chondrichthyans, such as stethacanthids and xenacanthids, the occurrence of this tissue in sinacanthid spines cannot be used to exclude them from the chondrichthyan crown group. Furthermore, it is clear that, for some primitive crown-group chondrichthyans, globular calcified cartilage was retained in parts of the skeleton, its total replacement by prismatic cartilage being an apomorphy that was acquired later in the history of the clade. However, there are insufficient detailed histological surveys of the whole skeleton of Palaeozoic chondrichthyans to determine the significance of this observation.

Limited data are available on the early history of the chondrichthyans. Chondrichthyan and chondrichthyan-like scales are known from the Ordovician and Silurian (e.g. Sansom, Smith & Smith 1996; Sansom *et al.*, 2000; Karatajūtė-Talimaa, 1973, 1992, 1995; Karatajūtė-Talimaa *et al.*, 1990; Karatajūtė-Talimaa & Novitskaya, 1992). Readily identifiable chondrichthyan teeth do not appear in the fossil record until the Early Devonian (Late Lochkovian) (Long, 2001), and an understanding of the chondrichthyan bauplan only becomes available in the Early and Middle Devonian (Emsian-Eifelian) through taxa such as *Doliodus, Antarctilamna* and *Pucapampella* (Miller *et al.*, 2003; Young, 1982; Maisey, 2001). This paucity of evidence poses a number of problems in the identification of chondrichthyan apomorphies. At present, anatomical data is heavily skewed towards crown-group chondrichthyans and, other than isolated scales from the
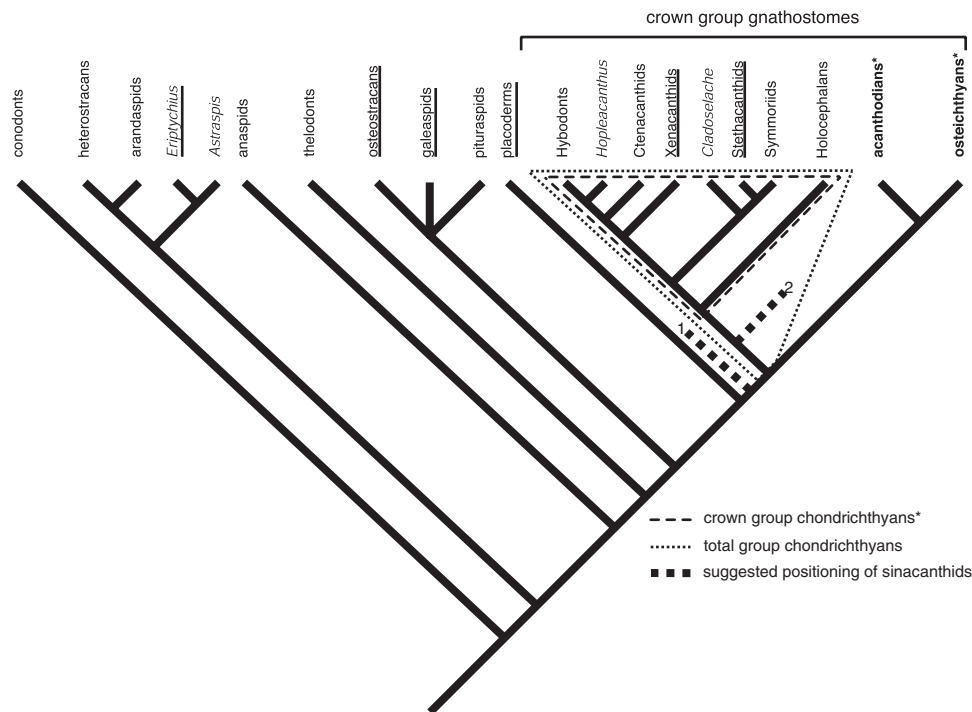

Figure 3. Hypothesis of phylogenetic relationships of lower vertebrates based upon the cladograms of Donoghue *et al.* (2000) for the lower vertebrates and Coates & Sequeira (2001b) for the chondrichthyans. Taxa underlined (e.g. *Eriptychius*) are known to have possessed globular calcified cartilage, whilst those in bold and asterisked (e.g. chondrichthyans*) possessed spines composed from single units. The distribution of these two characters, coupled with the growth model suggested in the main text for sinacanthid spines, suggest that they occupy a position close to the chondrichthyan node; either as a highly derived component of the gnathostome stem-group (crownward of the placoderms) (dashed line 1), or plesiomorphic or basal crown-group chondrichthyans (dashed line 2).

Siluro-Ordovician and the Silurian sinacanthid spines – we know almost nothing about plesiomorphic chondrichthyan taxa. It is hoped that subsequent work in the Tarim and South China regions will yield specimens that provide morphological details about sinacanthids and help to unravel their relationships and clarify the history of character acquisition around the chondrichthyan crown-group node.

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