BioOne COMPLETE

Morphology and Histology of Dorsal Spines of the Xenacanthid Shark Orthacanthus platypternus from the Lower Permian of Texas, USA: Palaeobiological and Palaeoenvironmental Implications

Authors: Beck, Kimberly G., Soler-Gijón, Rodrigo, Carlucci, Jesse R., and Willis, Ray E.

Source: Acta Palaeontologica Polonica, 61(1) : 97-117

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.00126.2014

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Morphology and histology of dorsal spines of the xenacanthid shark *Orthacanthus platypternus* from the Lower Permian of Texas, USA: Palaeobiological and palaeoenvironmental implications

KIMBERLY G. BECK, RODRIGO SOLER-GIJÓN, JESSE R. CARLUCCI, and RAY E. WILLIS



Beck, K.G., Soler-Gijón, R., Carlucci, J.R., and Willis, R.E. 2016. Morphology and histology of dorsal spines of the xenacanthid shark *Orthacanthus platypternus* from the Lower Permian of Texas, USA: Palaeobiological and palaeoenvironmental implications. *Acta Palaeontologica Polonica* 61 (1): 97–117.

Detailed studies on Carboniferous species of the xenacanth *Orthacanthus* have shown that the xenacanth dorsal fin spine can be used for skeletochronological analyses and provides valuable information about development, growth and environmental life conditions of those extinct sharks. We report here for the first time the histology and skeletochronology of Permian specimens, dorsal spines of *Orthacanthus platypternus* from the Craddock Bone Bed (lower Clear Fork Formation; Early Permian, Leonardian age) of northern Baylor County (north-central Texas, USA). Twelve dorsal spines of *O. platypternus* preserve a highly vascularized wall mainly composed of centrifugally growing dentine in a succession of dentine layers, probably deposited with an annual periodicity. As expected, spines of individuals with 1–2 dentine layers, presumably juveniles, present the smallest sizes. However, spines of individuals showing at least 3–4 dentine layers and interpreted to be subadults/young adults, are distributed in two spine-size clusters corresponding to females (probably the largest spines) and males, in agreement with the hypothesis of sexual size dimorphism proposed in a previous biometric analysis. Our comparative study of *O. platypternus* and the Stephanian species *O. meridionalis* further suggests that spine denticulation can be useful for distinguishing between species of *Orthacanthus* and sexually dimorphic forms (juvenile to adults) in each species. Total body length estimations of *O. platypternus* from the Craddock Bone Bed point to relatively large juveniles and small subadults/young adults (less than 2 m in total length), living as opportunistic predators in the pond-channel coastal plain environments represented by the bone bed deposits. The comparative analyses of the ontogenetic stages of the recorded specimens of *O. platypternus* and their distribution along different facies and localities indicate that this species was euryhaline, diadromous with a catadromous life-cycle which was strongly regulated by the semi-arid, seasonally dry tropical climate affecting western Pangaea during the Early Permian.

Key words: Chondrichthyes, Xenacanthiformes, *Orthacanthus*, dorsal spine, diadromy, histology, Permian, Texas.

Kimberly G. Beck [kimberly.beck@mwsu.edu] and Ray E. Willis [raymond.willis@mwsu.edu], Department of Biology, Midwestern State University, 3410 Taft Boulevard, Wichita Falls, TX 76308, USA.
Rodrigo Soler-Gijón [rodrigo.solergijon@gmail.com], Museum für Naturkunde–Leibniz Institute for Evolution and Biodiversity Science, Invalidenstrasse 43, 10115, Berlin, Germany.
Jesse R. Carlucci [jesse.carlucci@mwsu.edu], Department of Geology, Midwestern State University, 3410 Taft Boulevard, Wichita Falls, TX 76308, USA.

Received 30 September 2014, accepted 25 November 2014, available online 18 December 2014.

Copyright © 2016 K.G. Beck et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License (for details please see http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

The red beds of north-central Texas are well known for their preservation of Permian faunas in increasingly and seasonally xeric environments. These fossil beds have produced the fossil *Seymouria baylorensis* (Williston 1911) and have provided the source material for numerous historically well-known Permian vertebrate studies, including those of Cope (1878), White (1889), Sternberg (1903), Williston (1909), Case (1935), Olson (1952), and Romer (1957). Xenacanthid sharks are frequently found in stream depositional environments (Olson 1952, 1977) of the informally named Craddock Bone Bed in northern Baylor County (Fig. 1). Based on tooth morphology, Clear Fork xenacanthid sharks have been assigned to *Orthacanthus platypternus* (Murry and Johnson 1987;

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

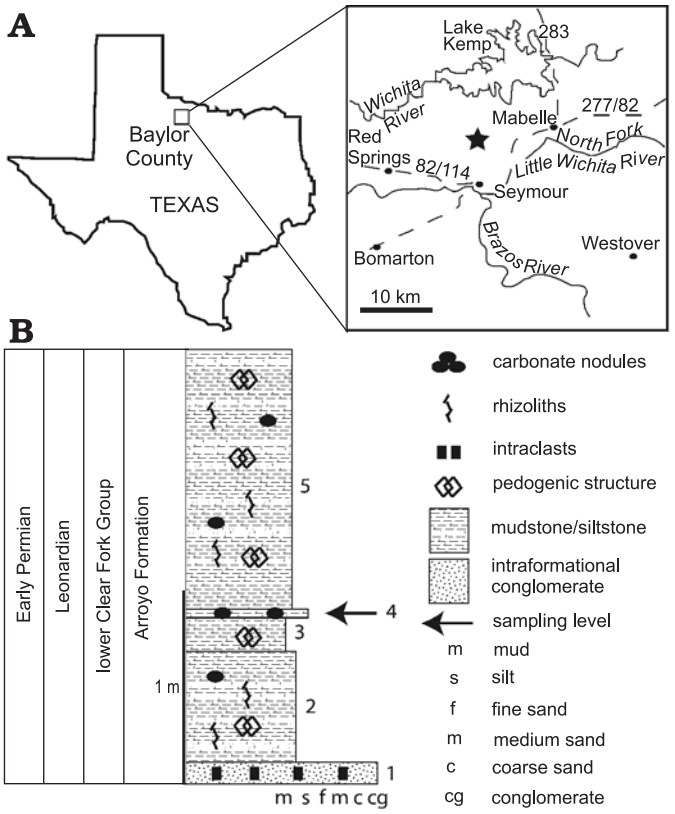


Fig. 1. Baylor County map (**A**) and stratigraphic section (**B**) at the Craddock Ranch (denoted with a star), Seymour Texas, lower Clear Fork Formation (cf. Nelson et al. 2013). Numbers 1–5 denote units through the sampled portion of the Craddock Ranch exposure.

Johnson 1999, 2012). An articulated, nearly complete skeleton of *Orthacanthus platypternus* is known from the Upper Carboniferous of Hamilton, Kansas, USA (Fig. 2A). This fossil, representing a juvenile, is the most complete xenacanth recovered in the Permo-Carboniferous American localities (Zidek 1993a, b) and shows the typical eel-like morphology of the derived xenacanthiforms (family Xenacanthidae), well-known from many articulated specimens of European localities (see Schneider and Zajíc 1994; Heidtke 2003 and references therein). As indicated in Fig. 2A, juvenile *O. platypternus* had a dorsal spine already contacting the occipital region of the neurocranium (but see the condition in early juvenile *O. bohemicus*; Fig. 2B), an elongated dorsal fin and two anal fins. Dorsal spines of *Orthacanthus*, the subjects of our study, are very common in the Craddock Bone Bed. Donelan and Johnson (1997) gave the first description and biometry referring the isolated spines to *O. platypternus* due to the association with numerous teeth of that species.

The xenacanth dorsal spine is a modified dorsal-fin spine, homologous to the fin-spine of fossil and modern phalacanthous sharks and structurally comparable with the fin spines of modern elasmobranchs lacking the ornamented mantle (e.g., *Oxynotus*; Soler-Gijón 2004). The xenacanth spine was developmentally connected to the dorsal-fin module, which was probably under the positional regulation of the *Hox* and *Tbx* genes, as occurs in modern sharks (Maisey 2009). The occipital/cervical location of the spine in late juvenile-adults of derived xenacanthiforms (*Orthacanthus*, *Xenacanthus*, *Triodus* = *Bohemiacanthus* and *Plicatodus*) is secondary, and a consequence of the forward differential growth of the proximal end of the spine early in ontogeny (Soler-Gijón 2004). Articulated skeletons of juvenile and adult primitive xenacanthiforms (*Diplodoselache*, *Lebachacanthus*) always exhibit the dorsal spine behind the pectoral girdle, in front of the dorsal fin (Dick 1981; Heidtke 1982, 2007); a postcranial location is also suggested for *Dicentrodus* and *Reginaselache*, until now only known by disarticulated remains (Hampe 2003; Hampe et al. 2006; Turner and Burrow 2011).

The function of the dorsal spine is usually accepted as a defensive structure (Evans 1924; Hampe 1997; Johnson 1999: 253) but it has also been proposed that the spine reduced lateral bending of the anterior body and therefore stabilized swimming (Soler-Gijón 2004). The xenacanth dorsal spine was a non-replaced structure, in similar fashion to the dorsal-fin spines of extinct and modern chondrichthyans (Maisey 1978, 1979; Soler-Gijón 1999; Clarke et al. 2002; Ramos 2007; Tovar-Avila et al. 2008; Barnett et al. 2009). As such, dorsal spines have been the subject of histological and skeletochronological studies (Dick 1981; Soler-Gijón 1999; Soler-Gijón and Siebert 2001; Turner and Burrow 2011). Past studies have noted cyclical deposition in xenacanth dorsal spines and fin spines, allowing the study of growth rates through ontogeny, as well as interpretation of environmental conditions (see Soler-Gijón 1999). Dorsal spine histology and skeletochronology have only been studied in detail in Late Carboniferous xenacanths (*Orthacanthus meridionalis* from the Puertollano coal basin, Spain and *Orthacanthus* sp. from the Robinson locality, Kansas, USA) living in tidally influenced, marginal marine environments with a humid tropical climate (Schultze 1995, 1998; Soler-Gijón and Moratalla 2001; Schultze and Soler-Gijón 2004). Permian *Orthacanthus platypternus* from the Craddock Bone Bed gives the opportunity to study xenacanth sharks that were growing, at least temporarily, in coastal plain environments under a semi-arid, seasonally dry tropical climate (Nelson et al. 2013).

Evidence for an increasingly dry and seasonal climate during the Permian in Baylor County and the surrounding area has been noted through the study of Permian floras (Chaney and DiMichele 2007; DiMichele et al. 2006) and palaeosols (Tabor and Montañez 2004). Evidence for cyclical growth has been found in the long bones of other vertebrates in the same bone bed (Beck 2014), and was expected in the hard structure of the xenacanth dorsal spine. The goals of this study were to (i) describe the morphology and histology of the dorsal spines of *O. platypternus*; (ii) determine if cyclical growth was recorded in the dorsal spines of *O. platypternus*; (iii) investigate if cyclical growth would correspond to spine size and answer previous questions about ontogeny and sexual size dimorphism in *O. platypternus* (Donelan and Johnson 1997); (iv) compare dorsal spine histology of *O. platypternus* with an earlier xenacanth, *O. meridionalis*, to

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

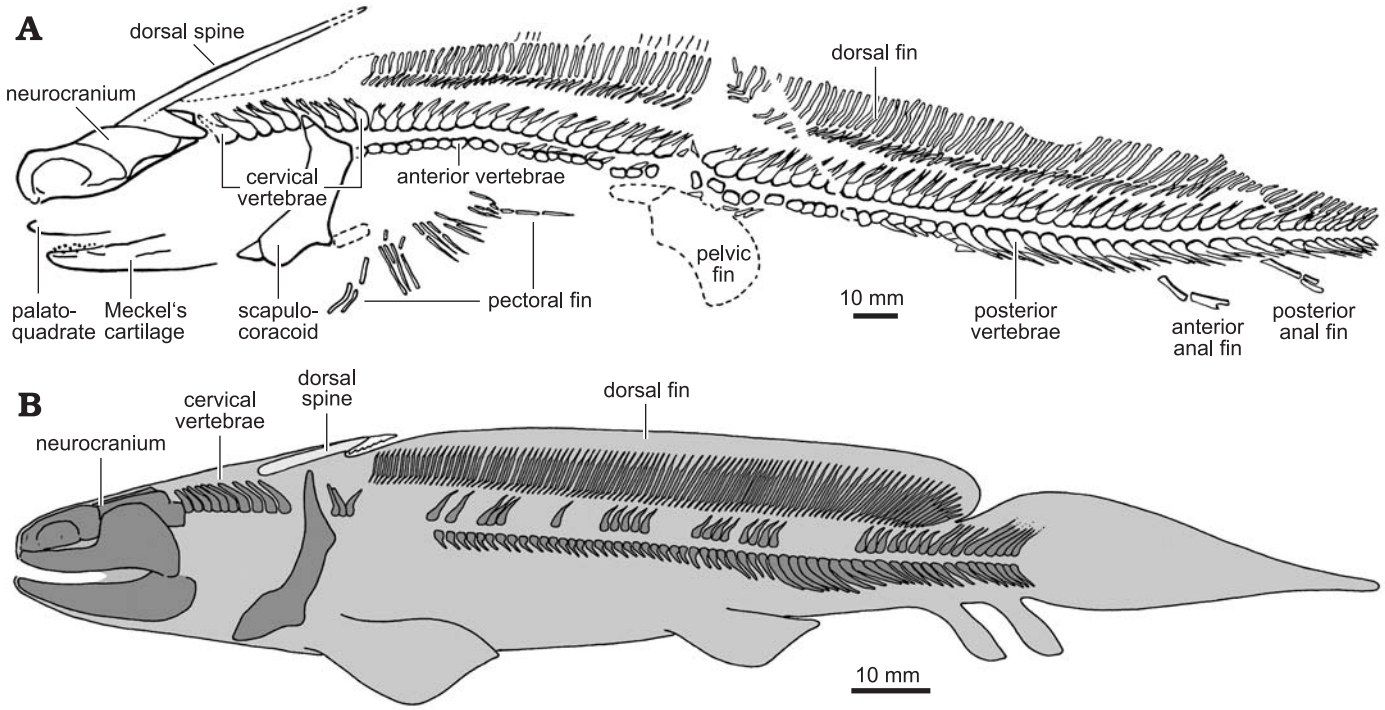


Fig. 2. Juvenile *Orthacanthus platypternus*, Stephanian B (Upper Carboniferous) of Hamilton, USA (**A**) compared to juvenile of *O. bohemicus*, Westphalian D (Upper Carboniferous) of Bohemia, Czech Republic (**B**), showing the relative position of the dorsal spine. A, modified from Zidek (1993b: fig. 1); B, modified from Soler-Gijón (2004: fig. 3C).

note any interspecific variability and test the hypothesis that spine denticle density corresponds to growth rates or is diagnostic of species within the genus; (v) discuss the possible diadromy and habitat of *O. platypternus* consistent with our histological and skeletochronological results.

Institutional abbreviations.—HMNS, Houston Museum of Natural Science, Houston, Texas, USA; KUVP, Museum of Natural History (Division of Vertebrate Paleontology), Lawrence, Kansas, USA; MCN, Museum of Natural Sciences, Madrid, Spain; PU-XE, Department of Paleontology (Vertebrates collection, Puertollano Basin), Universidad Complutense, Madrid, Spain; SMU, Southern Methodist University Dallas, Texas, USA.

Geological setting

The Early Permian of north-central Texas (Fig. 1) is characterized by a dynamic sequence of terrestrial red beds that grades into a coeval shallow marine shelf environment in the northern Midland basin. The Craddock Bone Bed (lower Clear Fork Formation; Nelson et al. 2013) exposes terrestrial dominated deposits that have previously attracted the attention of vertebrate specialists because of their articulated *Dimetrodon* and temnospondyl specimens. The bone beds are located approximately 12 km north of Seymour, TX on the Craddock Ranch. These Early Permian deposits have previously been assumed to have accumulated under a strongly seasonal climate that was undergoing a transition from wet conditions in the late Pennsylvanian to drier conditions in the Early Permian (Chaney and DiMichele 2007; Tabor and Montañez 2004). Tabor and Montañez (2004) noted that climate changes leading up to the deposition of the Clear Fork Group (e.g., the Wichita Group) were consistent with atmospheric circulation over western equatorial Pangaea. More specifically, Permian deposits possibly record the onset of monsoonal atmospheric circulation across this region.

A vertical stratigraphic column (Fig. 1) through the collection sectors at the main quarry of the Craddock Ranch reveals five distinct units. Unit 1 is an intraformational, polymict conglomerate that forms the quarry floor. The matrix is composed of clay and silt that surrounds mudstone and siltstone intraclasts, carbonate nodules, and other palaeosol debris. Secondary calcite forms the cement and coats many of the intraclasts. The conglomerate unit is interpreted as an event deposit, possibly deposited during large storm events that reworked underlying palaeosol deposits and concentrated them in ephemeral alluvial fans. Units 2, 3, and 5 are primarily siliciclastic mudstone and siltstone that display pedogenic structures, carbonate nodules, rhizoliths, and subangular aggregates. They vary slightly in clay content or degree of induration, but all are consistent with vertisols based on their v-shaped cracks and pedogenic carbonate (analogous to the type G profiles of Tabor and Montañez 2004.) The lack of redoximorphic features (e.g., hematite nodules) indicates that units 2, 3 and 5 were relatively well drained in between periods of prolonged drying. Broadly, these units represent floodplain fines or oxbow (abandoned) channel deposits typical of the lower Permian. Chaney and

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

DiMichele (2007) also noted that much of the "basal" and "lower" Clear Fork Group (both included now in the lower Clear Fork Formation; see Nelson et al. 2013: fig. 5) was consistent with vertisol and oxbow siltstone deposition. Unit 4 is a layer of slightly more indurated siltstone (minor clay and fine grained sand) with small carbonate nodules, containing the *Orthacanthus* spines, xenacanth calcified cartilage, scales of palaeonisciforms, and bones and teeth of *Trimerorhachis* and *Dimetrodon*. *Orthacanthus* spines were collected from two sectors of unit 4: the first consisting of a clay-rich mudstone and siltstone where many xenacanth spines and cartilage have been found among shed teeth of *Trimerorhachis* and *Dimetrodon*, and the second sector consisting of a carbonate-rich mudstone where the xenacanth spines are associated with large *Dimetrodon* bones (sectors are named "Tuffy" and "Jonathan", respectively, in Houston Museum of Natural Science records). The thin layer with *Orthacanthus* was likely deposited during overbank flooding events, or potentially in ephemeral streams or oxbow lakes formed during severe storms.

Material and methods

Twelve dorsal spine fragments of *Orthacanthus platypternus*, housed at the Houston Museum of Natural Science (HMNS) Craddock Bone Bed collections, form the main data set for this histological study. Three additional spines (SMU 68799–801), collected by Donelan and Johnson and housed at Southern Methodist University, were also examined in order to study the general morphology of spines of *O. platypternus* (Fig. 3). Due to the destructive nature of histological sampling, specimens selected for study were from non-articulated and incomplete spine fragments (many fragments were proximal to the denticulate region), and ranged in diameter from approximately 4 to 10 mm (see Table 1 for measurements and complete HMNS catalogue codes). Two specimens (HMNS-T1 and HMNS-T2) were collected in sector "Tuffy" of unit 4 (see Geological setting section above and Fig. 1). The rest of the studied specimens (HMNS-J1 through HMNS-J10) were collected in sector "Jonathan" of unit 4.

All spine fragments were photographed and measured prior to thin-sectioning. Measurements included length of fragments, width and height at their widest and narrowest points, and width at the site of thin-sectioning. Denticulate regions were present but poorly preserved on spines HMNS-T2 and HMNS-J3, so lengths of the denticulate regions, sizes of denticles, and distances between denticles could not be recorded. The denticulate region of HMNS-T1 was present and complete, but was not histologically sampled.

To protect and stabilize spines during thin-sectioning, specimens were vacuum embedded in a 15 × 15 cm (6 × 6 inch) polypropylene container of Silmar-41 polyester resin (U.S. Composites, Inc.) with methyl ethyl ketone peroxide catalyst at 0.7–1% by mass, according to the standard thin-sectioning procedures described by Lamm (2013). The resin was allowed to cure in a vent hood for 24–72 hours. Embedded spines were cut into thick sections with a diamond-embedded steel blade. The mounting sides of thick sections were ground and polished on an Ingram thin-section silicon carbide abrasion wheel (Ward's Natural Science Est., Inc.) with 220 grit per inch silicon carbide powder, followed by 400 grit per inch silicon carbide powder. Polished samples were mounted on frosted glass petrographic slides with clear 2-ton epoxy (Devcon) and allowed to cure for at least 24 hours. The backs of thick sections were cut off with a model 135 Ingram thin-section cut-off saw (Ward's Natural Science Est., Inc.) and thin-sections were ground to approximately 0.1 mm in thickness with a model 400 Ingram thin-section grinder (Ward's Natural Science Est., Inc.). Thin-sections were viewed and photographed through a Leica EZ4 D stereomicroscope (Leica Microsystems) with normal transmitted light, as well as through a Labophot-pol microscope (Nikon), using normal transmitted and polarized light. A small amount of water was added to each slide as it was viewed to enhance microstructure visibility.

All spines were sampled in cross-section, except for spine HMNS-T2, which was sampled as one proximal cross-section and a series of longitudinal sections through the denticulate region. Only spines HMNS-T2 and HMNS-J3 were sampled through denticulate regions; all other thin-sections were made from fragments proximal to denticulated regions (see Table 1).

Table 1. *Orthacanthus platypternus* dorsal spines sampled. Measurements are given for the most proximal point available and are rounded to the nearest millimeter. The measured cross-sections are from non-denticulated regions, except for specimen HMNS-J3, cut at the level of the denticulated region. With the exception of HMNS-T1 and HMNS-J3, dentine layer 2 is assumed to be the older layer recorded in the cross-sections of the spines because dentine layer 1, representing the juvenile stage SP1, becomes restricted to the distal part of the *Orthacanthus* spines during growth (cf. Soler-Gijón 1999) and it is already absent in the non-denticulated region of the small spine HMNS-T2 (see longitudinal section in Fig. 4). Abbreviation: dl, dentine layer of centrifugally growing dentine.

Specimen abbreviation	HMNS catalogue code	Spine width (mm)	Spine height (mm)	Number dentine layers (dl)	Estimated age (years)
HMNS-T1	CBB TUF X Spn 1	4	4	1 (dl1)	1
HMNS-T2	CBB TUF X Spn 2	6	6	1 (dl2)	2
HMNS-J1	CBB JON X Spn 1	9	10	3 (dl2–4)	4
HMNS-J2	CBB JON X Spn 2	8	8	?	?
HMNS-J3	CBB JON X Spn 3	7	7	2 (dl1–2)	2
HMNS-J4	CBB JON X Spn 4	7	6	2 (dl2–3)	3
HMNS-J5	CBB JON X Spn 5	6	6	?	?
HMNS-J6	CBB JON X Spn 6	8	6	2 (dl2–3)	3
HMNS-J7	CBB JON X Spn 7	10	8	>3 (dl2–n)	>4
HMNS-J8	CBB JON X Spn 8	7	7	>3 (dl2–n)	>4
HMNS-J9	CBB JON X Spn 9	7	8	?	?
HMNS-J10	CBB JON X Spn 10	8	8	3 (dl2–4)	4

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

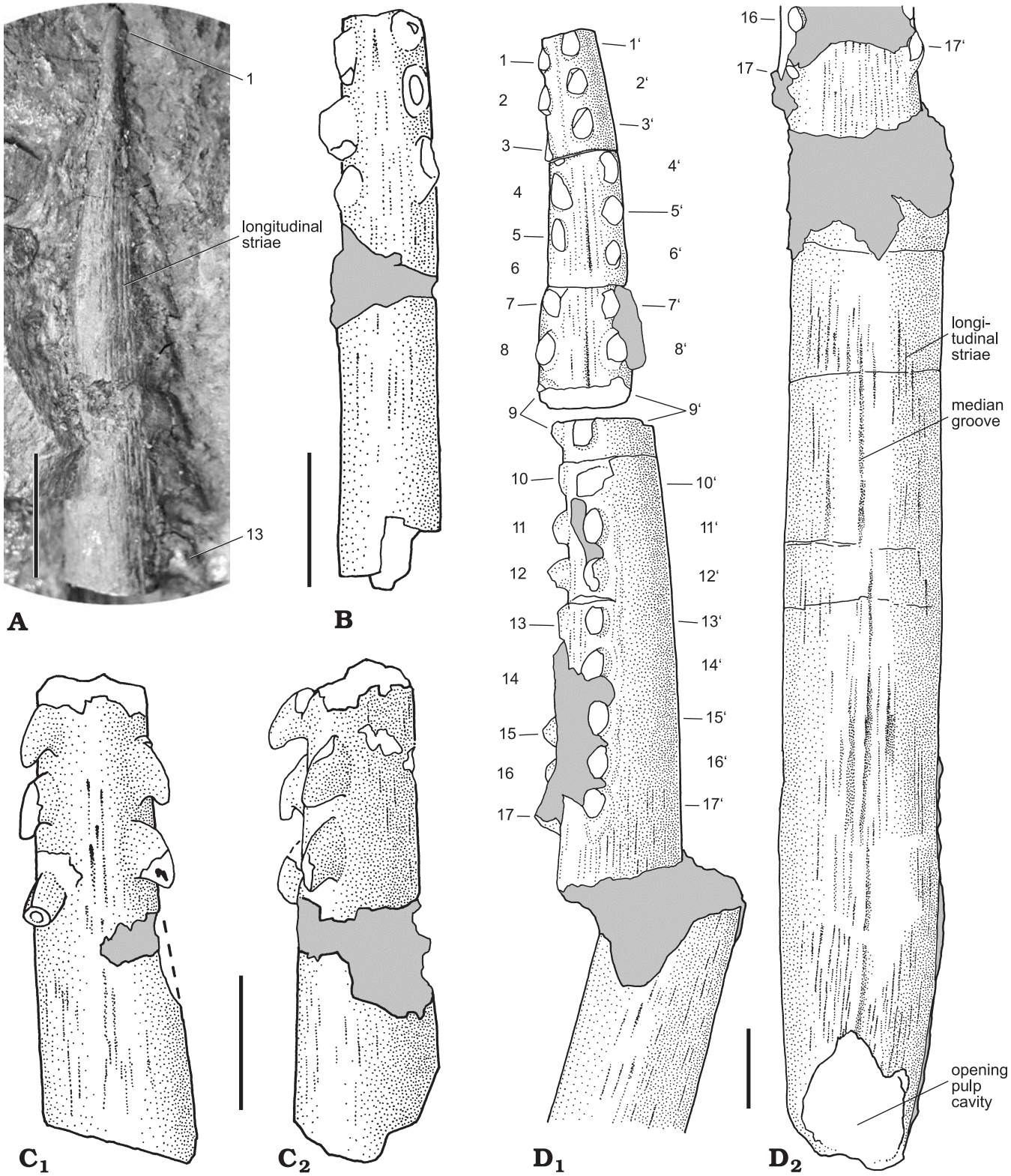


Fig. 3. External morphology of dorsal spines of *Orthacanthus platypternus* (Cope, 1884), Lower Permian, Craddock Bone Bed, Texas, USA. **A**. HMNS-T1, juvenile, lateral view. **B**. SMU 68799, juvenile, posterior view. **C**. SMU 68800, juvenile, posterior (C_1) and postero-lateral (C_2) views. **D**. SMU 68801, adult, denticulated, postero-lateral view (D_1) and non-denticulated, posterior view (D_2) regions. Numbers 1 to 17 point to the positions of the denticles along the posterior sides of the spines. Numbers 1' to 17' correspond to the right row of denticles. Grey areas in B–D_2 represent sedimentary matrix. Scale bars 5 mm.

The terminology used here to describe the morphology and microstructure of the xenacanth spines basically follows that of Soler-Gijón (1999). In this study, "major growth line" is used to describe a dark, hypomineralized line marking an unconformity in dentine deposition. "Minor growth lines" refer to finer lines within lamellar dentine usually arranged

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

in a close, but evenly spaced series. A dentine layer (dl) within the spine proper (SpPr) was identified as a band or zone of trabecular and lamellar dentine that was generally homogenous in appearance, especially in terms of colour and vascular structure, and usually separated from successive layers by a major growth line. Successive dentine layers (dl1–n) preserved in the outer (centrifugally growing) part of the wall of each spine proper represent the successive ontogenetic stages (SP1–n). "Lamellar" is used to describe less vascular dentine, such as that located immediately around the pulp cavity or around the periphery of the spine wall.

Systematic palaeontology

Class Chondrichthyes Huxley, 1880

Order Xenacanthiformes Berg, 1940 [= Xenacanthida Glikman, 1964]

Family Xenacanthidae Fritsch, 1889

Genus *Orthacanthus* Agassiz, 1843

Type species: *Orthacanthus cylindricus* (Agassiz, 1843), Late Carboniferous, Coal Measures, Manchester, England. See Hampe (2003) for additional information about this species and the Carboniferous biostratigraphy of the British localities.

Orthacanthus platypternus (Cope, 1884)

Figs. 3–7, 8A, 9.

Referred material.—15 isolated dorsal spines (HMNS-T1–2, HMNS-J1–10, SMU 68799–68801) from the Craddock Bone Bed (northern Baylor County, Texas, USA), lower Clear Fork Formation, Early Permian (Leonardian age; see Nelson et al. 2013).

Description

General morphology.—The external morphology of a dorsal spine of *Orthacanthus platypternus* is well represented by the specimen SMU 68801 (Fig. 3D), 114 mm long, and lacking the most distal region. Two posterior rows of denticles covered about 48 mm of the complete length of the spine, indicating that the denticulation could be extended for the distal half of the complete spine. The cross-section was oval near the opening of the pulp cavity but became circular to subtriangular in the distal part of the non-denticulated region and circular in the denticulated region. The spine was 8.4 mm wide at the proximal end of the denticulated region and reached a maximum width of 9.4 mm proximally, near the basal opening of the pulp cavity. The robustness index (maximum width to total length ratio) of the preserved spine is 1:12. The denticle sizes (base length) ranged 1.7–2.3 mm. A density of denticulation of 0.40 denticles/mm remained uniform through the spine SMU 68801 and in the much smaller fragmentary specimens SMU 68799 and 68800 (juveniles) that showed the most proximal denticles (Fig. 3B, C).

The most distal denticulation (Fig. 3A) of a juvenile spine was preserved on the smallest spine sampled (HMNS-T1). Thirteen denticles covered approximately 23.5 mm of the total spine fragment length (40 mm). These denticles increased in base length and denticle height proximally except for the most proximal denticle, which was approximately 1 mm shorter in length than the denticle before (distal to) it. Spacing between denticles on HMNS-T1 increased proximally until the 6th denticle, after which spacing between denticles fluctuated. The denticle sizes ranged from 0.4 mm (first denticle, distally) to 2 mm (denticle 13). The density of denticulation dramatically increased from 1.1 denticles/mm in the distal part to 0.32 denticles/mm in the proximal part.

Histology.—The general histology of spines thin-sectioned is shown in serial longitudinal sections (Fig. 4) and serial cross-sections (Fig. 5). The pulp cavity of many spines was filled with calcite and quartz, as well as opaque minerals such as iron oxides. The pulp cavity was located slightly off-center in the spine (as seen in cross-sections) at the proximal end of the denticulated region (Fig. 5), but became closer to the posterior side of the spine in the non-denticulated region (Figs. 6, 7). The wall of the spine was composed of two structural components—an outer layer of centrifugally growing dentine (growing outward from the periphery of the spine), and a layer of centripetally deposited dentine (growing inward) lining the pulp cavity.

The centrifugal dentine was composed primarily of highly vascular trabecular dentinal layers. Centrifugal lamellar dentine was in the most distal parts of the dentinal layers and at the periphery of large spines. Most spines had occasional enlarged vascular canals in the outer half of the spine wall (Fig. 6B, see also Fig. 5A, C). Dentinal tubules radiated out from the outermost lamellae of denteons, although some vascular canals were simple and did not have distinct lamellae. When a major growth line was present, denteons below the growth line were more developed than those outside of the line. Colour banding was apparent in most spines (Figs. 5A–D, 6A, 7).

The centripetal dentine mainly exhibited a lamellar structure with incremental deposition of hard tissue (Figs. 4, 5). Centripetal lamellar dentine thickened distally, and filled the pulp cavity of the most distal sections. Spines HMNS-T2 and HMNS-J3, shown in Figs. 4 and 5, respectively, each had a region of centripetal trabecular dentine in the pulp cavity near the distal end.

Though the smallest spine sampled (HMNS-T1) was sectioned just proximal to the denticulate region, only one dentine layer (SP1) was present. This layer contained no growth lines, changes in colour or vascular patterns, or lamellar dentine (Fig. 6A). However, in thin-sections made near or through the denticulate region of larger spines, centrifugal and centripetal lamellar dentine were present, and in some cases, the dentine could be divided into two depositional layers, separated by a major growth line (see Figs. 4–6). Dentine layer SP1 was thickest in the distal portion of spines, gradually became thinner proximally, and was not present in most fragments proximal to the denticulate region. Dentine layer SP2 was thickest proximally and was not present in the most distal portions of

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

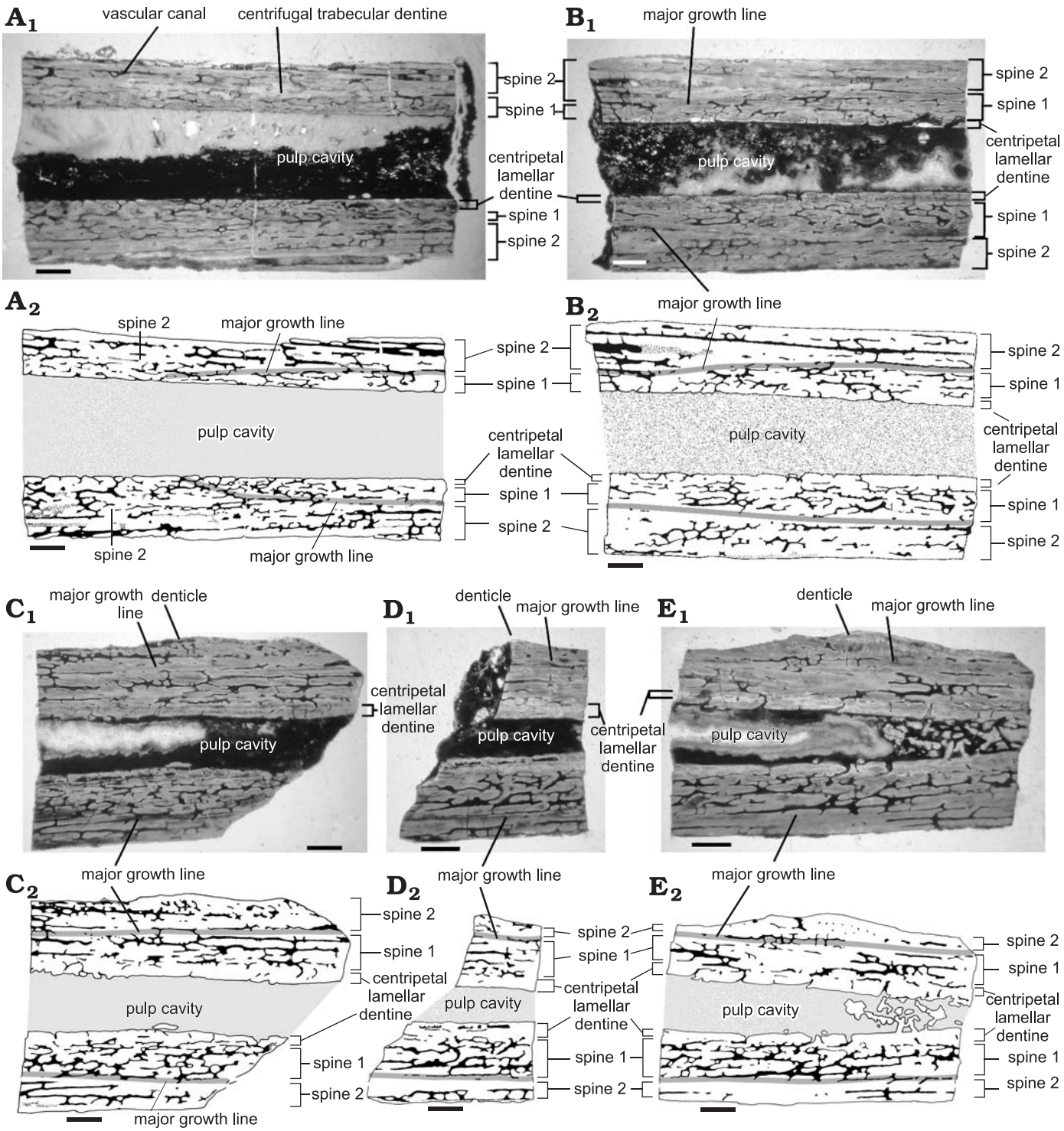


Fig. 4. Serial longitudinal sections of dorsal spine of *Orthacanthus platypternus* (Cope, 1884), Lower Permian, Craddock Bone Bed, Texas, USA; specimen HMNS-T2, where A represents the most proximal section and E is the most distal. Samples C–E include the denticulate region. Photos of the sections (A_1–E_1), interpretative drawings (A_2–E_2). Scale bars 1 mm.

denticulate regions (see Fig. 5). Where both dentine layers were present, a major growth line separated them.

Major growth lines were most evident in spines HMNS-T2 and HMNS-J3 (Figs. 4, 5). A growth line was evident in four out of five cross-sections of specimen HMNS-J3 (all except for the most distal) and can be seen most clearly in Fig. 5A. Vascular canals to the inside of the growth line were lined with lamellae, whereas vascular canals to the outside of the ring were not. In serial longitudinal sections (Fig. 4), the major growth line gradually projected toward and eventually contacted the pulp cavity, proximally.

Some of the larger spines also had minor growth lines

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

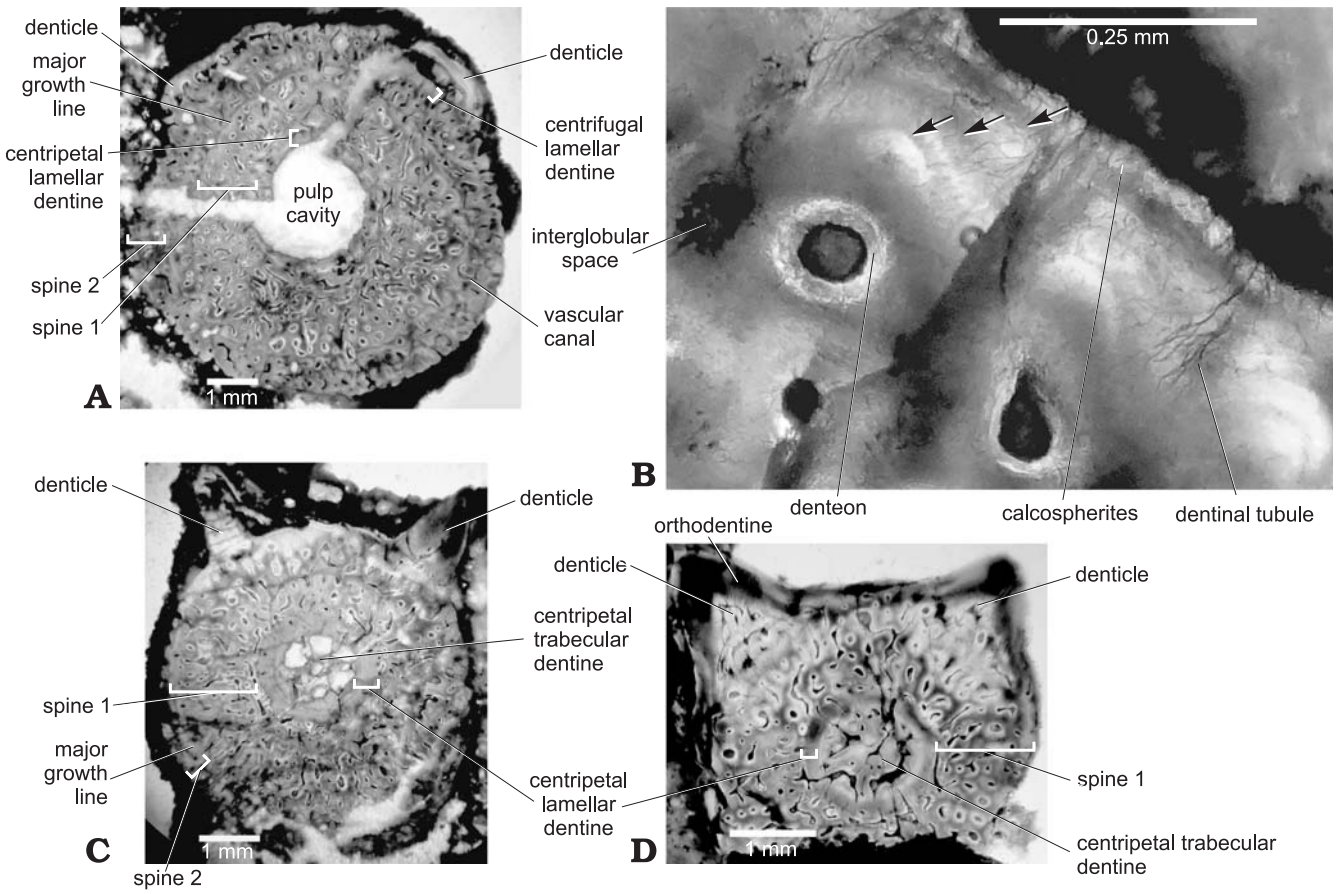


Fig. 5. Serial cross-sections (**A**, **C**, **D**) of dorsal spine of *Orthacanthus platypternus* (Cope, 1884), Lower Permian, Craddock Bone Bed, Texas, USA; specimen HMNS-J3, where A represents the most proximal section and D is the most distal. **B**. Detail of section in A showing three minor growth lines close to the base of the right denticle in the figure (arrows).

in the lamellar dentine at the periphery of SP2 (Fig. 5, 7). In specimen HMNS-J3, three minor growth lines were fine, dark and evenly spaced (Fig. 5B). In specimen HMNS-J7, growth lines were arranged in at least three pairs (Fig. 7B), although the spine fragment was not long enough to determine if these growth lines were major or minor growth lines.

Growth lines, such as those seen in Fig. 5B, were also present in the lamellar dentine around the pulp cavity of four spines (specimens HMNS-J1, J3, J7, J8). In most specimens, colour-banding and growth lines usually circumvented vascular canals.

Cross-sections of specimen HMNS-J3 show the orthodentine (dark colour) forming the distal part of the denticles (see Fig. 5D). The inner region of denticles consisted of white dentine, with many long dentinal tubules radiating outward from at least one vascular canal at the base of or in the innermost region of the denticle. In serial longitudinal sections of HMNS-T2, the denticulate region did not extend to the entire length of SP1 and all denticles present on the available fragment were added to SP2 (Fig. 4).

Interglobular spaces were found in interdenteonal areas of all spines. These spaces were generally more numerous near the pulp cavity of all spines, and were especially dense in proximal sections, near the pulp cavity of larger spines. In proximal specimen HMNS-J7, interglobular spaces and iron oxides were extremely dense in some regions near the pulp cavity and also markedly decreased in number and size at the border between the innermost layer of white centripetal dentine and the following, darker coloured trabecular dentine of the spine wall (Fig. 7D). Spine HMNS-J8 had a similar distinct decrease in interglobular spaces where the centripetal lamellar dentine lining the pulp cavity met the centrifugal trabecular dentine of the spine wall.

In several spines, calcospherites on the periphery of the spine wall formed a translucent border (Fig. 5B). Globular calcospherites were most clearly visible on the outer edge of specimen HMNS-J3, and were associated with numerous small interglobular spaces. Interglobular spaces represent poorly mineralized regions between calcospherites, which did not completely fuse during dentinogenesis (Currey 2006). In most cases, interglobular spaces were distributed sporadically through the spine wall, and in the highest numbers and density near the pulp cavity of spines. The high density of interglobular spaces within the centripetal lamellar dentine of specimens HMNS-J7 and HMNS-J8 supports the hypothesis that younger dentine was hypomineralized and became more mineralized as the individual aged (as suggested by Soler-Gijón 1999). Hypomineralized dentine

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

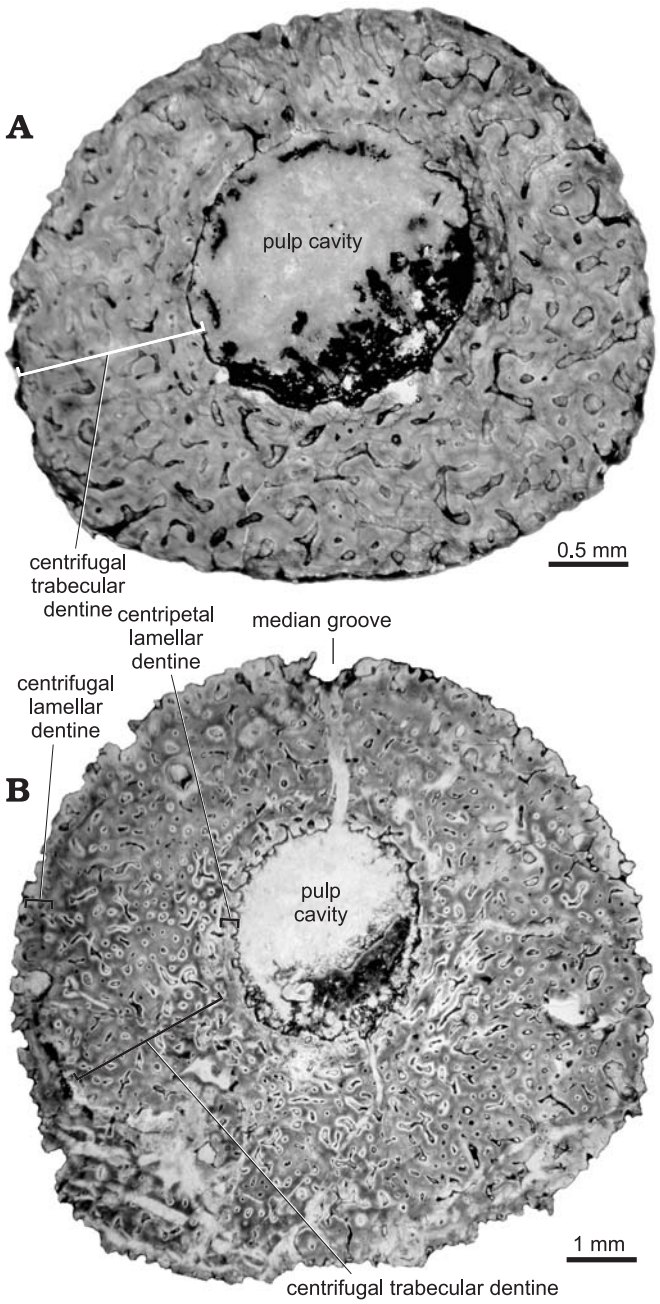


Fig. 6. Cross-sections of dorsal spines (non-denticulated region) of *Orthacanthus platypternus* (Cope, 1884), Lower Permian, Craddock Bone Bed, Texas, USA. Comparison between the smallest, specimen HMNS-T1 (**A**), and the largest *Orthacanthus* dorsal spine sampled, specimen HMNS-J1 (**B**). Posterior sides of the spines are pointing to the top of the figure.

(particularly that near the pulp cavity) was probably more susceptible to diagenesis and degradation following invasion of microorganisms, leading to the deposition of dark, opaque minerals (such as iron oxide) seen associated with interglobular spaces of the centripetal lamellar dentine of some spines (Fig. 7D) (Turner-Walker 2008). Altered dentine and interglobular spaces filled by authigenic minerals are relatively common in fossil chondrichthyan and acanthodian fin-spines (see discussion and references in Botella et al. 2012).

The colour-banding present in almost all spines was also noted by Maisey (1978) in finspines of hybodont sharks. The colour of fossil dentine can be related to diagenesis, where well-preserved dentine often appears reddish in colour, whereas layers of dentine exposed to the environment may be white-coloured. However, in some cases in this study, a major growth line separated two colour bands as well as two different stages in denteon development (such as in Fig. 5A), suggesting that colour banding can also be related to dentine deposition. The smallest spine sampled here (HMNS-T1) corresponded to a very young juvenile individual as indicated by the short denticulation, and lacked colour banding. The largest spine sampled (HMNS-J1) also showed weaker colour banding than most other spines, probably due to a very fast mineralization during dentinogenesis (see discussion below, in section "Histology and skeletochronology").

Discussion

Growth and ontogeny.—The xenacanth spine appears to be structurally comparable to the dentinal trunk (stem) of the dorsal-fin spines of holocephalians and phalacanthous sharks (Soler-Gijón 2004; Maisey 2009). The comparative information concerning skeletochronology and growth patterns in Recent chondrichthyans facilitates a more objective interpretation of the fossil forms. In this respect, the recent publication on *Heterodontus portusjacksoni* by Tovar-Avila et al. (2008) is especially relevant to our study. The authors found evidence of annual growth increment banding in both inner (centripetal) and outer (centrifugal) trunk dentine. Interestingly, the model of chondrichthyan dorsal-fin spine growth proposed by Tovar-Avila et al. (2008: fig. 6) is basically similar to the pattern of deposition of dentinal layers described for xenacanths (compare with Soler-Gijón 1999: fig. 10 and Fig. 8 in this paper). In both *Heterodontus* and xenacanths, the successively deposited dentinal layers of the outer trunk do not reach the apex of the spine but instead extend more proximally. The most distal part of the spine contains the first spine (termed SP1 for xenacanths, cf. Soler-Gijón 1999). Successive dentinal layers represent the successive ontogenetic stages (SP1–n). Fluorescent (oxytetracycline) marking in sections of *Heterodontus* spines suggests the annual timing of dentine deposition and shows how the outer trunk dentine always surrounds the inner trunk dentine lining the pulp cavity, in a fashion similar to that observed in the sections of xenacanth spines. These comparative results suggest that the centripetal lamellar dentine of xenacanth spines can also be useful for age estimations. However, there is no correlation between the growth marks of centrifugal and centripetal dentine in the cross-sections of spines of xenacanths, in contrast to those described in *Heterodontus* (Tovar-Avila et al. 2008: fig. 5; see also Ramos 2007: pl. 4.2). Centripetal lamellar dentine was not produced at the same rate or at the same time as centrifugal lamellar (and trabecular) dentine in the same cross-section (Soler-Gijón

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

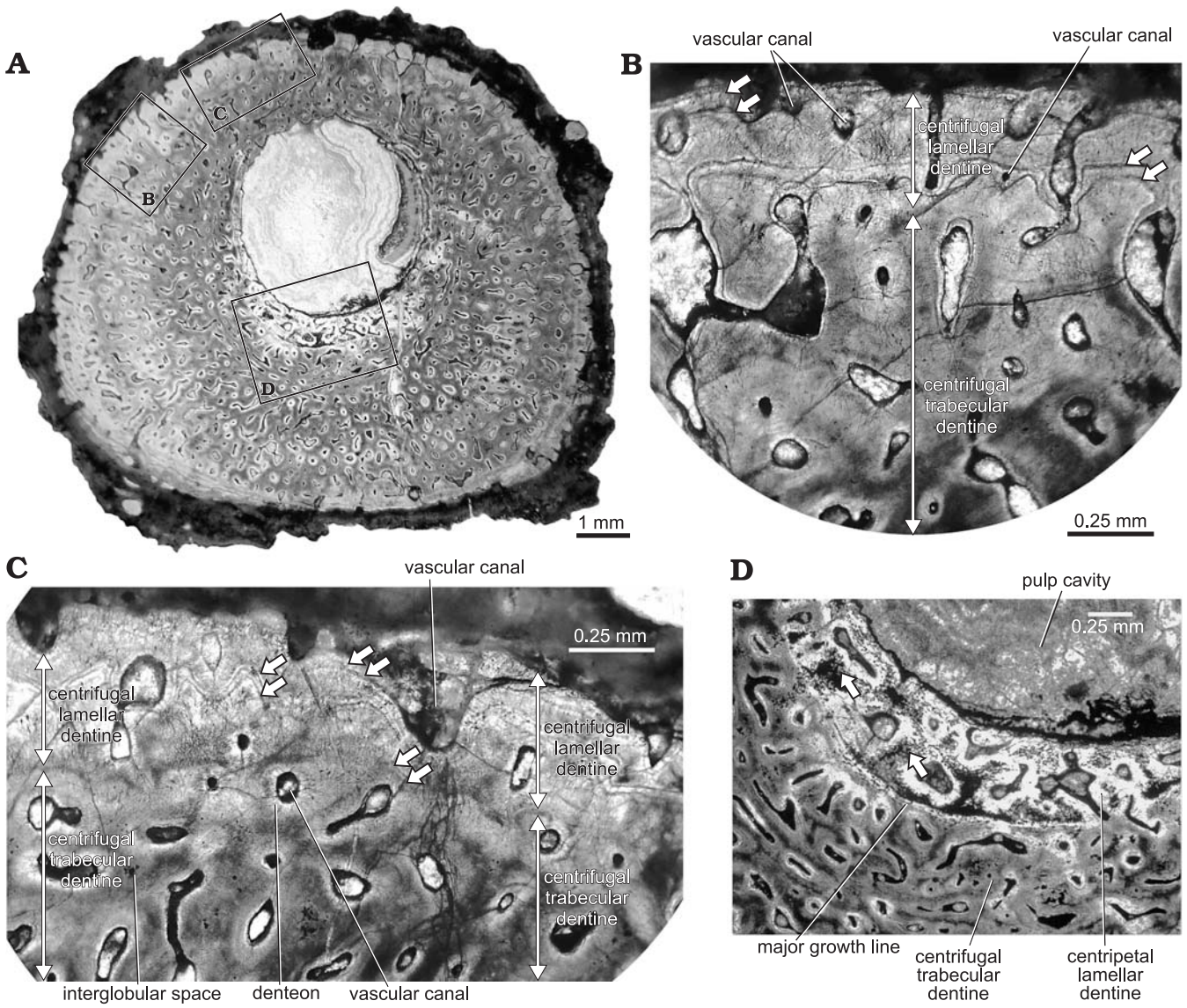


Fig. 7. Cross-section of dorsal spine of *Orthacanthus platypternus* (Cope, 1884), Lower Permian, Craddock Bone Bed, Texas, USA; specimen HMNS-J7 (non-denticulated region) showing color-banding in centrifugal trabecular dentine and growth lines in lamellar dentine. **A**. General view (posterior side of spine towards the top of the figure). **B**, **C**. Details of periphery showing pairs of growth lines (marked by arrows) in the centrifugal lamellar dentine. **D**. Detail of interglobular spaces within the centripetal lamellar dentine (arrows denote interglobular spaces).

1999), as observed by the difference in thickness and number of growth lines within both kinds of dentine on the same thin-section. This apparent asynchrony in the deposition of dentine in the xenacanths can be explained by the histological differences between outer (centrifugal) and inner (centripetal) dentines: the centrifugal trabecular dentine grew faster than the centripetal lamellar dentine. In *Heterodontus*, and other neoselachians, the complete spine trunk is composed of lamellar dentine. For clarity, the succession of dentinal layers (SP) of the outer part of the spine (probably deposited with an annual periodicity) is chosen for skeletochronological and developmental studies in *Orthacanthus platypternus* (cf. Soler-Gijón 1999), as well as to test the hypothesis of sexual size dimorphism by Donelan and Johnson (1997).

Donelan and Johnson (1997) presented the first biometric analysis of the ontogenetic and sexual size variations in the species *Orthacanthus platypternus* based on the measurement (width × height of cross-sections) of a relatively large collection (65 specimens) of isolated dorsal spines. The obtained data, ranging from 3.5 × 3.2 mm to 9.9 × 9.6 mm (fitting the linear regression $y = 0.91x + 0.15$, where y and x represent height and width, respectively, of the spine cross-sections; see Fig. 9), are grouped in three clusters that are assigned by Donelan and Johnson (1997) to juveniles (38 smallest analyzed specimens), and sexually dimorphic adults (17 specimens of intermediate sizes and 9 specimens of the largest sizes).

It was expected that juvenile shark spines would differ histologically from adult spines, and those differences would correlate with morphological and biometric differences proposed previously by Donelan and Johnson (1997) for dorsal spines from the same bone bed. Also, based

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

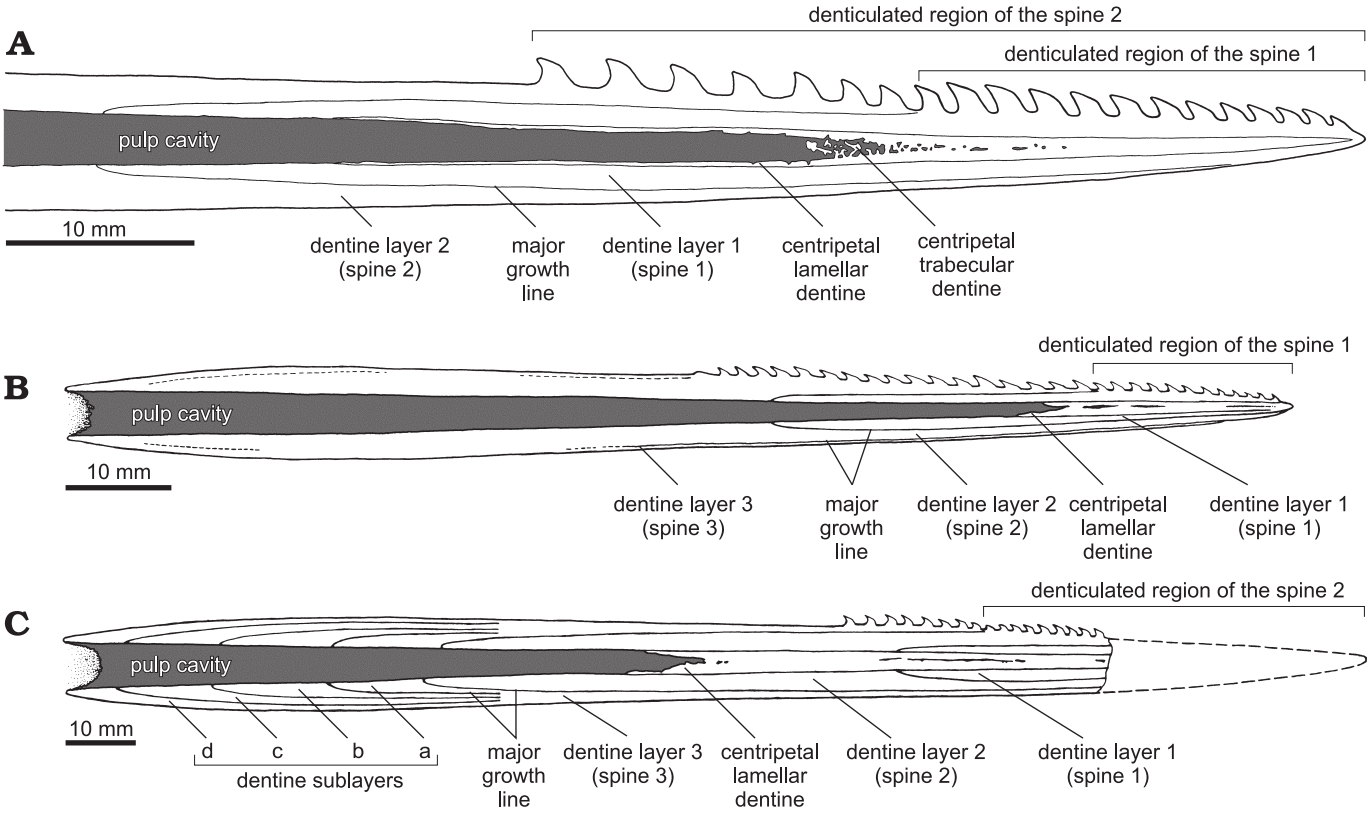


Fig. 8. **A**. Reconstruction of the dorsal spine (mainly the denticulated region) of *Orthacanthus platypternus*, based on specimens HMNS-T1 and HMNS-T2. **B**, **C**. Reconstructions of the dorsal spine of *Orthacanthus meridionalis* (modified from Soler-Gijón 1999: fig. 10); PU-XE76 (**B**) PU-XE19 (**C**). Note that distal denticles belong to the first spine (juvenile). The intersection of the first major growth line and the denticulated border of the spine indicate the proximal end of the denticulated region of the first spine; the following "spines" exhibit the distal denticles and those corresponding to each new growth stage.

on several histological studies of fossil and extant shark spines, (such as those including xenacanthid dorsal spines (Soler-Gijón 1999), ctenacanth fin spines (Stamberg 2001), hybodont fin spines (Maisey 1978), and neoselachian fin spines (Tovar-Avila et al. 2008 and references therein), it was expected that juvenile and adult spines would show a cyclical growth pattern.

Our histological and skeletochronological analyses support the conclusion of Donelan and Johnson (1997) concerning the smallest, juvenile remains. However, our data and the comparative analyses with ontogenetic data from other xenacanths and Recent sharks reveal a growth pattern in the subadults/adults of *Orthacanthus platypternus* from the Craddock Bone Bed that is far more complex than that indicated by the biometric analyses of Donelan and Johnson (1997). We considered two different aspects in the discussion of the Craddock material: (i) comparative study of the histology and skeletochronology of the isolated spines in order to analyze the relationship between size (width × height of cross sections) and ontogenetic age, development and possible sexual dimorphism, and (ii) inference of the body size of the sharks for each ontogenetic stage in order to discuss the structure of the shark population, sexual size dimorphism, and ontogenetic habitat partitioning.

Histology and skeletochronology: We integrate the skeletochronological and biometric data from *Orthacanthus platypternus* and two very well-known species *O. meridionalis* (Puertollano basin) and *Orthacanthus* sp. (Robinson locality), including information of the ontogenetic trajectories of several individuals as indicated by the measurements of histological sections (Fig. 9).

Many spine fragments sampled in this study were proximal to their respective denticulate regions and therefore did not record juvenile growth stages. However, two large spines with denticulate regions thin-sectioned as serial cross-sections and serial longitudinal sections, as well as one small spine sampled, were supportive of the hypotheses proposed above. The smallest spine sampled (HMNS-T1) was comparable in diameter to the smallest spines collected by Donelan and Johnson (1997) (Fig. 9A), and was therefore assumed to be juvenile. This assumption was supported by the histology of the spine, in that no growth lines were present, the dentine structure (as well as colour) was homogeneous through the entirety of the spine wall, and the diameter of the spine was comparable to SP1 in larger spines sampled at a similar location (just proximal to the denticulate region). No centripetal lamellar dentine was present in HMNS-T1, in contrast to larger spines sampled at a corresponding location. Specimen HMNS-T1 then, represents the first dentine layer, or SP1, and the ontogenetic stage of a juvenile (Fig. 9A).

Spines HMNS-T2, HMNS-J3, and HMNS-J8 were comparable in diameter to the smaller of two spine-size clusters

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

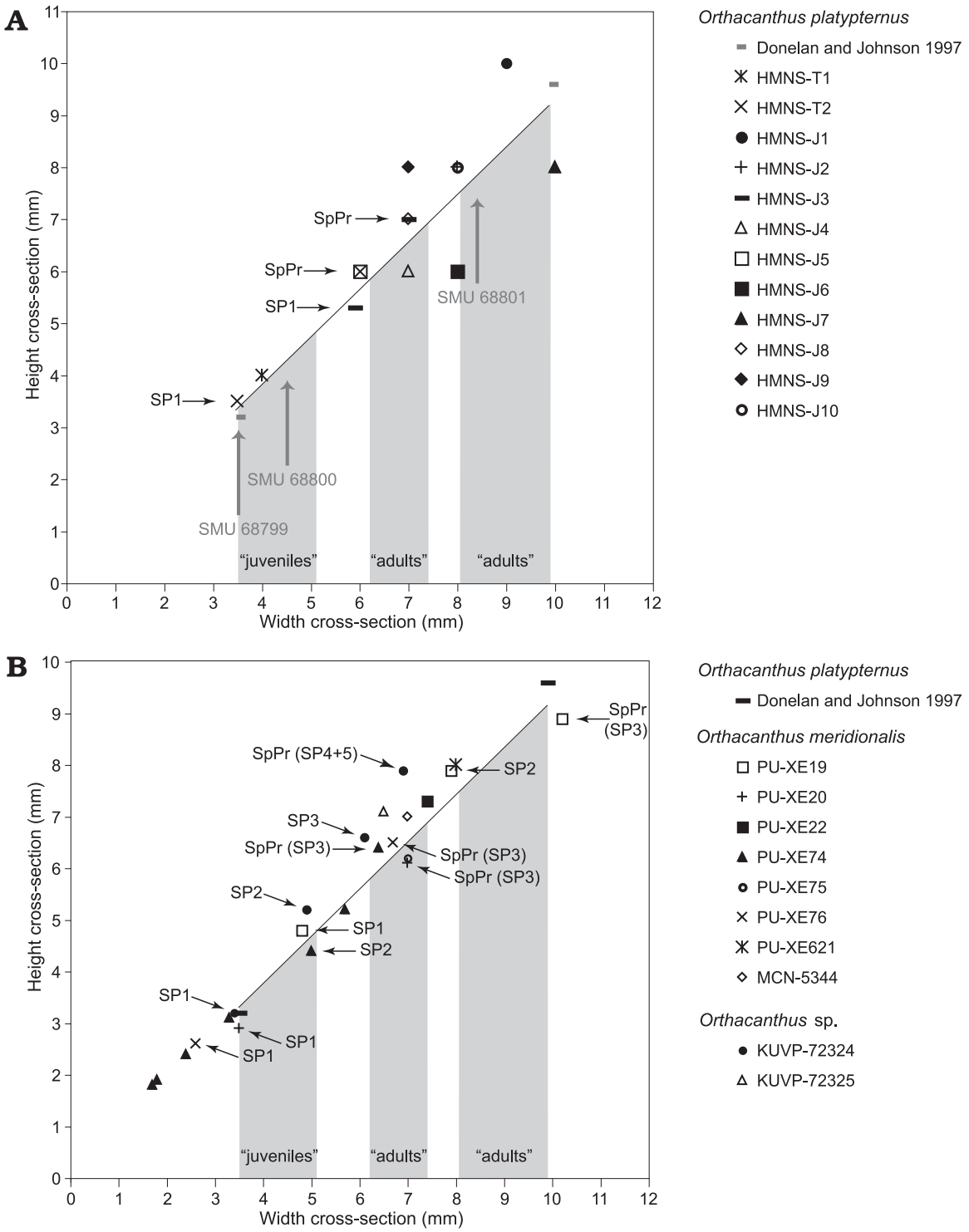


Fig. 9. Bivariate plots of relationship between width and height in cross sections of *Orthacanthus* dorsal spines. **A**. *Orthacanthus platypternus* (Lower Permian, Craddock Bone Bed, Texas, USA). **B**. Comparison of *O. platypternus* with *O. meridionalis* (Upper Carboniferous, Puertollano, Spain) and *Orthacanthus* sp. (Upper Carboniferous, Robinson, Kansas, USA). Note the linear regression ($y = 0.91x + 0.15$; $n = 65$, $r^2 = 0.98$) calculated by Donelan and Johnson (1997) for the isolated dorsal spines of *O. platypternus*. The maximum and minimal values are also included here for a comparative reference; values of the rest of the specimens are not included for clarity. Grey shaded areas indicate approximate intervals of the three size clusters corresponding to juveniles and adults according the biometric analysis by Donelan and Johnson (size intervals are based on unpublished data presented in a poster at 57th Annual Meeting of the Society of Vertebrate Paleontology, Chicago, October 1997). Note the ontogenetic trajectories of several individuals of *O. platypternus* (HMNS-T2 and HMNS-J3), *O. meridionalis* (PU-XE19, 20, 74 and 76) and *Orthacanthus* sp. (KUVP-72324) showing stages SP1–n (spine proper). Data from *O. meridionalis* and *Orthacanthus* sp. after Soler-Gijón (1999: table 1 and figs. 4–8). Vertical grey arrows point to the position in the linear regression for SMU specimens according the maximum width values at the proximal end of denticulated regions: 3.5 mm (SMU 68799), 4.5 mm (SMU 68800) and 8.4 mm (SMU 68801). Abbreviations: SP1–5, spines 1–5; SpPr, spine proper.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

attributed to adults by Donelan and Johnson (1997) (Fig. 9A). However, despite their similarity in sizes, the internal structures of these spines correspond to two different ontogenetic stages (juveniles and subadult/adults). Specimen HMNS-J8 appears to fit in the model proposed by Donelan and Johnson as a spine belonging to a relatively small, but already adult individual (indicated by the number of preserved dentinal layers) (Table 1). Spines HMNS-T2 and HMNS-J3, which may be considered adults due to their sizes, actually correspond to young, juvenile individuals according to the histological and skeletochronological examinations. Both spines had one major growth line separating two dentine layers (see Figs. 4, 5). This growth line was not visible in the most distal sections of HMNS-J3, where only SP1 was present, or the most proximal part of HMNS-T2, where only SP2 was present. The second and more recent layer of dentine (SP2) thickened proximally and in some areas, contained minor growth lines within the centrifugal lamellar dentine (Fig. 5B).

A complete denticulate region is needed to associate major growth lines with growth rates, but the presence of one growth line indicates that both HMNS-J3 and HMNS-T2 are between one and two years old. The denticulate region of HMNS-T2 does not extend the entire length of SP1 (Fig. 8), as has been described for *Orthacanthus* by Soler-Gijón (1999) and so it is likely that HMNS-T2, the similarly sized HMNS-J3, and part of the middle spine-size cluster of Donelan and Johnson (1997) represent juveniles. Interestingly, the ontogenetic stage SP1 of HMNS-T2, as measured at the level of most distal part of the preserved spine proper, appears close to juvenile spine HMNS-T1 in Fig. 9A, though the two spines' sizes place them in different size clusters of Donelan and Johnson (1997.)

Finally, spines HMNS-J1, HMNS-J7, and HMNS-J10 were comparable in diameter to the largest spine cluster reported previously (Donelan and Johnson 1997) (Fig. 9A). The three specimens show at least three dentinal layers pointing to larger and relatively older animals than those in the smaller clusters, in agreement with the biometric model. Spine HMNS-J7 corresponds to the oldest individual in the collection, showing several growth lines arranged in pairs in the centrifugal lamellar dentine, which suggests multiple dentine layers. In spite of its large size (almost of the same width as HMNS-J7), spine HMNS-J1 represents a relatively young individual recording only three dentinal layers and weakly developed growth lines. Such histology can be explained by a very fast deposition of hard tissue.

Our results indicate that size does not always correlate with ontogenetic age and degree of development. The cluster of spines with intermediate sizes includes relatively old and small "adult" individuals, as proposed by Donelan and Johnson (1997), but also younger individuals relatively large in size, which correspond to juveniles of the second group of "adults". This conclusion for *Orthacanthus platypternus* is also supported by the comparative study of *Orthacanthus meridionalis* from Puertollano (Spain) and *Orthacanthus* sp. from Robinson (Kansas, USA) (see Fig. 9B). In similar fashion to *O. platypternus*, there are two groups of spines of *O. meridionalis* belonging to old, adult individuals, which differ in size and growth pattern. Spines PU-XE19 and PU-XE621 correspond with the large "adults" of *O. platypternus* whereas the rest of the Spanish spines are located in or close to the interval of small "adults" of *O. platypternus* (cf. Donelan and Johnson 1997). Specimens KUVP-72324 and KUVP-72325 of *Orthacanthus* sp. are located in the small-adults cluster in Fig. 9B. The ontogenetic trajectories of spines of *O. meridionalis* and *Orthacanthus* sp. (e.g., Fig. 9B: specimens PU-XE19, PU-XE74, and KUVP-72324) show a typical decrease in growth rate, indicating the gradual ontogenetic change into sexual maturity. This ontogenetic trend is very well known from dorsal fin spines of Recent neoselachians (Guallart-Furió 1998; Ramos 2007; Irvine et al. 2006a, b). According to the record of complete articulated xenacanths (Schwind 1991; Schneider and Zajíc 1994; Heidtke 1999, 2007; Heidtke and Schwind 2004; Heidtke et al. 2004), there are no significant differences in the relative sizes of the spines between males and females; consequently the two "adult" groups of isolated spines can be correlated with two groups of individuals differing in total length because of sexual size dimorphism (see discussion below).

The denticulation of spines also provides ontogenetic information. As indicated by Soler-Gijón (1999), the denticles were added successively to the developing spines in the proximal direction (Fig. 8). Size and rate of denticle deposition are developmentally linked to the growth rate of the spine proper. Because spine histology just proximal to the denticulate region of HMNS-T1 does not show a second dentine layer, the thirteen denticles of HMNS-T1 can also be attributed to SP1, or the "first" spine. The most proximal denticle is shorter than the preceding denticle. In another study, a decrease in denticle size occurred near a major growth line and was associated with a decreased growth rate (see Soler-Gijón 1999). It is then possible that the most proximal denticle of HMNS-T1 could indicate a change in growth rate. Such timing in the first decrease in the growth rate (between in the twelfth and thirteenth denticle) is similar to a spine of *Orthacanthus meridionalis*, in which the first decrease in denticle size and corresponding major growth line occur at the twelfth denticle (Fig. 8B).

In addition to the similarity in number of denticles deposited per unit of time, we have to point out a more important conclusion after the comparison of SP1 in *O. platypternus*, as indicated by specimen HMNS-T1, and SP1 of *O. meridionalis*: the American species deposited larger denticles and grew faster than the European species from the very early ontogenetic stage on (see Fig. 8 and Soler-Gijón 1999: figs. 22, 23). Consequently, in spite of the typical seasonal variations of the growth rate (e.g., Soler-Gijón 1999: fig. 9A for *O. meridionalis*), the two species differed in the speed of growth and morphogenesis of denticulation. This conclusion supports the idea that the analysis of the denticulation (relative size of denticles and denticle density) of the dorsal spines can be very useful for distinguishing species

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

of *Orthacanthus* and sexually dimorphic forms (juvenile to adults) in each species, after a careful examination of the ontogeny (as reported by the histology and skeletochronology). As shown in Soler-Gijón (1999: fig. 22; compare with Fig. 9B), two well-defined groups of spines have been reported for *O. meridionalis*, differing in the relative sizes and density of denticles. Specimens PU-XE20, PU-XE74, and PU-XE76 of *O. meridionalis* present relatively small denticles from the distal (juvenile spine) to the proximal parts (density: 0.55–0.60 denticles/mm), in clear contrast with PU-XE75, PU-XE22, and PU-XE621 which exhibit a larger general size and bigger denticles all along the spine (density: 0.38–0.41 denticles/mm). These two groups could correspond to males and females (or vice versa), but still are distinct from *O. platypternus*. The denticulated region corresponding to stage SP1 in the largest spine of *O. meridionalis* (PU-XE621) is less than 2 cm long, significantly shorter than in *O. platypternus* HMNS-T1 (2.3 cm). The denticle density is 0.85 denticles/mm (12 denticles) for PU-XE621 but 0.55 denticles/mm for HMNS-T1. Donelan and Johnson (1997) even reported spines of *O. platypternus* with a density of 0.21 denticles/mm (for most proximal denticles) for large spines, far distant from the maximal values reached by *O. meridionalis*. Interestingly, the relationship between width and height of the cross-sections of spines of *O. meridionalis* group specimens together with very different patterns in the denticulation (PU-XE74, PU-XE75, PU-XE76, PU-XE20) and separate others with similar denticulations because of the size differences (Fig. 9B). In conclusion, our results suggest that the analysis of the denticulation can be adequate to distinguish between sexes in *Orthacanthus* species even with a relatively small number of examined specimens.

Body sizes, sexual size dimorphism, and ontogenetic habitat partitioning: The study of the ontogenetic variation of the total animal length in *Orthacanthus platypternus* is greatly constrained by the quality of the fossil record. In contrast to *Lebachacanthus*, *Xenacanthus*, and *Triodus*, known by numerous nearly complete articulated skeletons, *Orthacanthus* is represented mainly by isolated dorsal spines and teeth. Rare articulated juvenile skeletons come from *O. platypternus* (Zidek 1993a, b; Fig. 2A) and *O. bohemicus* (Westphalian D of Bohemia; see Soler-Gijón 2004; Fig. 2B). Semiarticulated partial skeletons or isolated cranial remains of subadult/adult individuals are recorded from *O. platypternus* (Cope 1884; Broili 1904; Hotton 1952), *O. bohemicus* (Fritsch 1889; Heidtke 1998; Soler-Gijón 2000), *O. buxieri* (Lower Permian of French Massif Central; see Heyler and Debriette 1986; Poplin and Heyler 1989) and *O. meridionalis* (Soler-Gijón 1993, 1997b). Despite those limitations, we can infer the complete sizes of juvenile and adult individuals in *O. platypternus* from the isolated dorsal spines and neurocrania after the analysis of the allometric relationships between those dermal and endoskeletal elements and the complete body in different xenacanth taxa.

The smallest spines found in the Craddock Bone Bed (e.g., HMNS-T1) and ontogenetic stage SP1 recorded in the histological structure of larger spines (Figs. 8A, 9A) correspond in dimension (about 60 mm long, 4 mm in maximum width) and development with the dorsal (occipital) spine of a nearly complete late juvenile individual of *O. platypternus*, 345 mm in total length, from the Late Carboniferous of Hamilton (Fig. 2A; Zidek 1993a). There is no evidence of newborns in the Craddock Bone Bed. We expect much smaller spines (less than 2 cm long, less than 2 mm maximum width) with short or no denticulation for neonates or early juveniles less than 20 cm in total length, as suggested by the articulated material of *O. bohemicus* (see Fig. 2B; Soler-Gijón 2004).

Total body length estimation of larger (older) individuals of *O. platypternus* is problematic because of the absence of complete subadult/adult specimens of any *Orthacanthus* species for comparison. Soler-Gijón (1999) was incorrect in giving a total length of 75–90 cm to the largest individual of *O. platypternus* from the Craddock Bone Bed after the application of the ratio 1:5–1:6 (dorsal spine length:total animal length ratio; cf. Zidek 1992) to the largest dorsal spine, 15 cm long. That ratio matches the data of juvenile *O. platypternus* and the *Xenacanthus* species but underestimates the dimensions of subadult/adult individuals of *Triodus*, *Orthacanthus*, and *Lebachacanthus*. Descriptions of numerous articulated xenacanths, mainly from the Lower Permian of Saar-Nahe basin (Germany) reveal the large variation of the "dorsal spine length:total animal length" ratio in xenacanth sharks in correlation with the phylogenetic position of the taxa (see Turner and Burrow 2011: fig. 9) and the morphological features of the spines (i.e., robustness and extent of denticulation; see Soler-Gijón 2004: table 1). The primitive *Lebachacanthus* has a relatively short, robust spine and a ratio spine/animal of 1:13–1:22 (Probst 1986; Soler-Gijón 1997a; Heidtke 1999, 2007; Krätschmer 2004), whereas the derived *Xenacanthus* presents a slender relatively long spine and a ratio spine/animal of 1:4–1:6 (Schwind 1991; Heidtke and Schwind 2004; Krätschmer 2005). *Orthacanthus*, as represented by fragmentary specimens of *O. meridionalis* and *O. buxieri*, exhibits an intermediate ratio spine/animal between *Lebachacanthus* and *Xenacanthus*. The most complete remains of *O. meridionalis* come from the bituminous layer B, above coal seam V in the "Calvo Sotelo" quarry at the Puertollano basin, Spain (Soler-Gijón 1997b). An X-ray examination of one of the bituminous slabs from Puertollano (unpublished material, collected by Alex Ritchie and currently housed in Australian Museum, Sydney) shows the postcranial articulated skeleton of a mature male of *O. meridionalis* including a dorsal spine about 11 cm long and 8 mm in maximum width. The preserved specimen is 90 cm long but lacks the cranial, anal, and caudal parts so that the living animal could be about 150 cm in total length, suggesting a ratio spine/animal of ca. 1:13. Interestingly, the holotype of *O. buxieri* showing a neurocranium of 18 cm in total length and a slender dorsal spine 17 cm long and 13 mm in maximum width (Heyler and Debriette 1986; Poplin and Heyler 1989), represents a mature individual which reached 140–180 cm in total length

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

(as estimated from the dimension of the neurocranium; cf. Zidek 1993a) pointing out a ratio spine/animal of 1:8–1:11, in agreement with the articulated *O. meridionalis*.

Surprisingly, the application of the ratios spine/animal of mature individuals of *O. meridionalis* and *O. buxieri* to the large spines of *O. platypternus* from the Craddock (no more than 15 cm long; e.g., SMU 68801; Figs. 3E, F, 9A) gives total animal length values of less than 2 m, still far lower than the estimates of 2.5 to 3 m based in the sizes of large cranial remains found in other localities of the Arroyo Formation (Zidek 1993a). This result appears to indicate that the stream channels and ponds in the coastal plain were inhabited by relatively small individuals (juveniles to subadults/young adults.)

The detailed sampling by Donelan and Johnson (1997) with a relatively high number of collected spines (all belonging to different individuals) and the distribution of the sizes as indicated by the biometric analyses, strongly suggests that the absence of very small and large spines indicative of newborn/early juveniles and very old individuals, respectively, is not due to taphonomic biases or sampling artifacts but to biological reasons such as absence of very young and mature old individuals because of habitat partitioning (cf. Recent euryhaline sharks; Simpfendorfer et al. 2005; Phillips 2012; for examples with fossil forms, see Fischer et al. 2011 and references therein). Our conclusions are also supported by the recent biometric analyses of isolated teeth *O. platypternus* from the Geraldine bonebed (Nocona Formation, Wichita Group, Sakmarian age) (Johnson 2013). The measured *O. platypternus* teeth from Geraldine range from 0.84 to 5.39 mm in anteromedial-posterolateral (am-pl) dimension, denoting small animals in comparison with the large (very old) animals with teeth up to 14 mm in am-pl dimension described in other localities (Cope 1884; Broili 1904; Hotton 1952; Olson 1989). Ontogenetic habitat partitioning might also explain the absence of large *O. compressus* teeth in the Upper Carboniferous faunas of Nebraska and Pennsylvania (Johnson 1999: 254, figs. 2, 3, tables 1, 2).

A palaeobiological aspect closely related to the ontogenetic habitat partitioning and reproduction concerns the size differences between sexes. The skeletochrological studies in Recent chondrichthyans show that females are usually larger than males, growing faster and/or for a longer time (Guallart-Furió 1998; Cailliet and Goldman 2004; Irvine et al. 2006a, b; Ramos 2007). Despite the fact that some Palaeozoic chondrichthyans show the opposite pattern with smaller females (e.g., the holocephalian *Echinochimaera meltoni*; Grogan and Lund 2004) the fossil record of articulated complete xenacanths indicates that the females attained the largest sizes. Importantly, this pattern in xenacanths is shown by primitive and derived taxa and by large and small species. For example, females of the primitive *Lebachacanthus colosseus* could reach 3 m in total length whereas the males reached 2.5 m in maximum total length; females of smaller *L. pollichiae* attained 1.75 m in total length, in contrast to the males which reached 1.3 m in maximum total length (Heidtke 2007). Females and males belonging to the derived genera *Xenacanthus* and *Triodus* were relatively small sharks, never larger than 2 m in total length (Soler-Gijón 2004), but exhibited a pattern of sexual size dimorphism similar to that in *Lebachacanthus* species (Schwind 1991; Schneider and Zajíc 1994; Heidtke and Schwind 2004; Heidtke et al. 2004). Given the phylogenetic position of *Orthacanthus* (more derived than *Lebachacanthus* and sister-group of *Xenacanthus* + *Triodus*; see Soler-Gijón 1997a, 2000; Turner and Burrow 2011), it is most parsimonious to conclude that the females of *Orthacanthus* were also larger than the males in similar fashion to the rest of xenacanths. Consequently, the clusters of *Orthacanthus* spines with largest sizes, in *O. platypternus* and *O. meridionalis* (Fig. 9) appear to correspond to females.

Habitat of *Orthacanthus platypternus*.—The determination of the life conditions (e.g., osmotic tolerance) of the aquatic vertebrate taxa located in floodplain pond bone beds is always a complex work because (i) the bone beds are usually composed of remains of organisms from very diverse ecological contexts and (ii) the remains, usually disarticulated, are accumulated by very different biotic and abiotic processes. The Early Permian bone beds in southwestern USA were generally formed in fluvio-lacustrine areas on the coastal plain, close to an epicontinental sea (Midland Basin) (Fischer et al. 2014b: fig. 1A). These particular palaeogeographical locations (freshwater/brackish areas in spatial proximity of the sea; Parrish 1978) explain some of the features of the bone beds. For example, predation of *Orthacanthus* on *Xenacanthus*, which may have been restricted to a near-shore marine habitat, could explain the presence of numerous dorsal spines of *Xenacanthus* (but not teeth) associated with teeth and spines of *Orthacanthus* in Archer City Bone Bed 3 and Conner Ranch Bonebed (Johnson 2012; see also Sander 1989 for a general description of these bone beds.)

The xenacanth sharks are considered as euryhaline organisms (Olson 1989; Johnson 1999; Schultze 1985, 1995, 1998, 2009, 2013; Soler-Gijón 1993; Schultze and Soler-Gijón 2004; Soler-Gijón and Moratalla 2001; Hampe et al. 2006; Laurin and Soler-Gijón 2010; Carpenter et al. 2011; but see Fischer et al. 2013, 2014b for a different conclusion). *Orthacanthus platypternus* was diadromous, as indicated by its presence in the fresh-brackish alluvial channel facies of the Clear Fork Group but also in the marine facies of the Arroyo Formation (Olson 1989; Johnson 1999). As discussed below, the palaeobiogeographical and palaeoenvironmental distribution of the different ontogenetic stages of *O. platypternus* indicate that the species was catadromous, a conclusion already suggested by Johnson (1999: 253) based in the low palaeolatitude of the Texas Permian localities.

Though the depositional environment of the Craddock Bone Bed differs from that in previous histology studies of *Orthacanthus*, a cyclical, environmentally influenced growth pattern in the dorsal spine was expected. In a large temporal scale, major growth marks are produced in modern sharks by periodical (seasonal) changes in three main

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

physical and biological factors: water temperature, food resources and breeding behavior (Cailliet and Radtke 1987; Soler-Gijón 1999; Ramos 2007; Tovar-Avila et al. 2008). The presence of major growth marks in immature specimens of *O. platypternus* (and the juveniles of other xenacanth species; see Soler-Gijón 1999) indicates that the growth cyclicity as recorded in the hard tissues was related to water temperature and food availability rather than reproduction. Water temperature as a primary factor affecting many physiological parameters, could directly influence the food consumption according the seasonal metabolic requirements in a similar fashion to that observed in Recent tropical sharks (Luer et al. 1990). On the other hand, seasonal variations in accessibility and abundance of prey according to rainy-dry cycles was probably one of the main factors modulating the growth in *O. platypternus*, as occurs today in fishes from non-marine and marginal marine tropical/subtropical regions (e.g., Lowe-McConnell 1964; Lecomte et al. 1993; Robins et al. 2006). As opportunistic predators, the xenacanths could move between the diverse aquatic environments of the coastal plain, intermittently connected by seasonal floodings, and exploit the high productivity of those freshwater/brackish habitats.

Increasing aridity during the deposition of the Early Permian bone beds is also pointed out by Fischer et al. (2014b) in their isotopic analyses of shark teeth from several localities of Texas and Oklahoma. Interestingly, oxygen and strontium isotope analysis of teeth of the xenacanths *Orthacanthus texensis* (Waurika, southern Oklahoma; latest Sakmarian) and *Barbclabornia luedersensis* (Spring Creek B, northern Texas; Kungurian) indicate that during the time of dental mineralization, the sharks were living in shallow ponds of non-marine waters with significant evaporative enrichment of ^{18}O, and quite close to the nearshore on the coastal plain (see Fischer et al. 2014b: fig. 8).

There is no evidence supporting the idea that *Orthacanthus* and *Barbclabornia* had an "obligate lifestyle in freshwater without euryhaline behavior" as claimed by Fischer et al. (2014b: 721). These authors obtained $^{87}Sr/^{86}Sr$ ratios in the shark teeth more radiogenic than $^{87}Sr/^{86}Sr$ of contemporaneous seawater, correctly concluding non-marine conditions for the pond water visited by the sharks. However, the obtained values do not automatically exclude the possibility of brackish conditions (e.g., oligohaline to mesohaline) in the ponds according to Carpenter et al. (2011), who interpreted the non-marine $^{87}Sr/^{86}Sr$ ratios from xenacanths of the Upper Pennsylvanian Cohn Coal Member, Mattoon Fm., Illinois (USA) as indicative of brackish (estuarine) water. Dipnoans (e.g., *Gnathorhiza*) and aquatic tetrapods (e.g., *Trimerorhachis*), associated with the xenacanths in the bone beds, also could tolerate brackish and even saline waters (Laurin and Soler-Gijón 2010; Schultze 2013) in a typical coastal plain ecosystem, in proximity to the sea and consequently affected by the dynamics of fluvial and marine (tidal) waters (Parrish 1978). Recently, Johnson (2013) reported for first time *Orthacanthus platypternus* and petalodonts (probably *Janassa*), a typical marine component, in the Geraldine Bonebed (Nocona Formation, Wichita Group, Sakmarian age) in association of other xenacanths (*Orthacanthus texensis*, *Xenacanthus* sp.), hybodont sharks, *Helodus*, acanthodians, actinopterygians, dipnoans (*Sagenodus*) and numerous tetrapods including *Trimerorhachis* and *Dimetrodon*. Johnson (2013) concluded that the depositional area of the Geraldine Bonebed was closer to the marine palaeoshore than suggested in previous studies (see Sander 1987).

The climatic conditions with a strong wet-dry seasonality (as indicated by the xenacanth teeth isotopes, palaeosols and palaeoflora) and the inferred small sizes of the depositional bone bed areas ("shallow ponds or backswamp areas generally smaller than one square mile" Fischer et al. 2014b: 721) suggest that the sharks, as euryhaline organisms, could move away from the ponds for reproduction and feeding (see Johnson 2012). This conclusion is also indicated by Zidek et al. (2004) who described the association of *Orthacanthus platypternus* with *O. texensis*, *B. luedersensis* and other chondrichthyans (the holocephalian *Helodus* sp., and diverse hybodont sharks) in fluvio-lacustrine deposits of Northeast Frederick and Lake Frederick (Early Permian, upper Garber Sandstone, Tillman County, southwestern Oklahoma, USA). According to Zidek et al. (2004: 136–138) who cite the works of Simpson (1976, 1979), most of the Permian lakes of the coastal plain, as represented in the deposits of the Garber Sandstone, were intermittent, killing their aquatic inhabitants in dry seasons. The authors concluded (Zidek et al. 2004:146) that the lakes represented by Northeast Frederick and Lake Frederick sites, covering about 160 acres each, were not large enough to sustain a breeding population of large predatory fishes.

Certainly the palaeobiogeographical distribution of *Orthacanthus platypternus* suggests ontogenetic habitat partitioning in this xenacanth. As indicated above, the dorsal spines and teeth of *O. platypternus* recorded in the Craddock and Geraldine bone beds point to relatively small individuals, juveniles (but not newborn) to subadult/young adults, less than 2 m in total length, which probably inhabited shallow waters of small ponds and stream channels of the upper part of a lower coastal plain. Large dermal and cranial remains of larger individuals up to 3 m in total length are known from other Early Permian localities from Texas (Zidek 1993a). Medium size teeth of *O. platypternus* are reported from marine limestone from the Arroyo Formation, representing estuarine-lagoonal near-shore conditions (Olson 1989). Most importantly, the articulated skeleton of a juvenile of *O. platypternus* (Fig. 2A) comes from estuarine facies of the Upper Carboniferous of Hamilton, Kansas (Zidek 1993a; Schultze 1995, 1998; Schultze et al. 1994). In summary, *O. platypternus* occurred in a wide range of environments, from near-shore marine areas (estuarine-lagoonal) to the fluvio-lacustrine systems of the coastal plain. Water bodies in the coastal plain presented a very complex development from very small, shallow ephemeral pools to relatively large lacustrine places as suggested by the pres-

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

ence of the giant *Barbclabornia luedersensis* which could reach 4.5 to 5 m in total length, according the estimations based in cranial remains from Northeast Frederick locality (Zidek et al. 2004).

The distribution of *O. platypternus* also suggests the migratory pattern of this diadromous xenacanth. Large, mature individuals bred in a marine marginal environment. Neonates and early juveniles inhabited estuarine areas before they moved into fresh-brackish habitats of the coastal plain. As a catadromous species, juveniles and subadult to young adults grew and developed in the ponds and channels of the coastal plain during several years before they returned to the sea for mating and spawning. We assume here that *O. platypternus* was an oviparous species as oviparity appears to be the general reproductive strategy in xenacanth sharks (see Fischer et al. 2014a and references therein).

Early juveniles of *O. platypternus* probably grew very fast in the estuarine waters, reaching more than 30 cm (total length) in less than one year, as indicated by the articulated material from Hamilton and the skeletochronological analyses from the isolated dorsal spines from Craddock (e.g., specimens HMNS-T1 and T2). Despite the risk of predation and cannibalism (for evidences in xenacanths see Soler-Gijón 1995; Heidtke 2012), the young *O. platypternus* spent a relatively long time in the marginal marine habitat before they migrated to the very low salinity areas of the coastal plain. With that behavior, the young xenacanths probably minimized the energetic costs of osmoregulation, using more energy on growth, in a fashion similar to that suggested for the neonates and early juveniles of the Recent euryhaline shark *Carcharhinus leucas* in the estuaries of the southwest Florida, USA (Simpfendorfer et al. 2005). The selection of brackish waters (salinities between 7‰ and 17.5‰) by the young *C. leucas* in order to meet optimal osmoregulation is logically connected to the fact that the smaller individuals have the highest surface-area-to-volume ratio and consequently, the highest energetic cost per unit weight for osmoregulating (Simpfendorfer et al. 2005: 83).

Two main factors probably triggered the migration of the juveniles of *O. platypternus* into the coastal plain habitats and far inland areas: protection against predation and food resources. These factors control the distribution of young Recent sharks (e.g., selection of nursery areas; see review of the topic and fossil examples in Fischer et al. 2011) and the migratory pattern of fishes in general (see Tsukamoto et al. 2009 and references therein). Additionally, the distribution of juvenile and subadult-young xenacanths in the coastal plain can be explained by the combination of two circumstances: (i) the low topography and large geographical dimension of that region as indicated by palaeogeographical locations of the Early Permian localities around the Midland Basin (Nelson et al. 2013; Fischer et al. 2014b), and (ii) the particular climatic conditions with marked seasonality in precipitations. Relevant in this respect is the comparison with the life conditions of the modern sawfish *Pristis microdon* in the Kimberley region of Western Australia, which presents an arid to semi-arid monsoonal climate, receiving the rains mainly during the wet season (Thorburn et al. 2007; Phillips 2012). While adults of *P. microdon* live and breed in marginal marine environments, the juveniles penetrate into the Fitzroy River, move very fast through the fluvial system and reach freshwater areas far inland where they find food but few large predators (Thorburn et al. 2007). These recent studies on *P. microdon* also conclude that the juvenile and subadult-young adult (small individuals less than 2.8 m in total length) stay several years (a maximum of four or five) in the freshwater rivers before they return to the marine regions for reproduction and growth (the species appears to reach up to 7 m in total length). The easy access to the Fitzroy River and wide distribution of immature *P. microdon* along the non-marine environments are due to high tides, high run-off and large catchment of the river, and a lowland topography. However, because of extreme climatic conditions, the seasonal fluctuations in the water level of the rivers constrain the developmental time and maximum growth of *P. microdon* in the fluvial system. Relatively small individuals appear to use pools as refuge habitats during the dry season (Martin 2005) but the large mature or nearly mature individuals move back to the sea. *Orthacanthus platypternus* and other xenacanth sharks (e.g., *O. texensis* and *B. luedersensis*; Zidek et al. 2004: 146) which grew very fast and reached several meters in total length, could already present such adaptive behavior migrating from one habitat to another in order to respond to the unstable palaeoenvironmental conditions of a broad, low relief coastal plain under the influence of tropical semi-arid to sub-humid climate with seasonal rainfalls (DiMichele et al. 2006).

Conclusions

Dorsal spines of the xenacanth *Orthacanthus platypternus* from the Permian Craddock Bone Bed preserve the typical histological structure of *Orthacanthus* spines, well known from Carboniferous species, mainly *O. meridionalis* of the Puertollano Basin (Spain) and *Orthacanthus* sp. of the Robinson locality, Kansas (USA). The wall of the spine, highly vascularized, is mainly composed by centrifugally growing dentine, which appears as a succession of dentine layers, usually bounded by growth lines. In several spines of *O. platypternus*, the growth lines are not clearly visible but a distinctive colour-banding shows the cyclical centrifugal deposition of dentine layers and allows the skeletochronological analyses. Dentine layers were probably deposited with an annual periodicity following the cyclical (seasonal) variations of two main environmental factors, the water temperature and food availability.

Despite the diagenetic alteration and fragmentation of the material, the dorsal spines of *Orthacanthus platypternus* provide valuable information about several ontogenetic stages in the sharks. The Craddock Bone Bed assemblages are composed of spines of juveniles (1–2 years old) and

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

small subadult/young adults (at least 3–4 years old) less than 2 m in total length. There is no evidence of newborns and large adults, about 3 m in total length as estimated by large cranial and dental remains reported from other Texas Permian localities. The palaeobiogeographical distribution of *O. platypternus* suggests ontogenetic habitat partitioning. The relatively small individuals represented by the studied spines from the Craddock Bone Bed probably inhabited shallow waters of small ponds and stream channels of the coastal plain. In contrast, large *Orthacanthus* (both *O. platypternus* and *O. texensis*) and *Barbclabornia* appear to correspond to deeper waters of the fluvio-lacustrine and marginal marine areas.

Our skeletochronological study partially confirms the ontogenetic categories (i.e., juveniles and sexually dimorphic adults) suggested by Donelan and Johnson (1997) in order to explain the variation in sizes shown by a biometric analysis of numerous isolated spines. The largest spines appear to belong to female subadult/adults. The cluster of intermediate size spines (cf. Donelan and Johnson 1997) includes the spines of male subadult/adults and relatively large juveniles, which represent ontogenetic stages of larger females. Finally, the smallest spines belong to smaller (young) juveniles, females and males, in agreement with the biometric results.

Comparisons of histology/skeletochronology and denticulation between dorsal spines of the Permian *O. platypternus* and the Late Carboniferous species *O. meridionalis* further suggest that the analysis of the relative sizes of denticles and denticle density can be useful for distinguishing between species of *Orthacanthus* and sexually dimorphic forms (juvenile to adults) in each species.

Orthacanthus platypternus was a euryhaline, diadromous shark with a catadromous life-style. The orientation of the migratory pattern is indicated by comparative analysis of the ontogenetic stages of the recorded specimens of *O. platypternus* and their distribution along the different facies and localities (estuarine facies from Hamilton and terrestrial coastal plain and marine facies from Texas localities). Neonates and small, early juveniles inhabited estuarine-lagoonal areas before they moved to the fresh-brackish aquatic habitats of the coastal plain. The sharks grew during several years in the highly productive fluvio-lacustrine environments of the coastal plain but they returned to the marginal marine areas for reproduction. Developmental time, maximum growth and migratory patterns of *O. platypternus* and other xenacanths of the fluvio-lacustrine systems of the low relief coastal plain around the Midland Basin, were regulated by the seasonal rainfalls of the semi-arid to sub-humid tropical climate that occurred on the western tropical Pangaea during late Early Permian.

The skeletochronological information from spines, more complete than that from teeth, can be used in future isotopic analyses of good preserved exemplars to describe in detail the migrations of the sharks along the non-marine/marginal marine environments.

Acknowledgments

We thank Bill and Judy Whitley, and Robert Bakker (all HMNS) for permission and encouragement to study and sample material from the HMNS Craddock Bone Bed collections. Thanks to Robert Bakker (HMNS) for sharing his expertise of the Permian red beds and Troy Bell, Chris Flis, Myria Perez, and David Temple (all HMNS) for their careful collection of xenacanthid dorsal spines. Gary D. Johnson (SMU) shared experience, research and resources useful to the study of sharks from the Craddock Bone Bed, as well as helpful suggestions to improve the manuscript. We thank him and SMU for the loan of specimens (SMU 68799–68801). Robert Jones (Australian Museum, Sydney, Australia) and Susan Turner (Queensland Museum, Brisbane, Australia) generously provided X-ray pictures of the unpublished articulated specimen of *Orthacanthus meridionalis* from Puertollano, Spain (Australian Museum collection). John Maisey (American Museum of Natural History, New York, USA) shared valuable literature and expertise, and many thought-provoking discussions about shark histology. Thanks to John Price (Midwestern State University, Wichita Falls, Texas, USA) for the use of Midwestern State University thin-sectioning equipment, Elke Siebert (Museum für Naturkunde, Berlin, Germany) for her support and creation of spine morphology diagrams, and William Cook and Michael Shipley (Midwestern State University, Wichita Falls, Texas, USA) for their constructive suggestions for improvement of the manuscript. Finally, we would like to thank John Maisey, Susan Turner, and editors of APP for their careful review of the manuscript.

References

Agassiz, L. 1843. *Recherches sur les Poissons fossiles. Volume 3. Contenant l'Histoire de l'Ordre des Placoïdes*. 422 pp. Petitpierre, Neuchâtel.

Barnett, L.A.K., Ebert, D.A., and Cailliet, G.M. 2009. Assessment of the dorsal fin spine for chimaeroid (Holocephali: Chimaeriformes) age estimation. *Journal of Fish Biology* 75: 1258–1270.

Beck, K. 2014. *Comparative Bone Histology Among Permian Vertebrates, Arroyo Formation, North Texas*. 104 pp. M.Sc. thesis, Midwestern State University, Wichita Falls, Texas.

Berg, L.S. 1940. Classification of fishes, both recent and fossil [in Russian]. *Trudy Zoologičeskogo Instituta Akademii Nauk* 5: 85–517.

Botella, H., Martinez-Perez, C., and Soler-Gijón, R. 2012. *Machaeracanthus goujeti* n. sp. (Acanthodii) from the Lower Devonian of Spain and northwest France, with special reference to spine histology. *Geodiversitas* 34: 761–783.

Broili, F. 1904. Ueber *Diacranodus texensis* Cope (= *Didymodus*? *compressus* Cope). *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 19: 467–484.

Cailliet, G.M. and Goldman, K.J. 2004. Age determination and validation in chondrichthyan fishes. *In*: J.C. Carrier, J.A. Musick, and M.R. Heithaus (eds.), *Biology of Sharks and Their Relatives*, 399–447. CRC Press LLC, Boca Raton.

Cailliet, G.M. and Radtke, R.L. 1987. A progress report on the electron microprobe analysis technique for age determination and verification in elasmobranchs. *In*: R.C. Summerfelt and G.E. Hall (eds.), *The Age and Growth of Fish*, 359–369. Iowa State University Press, Ames.

Carpenter, D., Falcon-Lang, H.J., Benton, M.J., and Nelson, W.J. 2011. Fishes and tetrapods in the Upper Pennsylvanian (Kasimovian) Cohn Coal Member of the Mattoon Formation of Illinois, United States: Systematics, paleoecology, and paleoenvironmnents. *Palaios* 26: 639–657.

Case, E.C. 1935. Description of a collection of associated skeletons of *Trimerorhachis*. *Contributions from the Museum of Paleontology, University of Michigan, Ann Arbor, Michigan* 4: 227–274.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Chaney, D.S. and DiMichele, W.A. 2007. Paleobotany of the classic redbeds (Clear Fork Group—Early Permian) of north central Texas. *In*: T.E. Wong (ed.), *Proceedings of the XVth International Congress of Carboniferous and Permian Stratigraphy, Utrecht, The Netherlands*, 357–366. Royal Netherlands Academy of Arts and Sciences, Amsterdam.

Clarke, M.W., Connolly, P.L., and Bracken, J.J. 2002. Age estimation of the exploited deepwater shark *Centrophorus squamosus* from the continental slopes of the Rockall Trough and Porcupine Bank. *Journal of Fish Biology* 60: 501–514.

Cope, E.D. 1878. Descriptions of extinct Batrachia and Reptilia from the Permian Formation of Texas. *Proceedings of the American Philosophical Society* 17: 505–530.

Cope, E.D. 1884. On the structure of the skull in the elasmobranch genus *Didymodus*. *Proceedings of the American Philosophical Society* 21: 572–590.

Currey, J.D. 2006. *Bones: Structure and Mechanics. Ed. 2.* 436 pp. Princeton University Press, Princeton.

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

DiMichele, W.A., Tabor, N.J., Chaney, D.S., and Nelson, W.J. 2006. From wetlands to wet spots: Environmental tracking and the fate of Carboniferous elements in Early Permian tropical floras. *In*: S.E. Grab and W.A. DiMichele (eds.), Wetlands Through Time. *Geological Society of America, Special Paper* 399: 223–248.

Donelan, C. and Johnson, G.D. 1997. *Orthacanthus platypternus* (Chondrichthyes: Xenacanthida) occipital spines from the Lower Permian Craddock Bonebed, Baylor County, Texas. *Journal of Vertebrate Paleontology* 17 (Supplement): 43A.

Evans, H.M. 1924. The defensive spine of fishes, living and fossil, and the glandular structure in connection therewith, with observations on the nature of fish venoms. *Philosophical Transactions of the Royal Society London, Series B* 212: 1–33.

Fischer, J., Licht, M., Kriwet, J., Schneider, J.W., Buchwitz, M., and Bartsch, P. 2014a. Egg capsule morphology provides new information about the interrelationships of chondrichthyan fishes. *Journal of Systematic Palaeontology* 12: 389–399.

Fischer, J., Schneider, J.W., Hodnett, J.-P.M., Elliott, D.K., Johnson, G.D., Voigt, S., Joachimski, M.M., Tichomirowa, M., and Götze, J. 2014b. Stable and radiogenic isotope analyses on shark teeth from the Early to the Middle Permian (Sakmarian–Roadian) of the southwestern USA. *Historical Biology* 26: 710–727.

Fischer, J., Schneider, J.W., Voigt, S., Joachimski, M., Tichomirowa, M., Tütken, T., Götze, J., and Berner, U. 2013. Oxygen and strontium isotopes from fossil shark teeth: Environmental and ecological implications for Late Palaeozoic European basins. *Chemical Geology* 342: 44–62.

Fischer, J., Voigt, S., Schneider, J.W., Buchwitz, M., and Voigt, S. 2011. A selachian freshwater fauna from the Triassic of Kyrgyzstan and its implications for Mesozoic shark nurseries. *Journal of Vertebrate Paleontology* 31: 937–953.

Fritsch, A. 1889. *Fauna der Gaskohle und der Kalksteine der Permformation Böhmens*, v. 2. 114 pp. F. Rivnác, Praha.

Glikman, L.S. 1964. Class Chondrichthyes, subclass Elasmobranchii [in Russian]. *In*: Û.A. Orlov (ed.), *Osnovy Paleontologii, 11. Agnathes, Pisces*, 195–236. Nauka, Moskva.

Grogan, E.D. and Lund, R. 2004. The origin and relationships of Early Chondrichthyes. *In*: J.C. Carrier, J.A. Musick, and M.R. Heithaus (eds.), *Biology of Sharks and Their Relatives*, 3–31. CRC Press LLC, Boca Raton.

Guallart-Furió, J. 1998. *Contribución al conocimiento de la biología y la taxonomía del tiburón batial* Centrophorus granulosus *(Bloch y Schneider, 1801) (Elasmobranchii, Squalidae) en el Mar Balear (Mediterráneo Occidental)*. 275 pp. Tesis Doctoral, Universitat de València, Valencia.

Hampe, O. 1997. Zur funktionellen Deutung des Dorsalstachels und der Placoidschuppen der Xenacanthida (Chondrichthyes: Elasmobranchii; Unterperm). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 206: 29–51.

Hampe, O. 2003. Revision of the Xenacanthidae (Chondrichthyes: Elasmobranchii) from the Carboniferous of the British Isles. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 93: 191–237.

Hampe, O., Johnson, G.D., and Turner, S. 2006. *Dicentrodus* (Chondrichthyes: Xenacanthida) from the Early Carboniferous (Visean: upper St Louis Formation) of Iowa, USA. *Geological Magazine* 143: 545–549.

Heidtke, U.-H.J. 1982. Der Xenacanthide *Orthacanthus senckenbergianus* aus dem pfälzischen Rotliegenden (Unter-Perm). *Mitteilungen der Pollichia* 70: 65–86.

Heidtke, U.-H.J. 1998. Revision der Gattung *Orthacanthus* Agassiz 1843 (Chondrichthyes: Xenacanthida). *Paläontologische Zeitschrift* 72: 135–147.

Heidtke, U.-H.J. 1999. *Orthacanthus* (*Lebachacanthus*) *senckenbergianus* Fritsch 1889 (Xenacanthida: Chondrichthyes): Revision, Organisation und Phylogenie. *Freiberger Forschungsheft* C481: 63–106.

Heidtke, U.-H.J. 2003. Neue Rekonstruktionen xenacanthider Haie aus dem Permokarbon des Saar-Nahe-Beckens (SW-Deutschland). *Mitteilungen der Pollichia* 90: 19–28.

Heidtke, U.-H.J. 2007. Neue Erkenntnisse über *Lebachacanthus* (Chondrichthyes: Xenacanthida) aus dem Unteren Rotliegend des südwestdeutschen Saar-Nahe-Beckens. *Mitteilungen der Pollichia* 93: 7–14.

Heidtke, U.-H.J. 2012. Weitere Erkenntnisse über *Lebachacanthus colosseus* (Elasmobranchii: Xenacanthida) aus der mittleren Meisenheim-Formation (Autunium, Unterperm) von Niederkirchen (Pfalz). *Mitteilungen der Pollichia* 96: 1–4.

Heidtke, U.-H.J. and Schwind, C. 2004. Über die Organisation des Skelettes der Gattung *Xenacanthus* (Elasmobranchii: Xenacanthida) aus dem Unterperm des südwestdeutschen Saar-Nahe-Beckens. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 231: 85–117.

Heidtke, U.-H.J., Schwind, C., and Krätschmer, K. 2004. Über die Organisation des Skelettes und die verwandschaftlichen Beziehungen der Gattung *Triodus* Jordan 1849 (Elasmobranchii: Xenacanthida). *Mainzer geowissenschaftliche Mitteilungen* 32: 9–54.

Heyler, D. and Debriette, P. 1986. Sur les Xénacanthiformes (Poissons, élasmobranches), à la lumière de découvetes récentes dans le Permo-Carbonifère de France. *Actes du lll^e Congrès National des Sociétés Savantes, Section des Sciences* 1: 89–109.

Hotton, N. III 1952. Jaws and teeth of American xenacanth sharks. *Journal of Paleontology* 26: 489–500.

Huxley, T.H. 1880. On the application of the laws of evolution to the arragement of the Vertebrata and more particularly of the Mammalia. *Proceedings of the Scientific Meetings of the Zoological Society of London* 1880: 649–652.

Irvine, S.B., Stevens, J.D., and Laurenson, L.J.B. 2006a. Comparing external and internal dorsal-spine bands to interpret the age and growth of the giant lantern shark, *Etmopterus baxteri* (Squaliformes: Etmopteridae). *Environmental Biology of Fishes* 77: 253–264.

Irvine, S.B., Stevens, J.D., and Laurenson, L.J.B. 2006b. Surface bands on deepwater squalid dorsal-fin spines: an alternative method for ageing *Centroselachus crepidater*. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 617–627.

Johnson, G.D. 1999. Dentitions of late Paleozoic *Orthacanthus* species and new species of ?*Xenacanthus* (Chondrichthyes: Xenacanthiformes) from North America. *Acta Geologica Polonica* 49: 215–266.

Johnson, G.D. 2012. Possible origin of the xenacanth sharks *Orthacanthus texensis* and *Orthacanthus platypternus* in the Lower Permian of Texas, USA. *Historical Biology* 24: 369–379.

Johnson, G.D. 2013. Xenacanth sharks and other vertebrates from the Geraldine Bonebed, Lower Permian of Texas. *New Mexico Museum of Natural History and Science, Bulletin* 60: 161–167.

Krätschmer, K. 2004. Überblick über die wichtigsten vertebratenführenden Fossilhorizonten im Rotliegend des südwestdeutschen Saar-Nahe-Beckens. Teil 1: Odernheim Schichten, Jeckenbach Schichten. *Geowissenschaftliche Beiträge zum Saarpfälzischen Rotliegenden* 2: 53–86.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Krätschmer, K. 2005. Überblick über die wichtigsten vertebratenführenden Fossilhorizonten im Rotliegend des südwestdeutschen Saar-Nahe-Beckens. Teil 2. *Geowissenschaftliche Beiträge zum Saarpfälzischen Rotliegenden* 3: 1–28.

Lamm, E.T. 2013. Preparation and sectioning of specimens. *In*: K. Padian and E.T. Lamm (eds.), *Bone Histology of Fossil Tetrapods, Advancing Methods, Analysis, and Interpretations*, 55–160. University of California Press, Berkeley.

Laurin, M. and Soler-Gijón, R. 2010. Osmotic tolerance and habitat of early stegocephalians: indirect evidence from parsimony, taphonomy, palaeobiogeography, physiology and morphology. *In*: M. Vercoli, G. Clément, and B. Meyer-Berthaud (eds.), The Terrestrialization Process: Modeling Complex Interactions at the Biosphere-Geosphere Interface. *Geological Society, London, Special Publication* 339: 151–179.

Lecomte, F., Boujard, T., Meunier, F.J., Renno, J.-F., and Rojas-Beltran, R. 1993. The growth of *Myleus rhomboidalis* (Cuvier, 1817) (Characiforme, Serrasalmidae) in two rivers of French Guiana. *Revue d'Ecologie (Terre Vie)* 48: 421–435.

Lowe-McConnell, R.H. 1964. The fishes of the Rupununi savanna district of British Guiana, South America. Part 1. Ecological groupings of fish species and effects of the seasonal cycle on the fish. *Journal of the Linnean Society, London* 45: 103–144.

Luer, C.A., Blum, P.C., and Gilbert, P.W. 1990. Rate of tooth replacement in the nurse shark, *Ginglymostoma cirratum*. *Copeia* 1990: 182–191.

Maisey, J.G. 1978. Growth and form of finspines in hybodont sharks. *Palaeontology* 21: 657–666.

Maisey, J.G. 1979. Finspine morphogenesis in squalid and heterodontid sharks. *Zoological Journal of the Linnean Society* 66: 161–183.

Maisey, J.G. 2009. The spine-brush complex in symmoriiform sharks (Chondrichthyes; Symmoriiformes), with comments on dorsal fin modularity. *Journal of Vertebrate Paleontology* 29:14–24.

Martin, R.A. 2005. Conservation of freshwater and euryhaline elasmobranchs: a review. *Journal of the Marine Biological Association of the United Kingdom* 85: 1049–1073.

Murry, P.A. and Johnson, G.D. 1987. Clear Fork vertebrates and environments from the Lower Permian of North-Central Texas. *The Texas Journal of Science* 39: 253–266.

Nelson, W.J., Hook, R.W., and Chaney, D.S. 2013. Lithostratigraphy of the Lower Permian (Leonardian) Clear Fork Formation of North-Central Texas. *New Mexico Museum of Natural History and Science Bulletin* 60: 286–311.

Olson, E.C. 1952. The evolution of a Permian vertebrate chronofauna. *Evolution* 6: 181–196.

Olson, E.C. 1977. Permian lake faunas: a study in community evolution. *Journal of the Paleontological Society of India* 20: 146–163.

Olson, E.C. 1989. The Arroyo Formation (Leonardian: Lower Permian and its vertebrate fossils. *Texas Memorial Museum Bulletin* 35: 1–25.

Parrish, W.C. 1978. Paleoenvironmental analysis of a Lower Permian bonebed and adjacent sediments, Wichita County, Texas. *Palaeogeography, Palaeoclimatology, Palaeoecology* 24: 209–237.

Phillips, N. 2012. *Conservation genetics of* Pristis *sawfishes in Australian waters*. 246 pp. Ph.D. Dissertation, Murdoch University, Perth, Western Australia.

Poplin, C. and Heyler, D. 1989. Èvolution et phylogénie des Xenacanthiformes (= Pleuracanthiformes) (Pisces, Chondrichthyes). *Annales de Paléontologie (Vertébrés-Invertébrés)* 75: 187–222.

Probst, E. 1986. *Deutschland in der Urzeit. Von der Entstehung des Lebens bis zum Ende der Eiszeit*. 479 pp. Orbis Verlag, München.

Ramos, R.O. 2007. *Age and growth estimates for the Port Jackson shark,* Heterodontus portusjacksoni *(Mayer, 1793) from New South Wales, Australia*. 222 pp. Ph.D. Dissertation, University of Newcastle, Newcastle.

Robins, J., Mayer, D., Staunton-Smith, J., Halliday, I., Sawynok, B., and Sellin, M. 2006. Variable growth rates of the tropical estuarine fish barramundi *Lates calcarifer* (Bloch) under different freshwater flow conditions. *Journal of Fish Biology* 69: 379–391.

Romer, A.S. 1957. The appendicular skeleton of the Permian embolomerous amphibian *Archeria*. *Contributions of the Museum of Paleontology, University of Michigan, Ann Arbor, Michigan* 13: 103–159.

Sander, P.M. 1987. Taphonomy of the Geraldine Bonebed in Archer County, Texas. *Palaeogeography, Palaeoclimatology, Palaeoecology* 61: 221–236.

Sander, P.M. 1989. Early Permian depositional environments and pond bonebeds in central Archer County, Texas. *Palaeogeography, Palaeoclimatology, Palaeoecology* 69: 1–21.

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 Forschungsheft* C452: 101–151.

Schultze, H.-P. 1985. Marine to onshore vertebrates in the Lower Permian of Kansas and their paleoenvironmental implications. *University of Kansas Paleontological Contributions, Paper* 113: 1–18.

Schultze, H.-P. 1995. Terrestrial biota in coastal marine deposits: Fossillagerstätten in the Pennsylvanian of Kansas, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 119: 255–273.

Schultze, H.-P. 1998. The Fossil Record of the Intertidal Zone. *In*: M.H. Horn, K.L.M. Martin, and M.A. Chotkowski (eds.), *Intertidal Fishes. Life in Two Worlds*, 373–392. Academic Press, San Diego.

Schultze, H.-P. 2009. Interpretation of marine and freshwater environments in Permo-Carboniferous deposits. *Palaeogeography, Palaeoclimatology, Palaeoecology* 281: 126–136.

Schultze, H.-P. 2013. The palaeoenvironments at the transition from piscine to tetrapod sarcopterygians. *New Mexico Museum of Natural History and Science Bulletin* 60: 373–397.

Schultze, H.-P. and Soler-Gijón, R. 2004. A xenacanth clasper from the ?uppermost Carboniferous–Lower Permian of Buxières-les-Mines (Massif Central, France) and the palaeoecology of the European Permo-Carboniferous basins. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 232: 325–363.

Schultze, H.-P., Maples, C.G., and Cunningham, C.R. 1994. The Hamilton Konservat-Lagerstätte: Stephanian terrestrial biota in a marginal-marine setting. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 84: 443–451.

Schwind, C. 1991. *Zur Organisation und zur Phylogenie der beiden Gattungen* Triodus *and* Xenacanthus. 201 pp. Unpublished Ph.D. Dissertation, Mainz University, Mainz.

Simpfendorfer, C.A., Freitas, G.G., Wiley, T.R., and Heupel, M.R. 2005. Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a southwest Florida estuary. *Estuaries* 28: 78–85.

Simpson, L.C. 1976. *Paleontology of the Garber Formation (Lower Permian), Tillman County, Oklahoma*. 216 pp. M.Sc. Thesis, University of Oklahoma, Norman.

Simpson, L.C. 1979. Upper Gearyan and lower Leonardian terrestrial vertebrate faunas of Oklahoma. *Oklahoma Geology Notes* 39: 3–21.

Soler-Gijón, R. 1993. *Estudio de los Vertebrados fósiles del Carbonífero superior de Puertollano, Ciudad Real*. 293 pp. Ph.D. Thesis, University of Complutense, Madrid.

Soler-Gijón, R. 1995. Evidence of predator-prey relationship in xenacanth sharks of the Upper Carboniferous (Stephanian C) from Puertollano, Spain. *In*: H. Lelievre, S. Wenz, A. Blieck, and R. Cloutier (eds.), Premiers vertébrés et vertébrés inférieurs. *Geobios, Mémoire Spécial* 19: 151–156.

Soler-Gijón, R. 1997a. New discoveries of xenacanth sharks from the Late Carboniferous of Spain (Puertollano Basin) and Early Permian of Germany (Saar-Nahe Basin): implications for the phylogeny of xenacanthiform and anacanthous sharks. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 205: 1–31.

Soler-Gijón, R. 1997b. *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.

Soler-Gijón, R. 1999. Occipital Spine of *Orthacanthus* (Xenacanthidae, Elasmobranchii): Structure and Growth. *Journal of Morphology* 242: 1–45.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Soler-Gijón, R. 2000. Phylogenetic relationships of Lebachacanthidae Soler-Gijón 1997 (Xenacanthiformes; Elasmobranchii). *Paläontologische Zeitschrift* 74: 363–377.

Soler-Gijón, R. 2004. Development and growth in xenacanth sharks: new data from Upper Carboniferous of Bohemia. *In*: G. Arratia, M.V.H. Wilson, and R. Cloutier (eds.), *Recent Advances in the Origin and Early Radiation of Vertebrates*, 533–562. Verlag Dr. Friedrich Pfeil, Munchen.

Soler-Gijón, R. and Moratalla, J.J. 2001. Fish and tetrapod trace fossils from the Upper Carboniferous of Puertollano, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 171: 1–28.

Soler-Gijón, R. and Siebert, E. 2001. Zeitmesser der Entwicklung. Skelettechronologische Untersuchungen an fossilen Haien. *Theatrum naturae. Paläontologie* 1: 32–34.

Stamberg, S. 2001. Fin spine of a ctenacanthoid shark (Elasmobranchii, Ctenacanthoidea) from the Upper Stephanian of the Krkonose Piedmont Basin (Bohemia). *Bulletin of the Czech Geological Survey* 76: 141–148.

Sternberg, C.H. 1903. The Permian life of Texas. *Transactions of the Kansas Academy of Science* 18: 94–98.

Tabor, N.J. and Montañez, I.P. 2004. Morphology and distribution of fossil soils in the Permo-Pennsylvanian Wichita and Bowie Groups, North Central Texas, USA: implications for western equatorial Pangean palaeoclimate during icehouse-greenhouse transition. *Sedimentology* 51: 851–884.

Thorburn, D.C., Morgan, D.L., Rowland, A.J., and Gill, H.S. 2007. Freshwater sawfish *Pristis microdon* Latham, 1794 (Chondrichthyes: Pristidae) in the Kimberley region of Western Australia. *Zootaxa* 1471: 27–41.

Tovar-Avila, J., Izzo, C., Walker, T.I., Braccini, J.M., and Day, R.W. 2008. Dorsal-fin spine growth of *Heterodontus portusjacksoni*: a general model that applies to dorsal-fin spines of chondrichthyans? *Canadian Journal of Fisheries and Aquatic Sciences* 65: 74–82.

Tsukamoto, K., Miller, M.J., Kotake, A., Aoyama, J., and Uchida, K. 2009. The origin of fish migration: the random escapement hypothesis. *American Fisheries Society Symposium* 69: 45–61.

Turner, S. and Burrow, C.J. 2011. A Lower Carboniferous xenacanthiform shark from Australia. *Journal of Vertebrate Paleontology* 31: 241–257.

Turner-Walker, G. 2008. The chemical and microbial degradation of bones and teeth. *In*: R. Pinhasi and S. Mays (eds.), *Advances in Human Palaeopathology*, 3–29. The Atrium, Southern Gate, Chichester.

White, C.A. 1889. On the Permian formation of Texas. *American Naturalist* 23: 109–128.

Williston, S.W. 1909. The faunal relations of the early vertebrates. *Journal of Geology* 17: 389–402.

Williston, S.W. 1911. Restoration of *Seymouria baylorensis* broili, an American cotylosaur. *Journal of Geology* 19: 232–237.

Zidek, J. 1992. Late Pennsylvanian Chondrichthyes, Acanthodii and deep-bodied Actinopterygii from the Kinney Quarry, Manzanita Mountains, New Mexico. *New Mexico Bureau of Mines & Mineral Resources Bulletin* 138: 145–182.

Zidek, J. 1993a. Juvenile *Orthacanthus platypternus* (Cope 1883) (Elasmobranchii: Xenacanthiformes) from the Upper Carboniferous near Hamilton, Kansas, U.S.A. *In*: U.-H.J. Heidtke (ed.), New Research on Permo-Carboniferous faunas. *Pollichia-Buch* 29: 53–65.

Zidek, J. 1993b. Xenacanth genera: How many and how to tell them apart? *In*: U.-H.J. Heidtke (ed.), New Research on Permo-Carboniferous faunas. *Pollichia-Buch* 29: 23–35.

Zidek, J., Johnson, G.D., May, W., and Claborn, A. 2004. New specimens of xenacanth and hybodont sharks (Elasmobranchii: Xenacanthida and Hybodontoidea) from the Lower Permian of Southwestern Oklahoma. *Oklahoma Geology Notes* 63 (4): 136–147.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use