

Vascular structure of the earliest shark teeth

CARLOS MARTÍNEZ-PÉREZ^{1, 2}, ALBA MARTÍN-LAZARO¹, HUMBERTO G. FERRÓN¹, MARTINA KIRSTEIN³, PHILIP C.J. DONOGHUE² and HÉCTOR BOTELLA¹

¹ Cavanilles Institute of Biodiversity and Evolutionary Biology, C/University of Valencia, Valencia, Spain.

E-mails: Carlos.Martinez-Perez@uv.es, alba.classe@gmail.com, Humberto.Ferron@uv.es,

Hector.Botella@uv.es

² School of Earth Sciences, University of Bristol, Life Sciences Building, 24 Tyndall Avenue, Bristol, BS8 1TQ, United Kingdom. E-mail: Phil.Donoghue@bristol.ac.uk

³ Department of Cellular Biology, Functional Biology and Physical Anthropology, and Interdisciplinary Research Structure for Biotechnology and Biomedicine-BIOTECMED, University of Valencia. C/Dr. Moliner, E-46100 Burjassot (Valencia), Spain. E-mail: Martina.Kirstein@uv.es

ABSTRACT:

Martínez-Pérez, C., Martín-Lazaro, A., Ferrón, H.G., Kirstein, M., Donoghue, P.C.J. and Botella, H. 2018. Vascular structure of the earliest shark teeth. *Acta Geologica Polonica*, **68** (3), 457–465. Warszawa.

Here we use synchrotron tomography to characterise dental vasculature in the oldest known tooth-bearing sharks, *Leonodus carlsi* Mader, 1986 and *Celtiberina maderi* Wang, 1993. Three dimensional reconstruction of the vascular system and microstructure of both taxa revealed a complex and dense network of canals, including horizontal, ascending and secondary bifurcated canals, as well as histological features consistent with an osteodont histotype. However, *L. carlsi* and *C. maderi* also exhibit significant morphological differences, showing *Leonodus* a typical diplodont tooth morphology with a linguo-labially elongated base, that contrast with *Celtiberina*'s teeth that show a single conical cusp curved lingually with a weak developed flat base mesio-distally extended, perhaps reflecting distant relationship. These data are compatible with a pre-Devonian diversification of the two main tooth types traditionally recognised in Palaeozoic sharks (i.e., “cladodont” vs “diplodont”). Finally, our data demonstrate that existing dental classification schemes based on styles of vascularisation are over-simplified, especially when Palaeozoic taxa are considered.

Key words: *Leonodus*; *Celtiberina*; Early chondrichthyans; Lower Devonian; Synchrotron tomography; Vascular system.

INTRODUCTION

Tooth replacement is a continuous dynamic process that occurs during the lifetime of a shark (with few exceptions, e.g., the Middle Devonian shark *Pucapampela Janvier* and Maisey, 2010). Teeth develop internally, as tooth buds produced at the dental lamina, in the lingual part of each tooth family, erupt into the mouth, and migrate, in a ‘conveyor belt’-like mechanism, towards the labial part (jaw margin) until occupying a functional position (Williams 1992). Teeth are functional for a period of time before being shed (or sometimes retained) and replaced by

the next tooth in the same family. This process of continuous production, and the fact that teeth are composed of highly resistant biogenic apatite, makes them the most abundant elements in the chondrichthyan fossil record. This bias is further accentuated by the fact that the chondrichthyan endoskeleton is cartilaginous and preserved only under exceptional circumstances. Consequently, the majority of extinct chondrichthyans (especially Palaeozoic taxa) are described on the basis of isolated teeth (see for example monographs of Cappetta 1987, 2012; Ginter *et al.* 2010 and references therein), and only few genera are known from relatively complete skeletons.

Fossil shark teeth are unique because they do not only preserve insight into feeding kinematics and ecology, but also a strong phylogenetic signal in form of useful diagnostic features for taxonomy and systematics (Schnetzer *et al.* 2016). However, descriptions of tooth-based fossil taxa have traditionally been established on the basis of external morphology, overlooking internal characters such as enameloid microstructure, shape of odontocyte lacunae and canaliculi, as well as the architecture of the vascularisation system, despite the fact that these features have been demonstrated to be effective in resolving taxonomic and phylogenetic problems (see e.g., Gillis and Donoghue 2007; Botella *et al.* 2009a; Cappetta 2012 for examples of studies on enameloid microstructure in Palaeozoic sharks).

Chondrichthyan teeth are composed of two principal, highly mineralised, tissue types, *viz.*, a core of dentine comprised of osteodentine or orthodentine, and an enameloid cap. Depending on the presence and location of the two types of dentine, and the presence or absence of a pulp cavity, shark teeth have traditionally been classified into two different histotypes: osteodonts or orthodonts (see Moyer *et al.* 2015 and references herein). In the orthodont histotype, the pulp cavity remains present in functional teeth, where orthodentine forms the crown under the enameloid cap, and trabecular dentine is present only at the root base. In osteodonts, the pulp cavity of a functional tooth is closed, filled by osteodentine and resembling highly vascularised bone. In this sense, not only the histology but also morphology of the root vasculature have shown potential in the taxonomic discrimination of otherwise similar tooth morphologies. Thus, Casier (1947) identified four structural grades based on the distribution of foraminae and the vascularisation of the root (later updated by Cappetta 2012), representing different evolutionary stages (anaulacorhize, hemiaulacorhize, holaulacorhize and polyaulacorhize) achieved by different groups. However, since these grades of organisation stages were based mainly on Mesozoic and Cenozoic shark taxa, Casier's (1947) subdivision is not suitable for Palaeozoic chondrichthyans. As noted by Ivanov and Nilov (2016), it is clear (despite the dearth of studies) that patterns of dental vasculature in Palaeozoic chondrichthyans were very diverse and show considerable differences to Mesozoic and Cenozoic hybodonts and neoselachian sharks. Until recently, reconstructions of dental vasculature in Palaeozoic sharks were limited to xenacanthids (Hampe 1988, 1993, 1995; Hampe and Heidke 1997) based on the application of traditional destructive techniques (histological

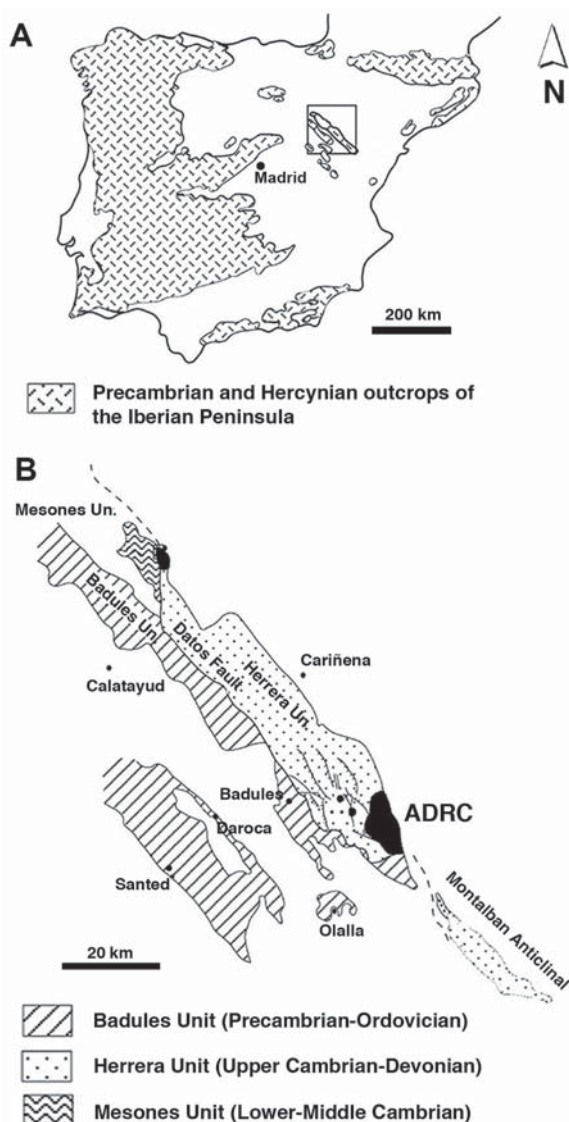
ground sections). However, the application of non-destructive X-ray based tomographic techniques has facilitated a broader taxonomic sampling and better three dimensional characterisation of the variety of dental vasculature exhibited by Palaeozoic sharks, including phoebodontiforms, symmoriiforms, ctenacanthiforms, hybodontiforms and other euselachians (Ivanov and Nilov 2016). Moreover, descriptions of dental vasculature have become incorporated to the description of new taxa (see e.g., Long *et al.* 2015; Ivanov 2016; Ivanov *et al.* 2017).

Within this context, we present a synchrotron-based characterisation of the dental histology and vasculature of the oldest known tooth-bearing sharks, *Leonodus carlsi* Mader, 1986 and *Celtiberina maderi* Wang, 1993 (Mader 1986; Wang 1993; Long 1995; Hampe and Long 1999; Williams 2001; Miller *et al.* 2003; Botella 2006; Botella *et al.* 2009a, b; among others). Synchrotron X-ray tomography has been demonstrated to be effective in the study of dentitions in several groups of early gnathostomes, including placoderms (Rücklin *et al.* 2012; Rücklin and Donoghue 2015), acanthodians (Qu *et al.* 2013), and the earliest bony fishes (Cunningham *et al.* 2012). Here, we apply this technique for the first time to study the earliest chondrichthyan teeth that, because of their antiquity, have the potential to provide insights into the condition from which the dental histology and vasculature of better known Palaeozoic and post-Palaeozoic chondrichthyans first evolved.

MATERIAL AND METHODS

The specimens of *L. carlsi* and *C. maderi* investigated were recovered as isolated elements after the acid digestion (10% formic acid) of limestone samples taken from the Noguerras Formation, lowermost Lockhovian (Lower Devonian) of the Iberian Chain (Spain), at the Poyales-East Locality at the Axial Depression of the Camaras River (Carls 1988; Dojen 2005) (Text-fig. 1; for a detailed geological and faunal succession, see Carls 1988, 1999; Carls and Valenzuela-Ríos 2002; Martínez-Pérez *et al.* 2010; and Dupret *et al.* 2011).

One specimen of *L. carlsi* (MGUV-36.141) and one specimen of *C. maderi* (MGUV-21.315) were characterised using Synchrotron Radiation X-Ray Tomographic Microscopy (SRXTM; Donoghue *et al.* 2006) at the X02DA TOMCAT beamline of the Swiss Light Source, Paul Scherrer Institute, Villigen, Switzerland. Both specimens were scanned using 2× and 4× objectives, with exposure times of 300 ms at



Text-fig. 1. A – Geographical setting of the studied area with indication of the distribution of Precambrian and Palaeozoic rocks in the Iberian Peninsula. B – Enlarged geological map of Palaeozoic rocks in the Iberian chains with the Devonian outcrops in black and indication of the studied area, the Axial Depression of the Camaras River (ADCR) (Carls 1988). Modified from Botella *et al.* (2012)

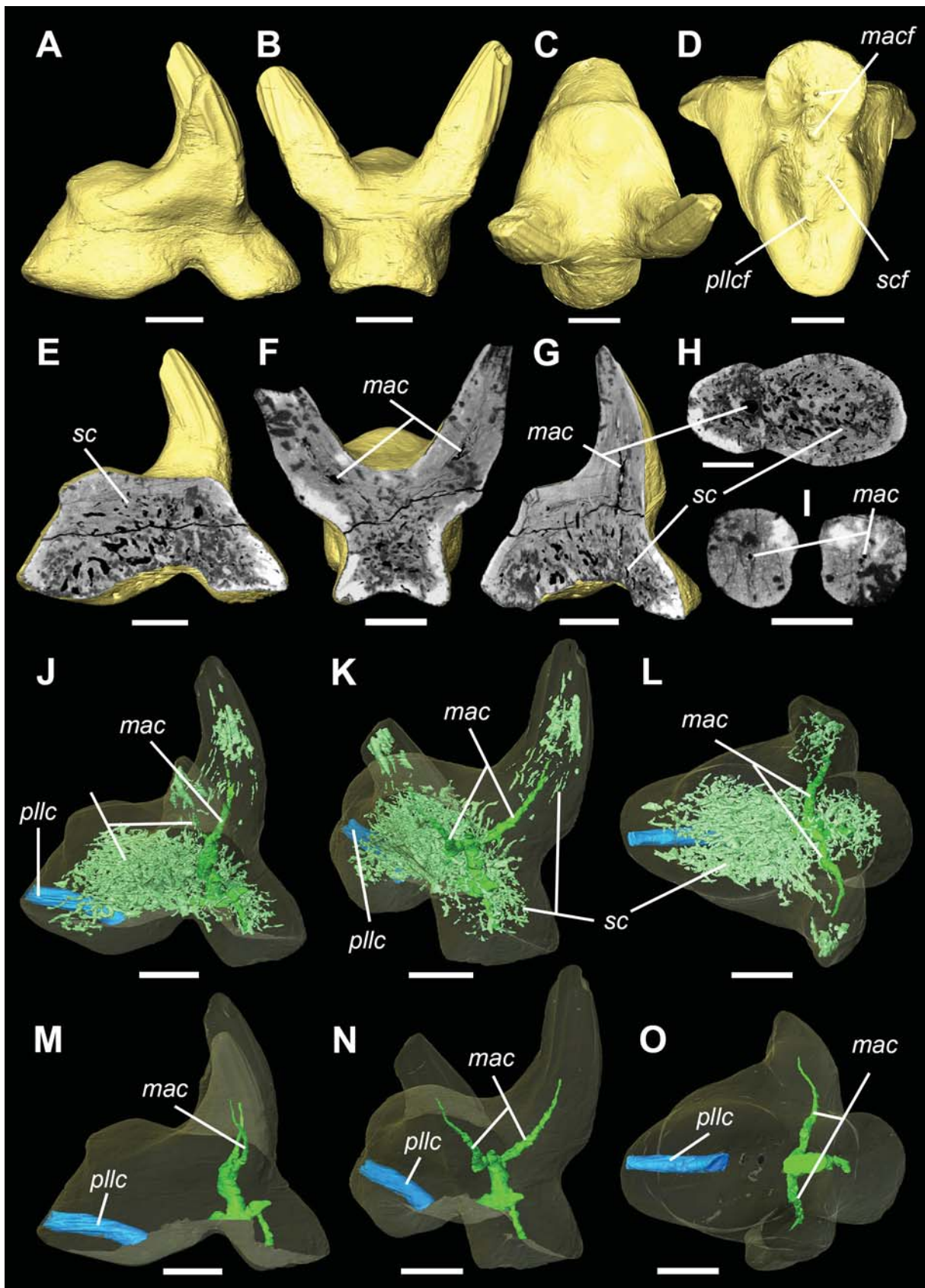
24 and 23 keV respectively, acquiring 1501 projections equiangularly over 180°. These data were post-processed and rearranged into flat- and dark-field-corrected sinograms. Reconstruction was performed on a Linux PC cluster using a highly optimised routine based on the Fourier transform method and a regridding procedure (Marone *et al.* 2010), resulting in volumetric data with voxel dimensions of 3.25 μm (2 \times objective) and 1.625 μm (4 \times objective). The reconstructed files produced were visualised, manipu-

lated and analysed using the computed tomography software package AVIZO Lite v.9 (VSG), allowing us to volumetrically characterise the three dimensional structure and arrangement of the dental vasculature, along with the hard tissue histology. The studied specimens are housed at the Museum of Natural History of the University of Valencia (former Museum of Geology at the University of Valencia – MGUV). The tomographic data are available from the University of Bristol data repository (data.bris) at <https://doi.org/10.5523/bris.1043tuuj66r2ebs2ae59xkys>.

RESULTS

Leonodus carlsi

The teeth of *L. carlsi* have a general diploidont morphology, possessing a characteristic peanut-shaped, linguo-labially elongated base. The cusps are rounded or oval in cross-section, lingually arched, and located on the labial edge of the base (Text-fig. 2A–D). Histologically, tooth cusps are composed of an osteodentine core covered by an undifferentiated enameloid cap that resembles Single Crystallite Enameloid (SCE). The tooth base has traditionally been interpreted to have been composed of trabecular dentine (Mader 1986; Botella *et al.* 2009a). The tomographic data reveal some taphonomic and diagenetic alteration of the internal structure, including recrystallisation of the lingual and labial margins of the base, fracturing, and evidence of endolithic microbial activity. Nevertheless, the general structure of the vascular system is clearly discernible, allowing a detailed description. The trabecular dentine of the base is comprised of a complex network of anastomosing secondary vascular canals (horizontal and ascending) of a similar moderate size that run through the entire tooth base, connected to the exterior by several foraminae at the lingual side of the base (Text-fig. 2D). The diameter of the canals in the network diminishes in size as they extend into the cusp (up to 10 μm diameter; Text-fig. 2J–O). No horizontal canals were observed in the cusps. In the centre of both cusps, a main ascendant vascular canal or pulp canal *sensu* Ivanov and Nilov (2016) is clearly visible (approx. 25 μm diameter), reducing its diameter towards the tip of the cusp (Text-fig. 2G, I–O). The pulp canals of each cusp join at the base of the tooth, and are connected directly to the exterior by an inverted “U”-shape canal (Text-fig. 2M). In addition, a large principal linguo-labial canal crosses the tooth in its lingual third (Text-fig. 2M–O).



Celtiberina maderi

The teeth of *C. maderi* have a single conical cusp curved lingually with a mesio-distally extended flat base (Text-fig. 3A–D). Histologically, teeth of *C. maderi* have been described to have a cap of Single Crystallite Enameloid with poorly discernible rounded crystallites that is readily distinguishable from the underlying dentine core (Botella *et al.* 2009a). Traditional histological studies describe a dentine core composed of osteodentine with numerous small canals (Botella *et al.* 2009a). The tomographic data reveal the same evidence of taphonomic and diagenetic alteration seen in the tooth of *L. carlsi* but, similarly, the vasculature can still be resolved (Text-fig. 3I–P). Indeed, the pattern of vascular canals in *C. maderi* is somehow similar to that seen in *L. carlsi*, with a complex mesh of secondary vascular canals (horizontal and ascending) that run through the entire tooth base, but these canals have a smaller diameter (Text-fig. 3I–L). This dense network extends into the cusp, maintaining approximately the same canal diameter (up to 3–5 µm wide), and running parallels to the main axis of the cusp, with a small number of oblique canals connecting some of the ascendant canals (Text-fig. 3I–K). In the centre of the cusps, a principal ascendant vascular canal (pulp canal) is clearly visible (approx. 40 µm diameter) (Text-fig. 3M–O). This ascendant canal is directly connected to the exterior by an open “U”-shape canal that crosses the base of the tooth linguo-labially (Text-fig. 3N–P). In addition, two large horizontal canals cross the tooth linguo-labially on either side of the base, parallel to the central canal that connects the main ascendant vascular canal with the exterior foramen (Text-fig. 3M–P). The external surface of the tooth base is characterised by small canal openings of the internal vascular network (Text-fig. 3A, B).

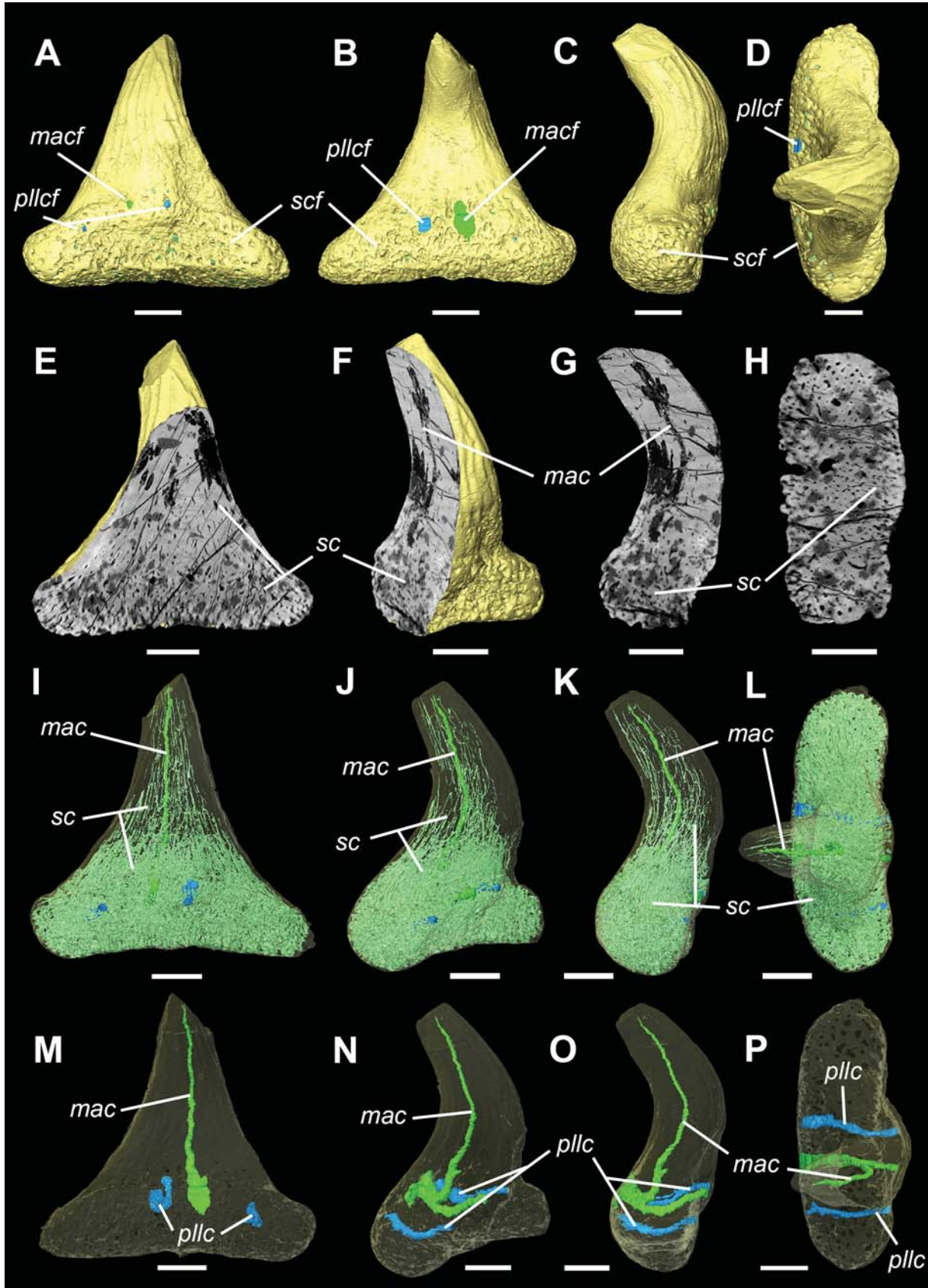
DISCUSSION

The teeth of both *L. carlsi* and *C. maderi* exhibit a complex and dense network of vascular canals, including horizontal, ascending and secondary bifur-

cated canals, as well as histological features consistent with an osteodont histotype. However, some differences between them stand out. In both taxa, the teeth possess a principal horizontal canal that transects the middle of the base linguo-labially, but in *Leonodus* this canal did not cross the tooth entirely, passing across the lingual torus but emerging from the aboral surface of the tooth base (Text-fig. 2N). We conclude that the same canal crosses again the labial region of the next tooth, bifurcating and connecting with the main pulp canals of the cusps (Text-fig. 2N). In *Celtiberina*, this canal crosses the entire tooth and connects directly with the ascendant pulp canal of the cusp (Text-fig. 3N–P). Additionally, in *Celtiberina*, a pair of horizontal parallel canals, similar in size to the main canal, cross the tooth base linguo-labially (Text-fig. 3M–P).

Leonodus was originally defined by Mader (1986) as a primitive xenacanthiform. However, the inclusion of *Leonodus* within Xenacanthiformes has been questioned previously by several authors (e.g., Soler-Gijón and Hampe 2003; Botella *et al.* 2005) who have suggested a closer phylogenetic relationship with Antarctilamniiformes, a group of earlier branching Chondrichthyes. *Leonodus* exhibits a vascular system that clearly differs from that seen in xenacanthids (Hampe 1988, 1993, 1995; Hampe and Heidtke 1997; see also synthetic fig. 53 in Ginter *et al.* 2010) showing, in general, a comparatively reduced vascular network at the base, with large cavities below the cusps that are connected to the exterior by parallel labio-lingual canals. Our data reveals a denser vascular system in *Leonodus*, with an interconnected network of canals filling most of the root base. This network extends into the cusp, associated with a reduction in the size of the canals, and run largely in parallel. In addition, a small number of principal ascendant pulp vascular canals are connected at the base of the tooth by a “T”-shape junction, and emerge at the base of the labial region. This pattern of vascularisation resembles (in terms of major or principal canals) that described in some Phoeodontiforms, with a single main nutrient canal transecting the apical button, emerging from the middle of the base, and connect-

← Text-fig. 2. *Leonodus carlsi* Mader, 1986 (MGUV-36.141) from Level 131-30 of the Poyales-East section (Santa Cruz de Nogueras, Teruel, Spain), Nogueras Fm (Lochkovian, Lower Devonian). A–D – Surface rendering derived from the tomographic data in lateral (A), labial (B), occlusal (C) and aboral (D) views. E–I – “virtual thin sections” based on SRXTM data; E – longitudinal cut between the two main cusps; F – transverse cut through the main cusp; G – longitudinal cut of one of the cusps; H – horizontal cut of the base; I – horizontal cut of the cusp. J–O – segmentation of the vascular system showing in light green the complex network of canals, in dark green the main ascendant vascular canals (pulp canals), and in blue the main linguo-labial canal; J–L – complete segmentation of the vascular system in lateral (J), labio-lateral (K) and occlusal views (L); M–O – principal vascular canals in lateral (M), labio-lateral (N) and occlusal views (O). Abbreviations: mac, main ascendant canal; pllc, principal linguo-labial canal(s); sc, secondary canals; macf, main ascendant canal foramina; pllef, principal linguo-labial canal foramina; scf, secondary canal foramina. Scale bar = 500 µm



ing with the main ascendant pulp canal (see Ivanov and Nilov 2016, fig. 3A–C). However, the structure of the vascular network is clearly different, with a more complex system of anastomosing secondary vascular canals in *Leonodus*.

The teeth of *Celtiberina* are of osteodont histotype, showing a vascular system composed by a complex canal network that differs from any known Palaeozoic shark tooth – though few have been characterised to date. The system is especially hyper-vascularised in the tooth-base with interconnected horizontal canals that run through the entire tooth base. This vascular network extends into the cusp, where it becomes more diffuse, with numerous small canals running parallel to the main axis of the cusp. In addition, a principal ascendant pulp canal is clearly visible (which is connected with the main linguo-labially canal that transects the tooth base, see Text-fig. 3M–P). Two laterally positioned, horizontally oriented (with respect to the base), longitudinal linguo-labial canals occur, running approximately parallel to plane of the main central canal (Text-fig. 3M–P). This configuration resembles that described from the ctenacanthiform *Glikmanius occidentalis* (Leidy, 1859) which has a dense network of strongly branched canals distributed within the crown, and several parallel horizontal canals (main and lateral) transecting the tooth base linguo-labially (Ivanov and Nilov 2016, fig 3A–C).

Celtiberina was originally identified as a chondrichthyan (Wang 1993), an assignment followed by most of latter authors (Turner 2004; Botella *et al.* 2009a, b; Ginter *et al.* 2010). However, Turner (2004) and Ginter *et al.* (2010) questioned the dental nature of these elements, suggesting that they instead represent modified dermal denticles, based mainly on its weakly developed base and the lack of evidence for overlapping tooth base. However, the absence of evidence for overlapping tooth bases does not preclude a tooth interpretation. The absence of a large overlapping area is indicated also by our 3-D vascular analysis. Thus, the principal basal canals in *Celtiberina* run horizontally, in the labio-lingual direction (Text-fig. 3O), and there is no basal opening. This suggests, rather, that the bases of these teeth did not overlap. Instead, they could have made contact only with their

labial and lingual faces. Non-overlapping tooth bases are rare in Palaeozoic shark teeth, but present in euselachian teeth (including hybodonts). In general, other aspects of the vascular structure of *Celtiberina* are entirely compatible with a tooth vascular system. Together with its generalized tooth-like morphology and clear evidence of wear (Botella *et al.* 2009a), these data support the interpretation of these skeletal elements of *Celtiberina* as teeth, however further analysis and discovery of additional skeletal remains will provide new opportunities for applying robust tests of this hypothesis. Thus, the important morphological and vascular system differences between the oldest putative shark teeth here discussed, reflecting perhaps distant relationship, are compatible with a Pre-Devonian diversification of the two main tooth types traditionally recognised in Palaeozoic sharks (i.e., “cladodont” vs. “diplodont”).

Finally, although both orthodont and osteodont teeth are widespread among Palaeozoic sharks, the presence of the osteodont histotype in *Leonodus* and *Celtiberina* challenges the view that orthodont tooth grade is plesiomorphic for chondrichthyans (Zangerl 1981). Following Ivanov and Nilov (2016), our data demonstrate that Casier’s (1947) classification of dental vascularisation grades is overly simplistic, especially when Palaeozoic taxa are considered. Further work is needed to establish the diversity and disparity of dental vascular architecture in Palaeozoic chondrichthyans and we provide further evidence that this variation may be sampled readily and non-invasively using X-ray microtomography. This work will likely yield a useful basis for discriminating taxonomically and systematically the relationships of early chondrichthyans which are known principally from isolated teeth.

Acknowledgements

We thank Vicent Gisbert Cardona and Nerea Vercher Capilla for their help developing the preliminary 3D models of the specimens here studied. This work was partially funded by the Research Projects CGL2014-52662-P (Spanish Ministry of Economy and Competitiveness) and GV/2016/102 (Generalitat Valenciana). Humberto G. Ferrón is a recipient of a FPU

← Text-fig. 3. *Celtiberina maderi* Wang, 1993 (MGUV-21.315) from Level 200 of the Poyales-East section (Santa Cruz de Noguerras, Teruel, Spain), Noguerras Fm. (Lochkovian, Lower Devonian). A–D – Surface rendering derived from the tomographic data in labial (A), lingual (B), lateral (C) and occlusal (D) views. E–H – “virtual thin sections” based on SRXTM data; E – transverse cut of the main cusp; F–G – longitudinal cut through the main cusp; H – horizontal cut of the base. I–P – segmentation of the vascular system, showing in light green the complex network of canals, in dark green the main ascendant vascular canals (pulp canals), and in blue the main linguo-labial canals; I–L – complete segmentation of the vascular system in labial (I), labio-lateral (J), lateral (K) and occlusal views (L); M–P – principal vascular canals in labial (M), labio-lateral (N), lateral (O), and occlusal views (P). For abbreviations see Text-fig. 2. Scale bar = 500 µm

Fellowship from the Spanish Ministry of Education, Culture and Sport [Grant FPU13/02660]. Assistance at the beamline was provided by Federica Marone (PSI-SLS), Martin Rücklin (Naturalis, Leiden), John Cunningham (Bristol Palaeobiology) and Joe Keating (Bristol Palaeobiology). We acknowledge the support of the Swiss Light Source and Paul Scherrer Institute, as well as access-funding provided by EU FP7 through CALIPSOplus.

REFERENCES

- Botella, H. 2006. The oldest fossil evidence of dental lamina in sharks. *Journal of Vertebrate Paleontology*, **26**, 1002–1003.
- Botella, H., Donoghue, P.C.J. and Martínez-Pérez, C. 2009a. Enameloid microstructure in the oldest known chondrichthyan teeth. *Acta Zoologica*, **90**, 103–108.
- Botella, H., Martínez-Pérez, C. and Soler-Gijón, R. 2012. *Mach-aeracanthus goujeti* n. sp. (Acanthodii) from the Lower Devonian of Spain and northwest France, with special reference to spine histology. *Geodiversitas*, **34**, 761–783.
- Botella, H., Valenzuela-Ríos, J.I. and Martínez-Pérez, C. 2005. Morfología e histología de escamas de *Leonodus carlsi* Mader, un condrichtio primitivo del Devónico Inferior de la Cordillera Ibérica (España) In: Meléndez, G., Martínez-Pérez, C., Ros, S., Botella, H. and Plasencia, P. (Eds), Miscelánea Paleontológica. *Publicaciones del Seminario de Paleontología de Zaragoza (SEPAZ)*, **6**, 205–219.
- Botella, H., Valenzuela-Ríos, J.I. and Martínez-Pérez, C. 2009b. Tooth replacement rates in early chondrichthyans: a qualitative approach. *Lethaia*, **42**, 365–376.
- Cappetta, H. 1987. Handbook of Paleichthyology, Vol. 3B: Chondrichthyes II, 193 p. Gustav Fischer Verlag; Stuttgart.
- Cappetta, H. 2012. Handbook of Paleichthyology, Vol. 3E: Chondrichthyes II (Mesozoic and Cenozoic Elasmobranchii: teeth), 512 p. Gustav Fischer Verlag; Stuttgart.
- Carls, P. 1988. The Devonian of Celtiberia (Spain) and Devonian paleogeography of SW Europe. In: McMillan, N.J., Embry, A.F. and Glass, D.J. (Eds), Devonian of the World, Memoir of the Canadian Society of Petroleum Geologist. *Proceedings of the 2nd International Symposium on the Devonian System*, **14**, 421–466.
- Carls, P. 1999. El Devónico de Celtiberia y sus fósiles. In: Gámez Vintaned, J.A. and Liñan, E. (Eds), Años de Paleontología Aragonesa, Homenaje al Prof. Leandro Sequeiros. *Memorias de Las VI Jornadas Aragonesas de Paleontología*, **25**, 101–164.
- Carls, P. and Valenzuela-Ríos, J.I. 2002. Devonian–Carboniferous Rocks from the Iberian Cordillera. In: García-Lopez, S. and Bastida, F. (Eds), Palaeozoic Conodonts from Northern Spain. *Serie Cuadernos del Museo Geominero*, **1**, 299–314.
- Casier, E. 1947. Constitution et évolution de la racine dentaire des Euselachii. III. Évolution des principaux caractères morphologiques et conclusion. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique*, **23**, 1–45.
- Cunningham, J. C., Rücklin, M., Blom, H., Botella, H. and Donoghue, P.C.J. 2012. Testing models of dental development in the earliest bony vertebrates. *Andreolepis* and *Lophosteus*, *Biology Letters*, **8**, 833–837.
- Dojen, C. 2005. Early Devonian ostracods of Celtiberia (NE Spain) taxonomy, palaeoecology, biostratigraphy, and biogeography, 1–256. PhD Thesis published electronically at the library of the Technical University of Braunschweig. <http://www.digibib.tu-bs.de/?docid=00000015>.
- Donoghue, P.C.J., Bengtson, S., Dong, X.-P., Gostling, N.J., Hultgren, T., Cunningham, J.A., Yin, C., Yue, Z., Peng, F. and Stamparoni, M. 2006. Synchrotron X-ray tomographic microscopy of fossil embryos. *Nature*, **442**, 680–683.
- Dupret, V., Carls, P., Martínez-Pérez, C. and Botella, H. 2011. First Perigondwanan record of actinolepids (Vertebrata: Placodermi: Arthrodira) from the Lochkovian (Early Devonian) of Spain and its palaeobiogeographic significance. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **310**, 273–282.
- Gillis, J.A. and Donoghue, P.C.J. 2007. The homology and phylogeny of chondrichthyan tooth enameloid. *Journal of Morphology*, **268**, 33–49.
- Ginter, M., Hampe, O. and Duffin, C. 2010. Handbook of paleoichthyology, Vol. 3D: Chondrichthyes. Paleozoic Elasmobranchii: Teeth, 1–168. Verlag Dr Friedrich Pfeil; München.
- Hampe, O. 1988. Über die Bezahnung des *Orthacanthus* (Chondrichthyes: Xenacanthida; Oberkarbon-Unterperm). *Paläontologische Zeitschrift*, **62**, 285–296.
- Hampe, O. 1993. Variation of xenacanthid teeth in the Permian–Carboniferous deposits of the Saar-Nahe Basin (SW-Germany). In: Heidtke, U. (Ed.), New Research on Permian–Carboniferous Faunas. *Pollichia*, **29**, 37–51.
- Hampe, O. 1995. *Plicatodus jordani* n.g., n.sp., a new xenacanthid shark from the Lower Permian of Europe (Saar-Nahe Basin, Germany). In: Arsenault, M., Lelièvre, H. and Janvier, P. (Eds), VIIth International Symposium, Studies on Early Vertebrates. *Bulletin du Muséum National d'Histoire Naturelle*, **17**, 209–226.
- Hampe, O. and Heidtke, U.H.J. 1997. *Hagenoselache sippeli* n. gen. n. sp., ein früher xenacanthider Elasmobranchier aus dem Oberkarbon (Namurium B) von Hagen-Vorhalle (NW-Sauerland/ Deutschland). *Geologie und Paläontologie in Westfalen*, **47**, 5–42.
- Hampe, O. and Long, J.A. 1999. The histology of Middle Devonian chondrichthyan teeth from southern Victoria Land, Antarctica. *Records of the Western Australian Museum Supplement*, **57**, 23–36.
- Ivanov, A.O. 2016. Chondrichthyans from the Lower Permian of Mechetlino, South Urals. *Bulletin of Geosciences*, **91**, 717–729.

- Ivanov, A.O., Duffin, C.J. and Naugolnykh, S.V. 2017. A new euselachian shark from the early Permian of the Middle Urals, Russia. *Acta Palaeontologica Polonica*, **62**, 289–298.
- Ivanov, A.O. and Nilov, S.P. 2016. Microtomographic research of the vascularization system in the teeth of Palaeozoic sharks. In: Abstract book of the 2016 Annual Bruker microCT User Meeting, pp. 203–206. Luxembourg.
- Janvier, P. and Maisey, J.G. 2010. The Devonian vertebrates of South America and their biogeographical relationships. In: Elliott, D.K., Maisey, J.G., Yu, X. and Miao, D. (Eds), *Morphology, phylogeny and paleobiogeography of fossil fishes*, pp. 431–459. Verlag Dr. Friedrich Pfeil; Munich.
- Leidy, J. 1859. Descriptions of *Xystracanthus arcuatus* and *Cladodus occidentalis*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, (unnumbered volume), 3.
- Long, J.A. 1995. The Rise of Fishes: 500 Million Years of Evolution, 1–223. Johns Hopkins Univ. Press; Baltimore.
- Long, J.A., Burrow, C.J., Ginter, M., Maisey, J.G., Trinajstić, K.M., Coates, M.I., Young, G.C. and Senden, T.J. 2015. First shark from the Late Devonian (Frasnian) Gogo Formation, Western Australia sheds new light on the development of tessellated calcified cartilage. *PLoS ONE*, **10**, 126066.
- Mader, H. 1986. Schuppen und Zähne von Acanthodien und Elasmobranchiern aus dem Unter-Devon Spaniens (Pisces). *Göttinger Arbeiten Zur Geologie und Paläontologie*, **28**, 1–59.
- Marone, F., Münch, B. and Stampanoni, M. 2010. Fast reconstruction algorithm dealing with tomography artifacts. In: Developments in X-Ray Tomography VII. *Proceedings SPIE*, **7804**, 780410.
- Martínez-Pérez, C., Dupret, V., Manzanares, E. and Botella, H. 2010. New data on the Lower Devonian chondrichthyan fauna from Celtiberia (Spain). *Journal of Vertebrate Paleontology*, **30**, 1622–1627.
- Miller, R.F., Cloutier, R. and Turner, S. 2003. The oldest articulated chondrichthyan from the Early Devonian period. *Nature*, **425**, 501–504.
- Moyer, K.M., Riccio, M.L. and Bemis, W.E. 2015. Development and microstructure of teeth histotypes in the blue shark, *Prionace glauca* (Carcharhiniformes: Carcharhinidae) and the Great White Shark, *Carcharodon carcharias* (Lamniformes: Lamnidae). *Journal of Morphology*, **276**, 797–817.
- Qu, Q., Sanchez, S., Blom, H., Tafforeau, P. and Ahlberg, P.E. 2013. Scales and tooth whorls of ancient fishes challenge distinction between external and oral 'teeth'. *PloS One*, **8**, e71890.
- Rücklin, M. and Donoghue, P.C.J. 2015. *Romundina* and the evolutionary origin of teeth. *Biology Letters*, **8**, 833–837.
- Turner, S. 2004. Early vertebrates: analysis from microfossil evidence. In: Arratia, G., Wilson, M.V.H. and Cloutier, R. (Eds), *Recent Advances in the Origin and Early Radiation of Vertebrates*, pp. 65–94. Verlag Dr. Friedrich Pfeil; München.
- Rücklin, M., Donoghue, P.C.J., Johanson, Z., Trinajstić, K., Marone, F. and Stampanoni, M. 2012. Development of teeth and jaws in the earliest jawed vertebrates. *Nature*, **491**, 748–751.
- Schnetz, L., Pfaff, C. and Kriwet, J. 2016. Tooth development and histology patterns in lamniform sharks (Elasmobranchii, Lamniformes) revisited. *Journal of Morphology*, **277**, 1584–1598.
- Soler-Gijón, R. and Hampe, O. 2003. *Leonodus*, a primitive chondrichthyan from the Early Devonian. *Ichthyolith Issues Special Publication*, **7**, 45.
- Wang, R. 1993. Taxonomie, Palökologie und Biostratigraphie der Mikroichthyolithen aus dem Unterdevon Keltiberiens, Spanien. *Courier Forschungsinstitut Senckenberg*, **161**, 1–205.
- Williams, M.E. 1992. Jaws, the early years; feeding behaviour in Cleveland. Shale sharks. *Explorer*, **32**, 4–8.
- Williams, M.E. 2001. Tooth retention in cladodont sharks: with comparison between primitive grasping and swallowing, and modern cutting and gouging feeding mechanisms. *Journal of Vertebrate Paleontology*, **21**, 214–226.
- Zangerl, R. 1981. Handbook of paleoichthyology, Vol. 3A: Paleozoic Elasmobranchi, 115 p. Gustav Fischer Verlag; Stuttgart–New York.

Manuscript submitted: 4th December 2017

Revised version accepted: 16th July 2018