

Research



Cite this article: Coates MI, Finarelli JA, Sansom IJ, Andreev PS, Criswell KE, Tietjen K, Rivers ML, La Riviere PJ. 2018 An early chondrichthyan and the evolutionary assembly of a shark body plan. *Proc. R. Soc. B* **285**: 20172418.
<http://dx.doi.org/10.1098/rspb.2017.2418>

Received: 27 October 2017

Accepted: 29 November 2017

Subject Category:

Palaeobiology

Subject Areas:

palaeontology, taxonomy and systematics, evolution

Keywords:

Chondrichthyes, gnathostomes, gill skeleton, scales, Middle Devonian, jaws

Author for correspondence:

Michael I. Coates

e-mail: mcoates@uchicago.edu

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.3952948>.

An early chondrichthyan and the evolutionary assembly of a shark body plan

Michael I. Coates¹, John A. Finarelli⁴, Ivan J. Sansom⁵, Plamen S. Andreev⁵, Katharine E. Criswell^{1,6}, Kristen Tietjen¹, Mark L. Rivers² and Patrick J. La Riviere³

¹Department of Organismal Biology and Anatomy, and ²Center for Advanced Radiation Sources, and

³Department of Radiology, University of Chicago, Chicago, IL 60637-1508, USA

⁴UCD School of Biology and Environmental Science, UCD Science Education and Research Centre (West), UCD Earth Institute, University College Dublin, Belfield, Dublin 4, Ireland

⁵School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham B15 2TT, UK

⁶Department of Zoology, Cambridge University, Cambridge CB2 3EJ, UK

id MIC, 0000-0003-2843-1075; IJS, 0000-0003-3043-8989; KEC, 0000-0002-4004-0192

Although relationships among the major groups of living gnathostomes are well established, the relatedness of early jawed vertebrates to modern clades is intensely debated. Here, we provide a new description of *Gladbachus*, a Middle Devonian (Givetian approx. 385-million-year-old) stem chondrichthyan from Germany, and one of the very few early chondrichthyans in which substantial portions of the endoskeleton are preserved. Tomographic and histological techniques reveal new details of the gill skeleton, hyoid arch and jaws, neurocranium, cartilage, scales and teeth. Despite many features resembling placoderm or osteichthyan conditions, phylogenetic analysis confirms *Gladbachus* as a stem chondrichthyan and corroborates hypotheses that all acanthodians are stem chondrichthyans. The unfamiliar character combination displayed by *Gladbachus*, alongside conditions observed in acanthodians, implies that pre-Devonian stem chondrichthyans are severely under-sampled and strongly supports indications from isolated scales that the gnathostome crown group originated at the latest by the early Silurian (approx. 440 Ma). Moreover, phylogenetic results highlight the likely convergent evolution of conventional chondrichthyan conditions among earliest members of this primary gnathostome division, while skeletal morphology points towards the likely suspension feeding habits of *Gladbachus*, suggesting a functional origin of the gill slit condition characteristic of the vast majority of living and fossil chondrichthyans.

1. Introduction

The early evolution of the Chondrichthyes (cartilaginous fishes) has long been obscured by an impoverished fossil record [1–3]. This has only recently been improved through discoveries of partly articulated bodies [4–7] and braincases from the Lower and Middle Devonian [8–10], coupled with computed tomography (CT) [11–16]. The Lower and Middle Devonian record of chondrichthyans remains sparse, but the influx of high-quality data from slightly younger material, especially from the Upper Devonian and Carboniferous [14–17], combined with insights from earlier studies [18–21] has transformed our understanding of the early evolution of the crown group (Holocephali and Elasmobranchii). In a complementary manner, the origin of total-group Chondrichthyes has been amended by serial large-scale analyses of early gnathostome phylogeny [22–27], which consistently recover acanthodians [28] as stem chondrichthyans. However, because the acanthodian and chondrichthyan taxa included in these data matrices are largely unaltered from Brazeau [29] and Davis *et al.* [30], these results are not truly independent.

Here, we present a CT analysis and redescription of *Gladbachus adentatus* [31] from the Middle Devonian (Givetian approx. 385-million-year-old) of Germany, one of the earliest chondrichthyans known from articulated remains. Unlike *Doliodus* [1,4–7], the earliest and most completely described ‘unambiguous’ stem chondrichthyan [32], *Gladbachus* has never been included among acanthodians, but, like *Doliodus*, recent analyses and discussion [16,32] suggest that it might illuminate conditions bridging the acanthodian–chondrichthyan transition. Thus, a primary aim of the present work is to test the assumed chondrichthyan affinity of *Gladbachus* in light of the current acanthodians-as-stem-chondrichthyans hypothesis. Here, we have constructed a new early gnathostome database, with an augmented chondrichthyan component with taxa and characters from analyses by Pradel *et al.* [14], Coates *et al.* [16] and Coates & Tietjen [17]. This analysis presents the most detailed context, thus far, to reconstruct the evolutionary assembly of the chondrichthyan morphotype: a body plan that has persisted, more or less conservatively, for at least 370 Myr.

2. Material and methods

(a) Specimens

The subject of this study, *Gladbachus adentatus* [31] is known from a single, dorsoventrally compressed individual, UMZC (University Museum of Zoology, Cambridge, UK) 2000.32 [31,33], collected from the Lower Plattenkalk, Upper Givetian, Upper Middle Devonian, of Unterthal, Bergisch Gladbach (Germany). The specimen (electronic supplementary material, figure S1) consists of three pieces embedded within a rectangular slab of resin, with only the dorsal surface visible for direct inspection.

(b) Computed tomography, anatomical reconstruction and histological thin sections

Whole specimen scans: large-scale scans were completed by the high-resolution X-ray CT facility at the University of Texas at Austin (UTCT, www.digimorph.org).

Scales, denticles, teeth and calcified cartilage were examined using synchrotron μ CT: all data were collected at beamline 13-BM-D at the Advanced Photon Source at Argonne National Laboratory. Image reconstruction used the GSECARS tomography processing software (<http://cars9.uchicago.edu/software/idl/tomography.html>), which dark-current corrects and white-field normalizes acquired data prior to performing gridding-based image reconstruction. Further details are provided in the electronic supplementary material.

Histological thin sections: doubly polished thin sections were studied using a Zeiss Axioskop Pol microscope equipped with Nomarski DIC optics.

Anatomical reconstruction: Mimics v. 17 (biomedical.materialise.com/mimics; Materialise, Leuven, Belgium) was used for the three-dimensional modelling, including segmentation, three-dimensional object rendering, STL polygon creation and kinematics. 3D Studio Max (Autodesk.com/products/3ds-max; Autodesk, San Rafael, USA) was used for further editing of the STLs (colour, texture, lighting), kinematics and mirroring for the final restoration.

(c) Phylogenetic and phenetic analysis

The phylogenetic data matrix are developed from sources including iterations of the early gnathostome data matrix by Brazeau [29], Davis *et al.* [30] and Zhu *et al.* [22]; most recently updated by Lu *et al.* [23], Qiao *et al.* [26], Zhu *et al.* [27] and Burrow *et al.* [34]. Chondrichthyan content includes substantial additions

of new data drawn from Pradel *et al.* [14,15], Coates *et al.* [16] and Coates & Tietjen [17], and observation of original specimens (electronic supplementary material).

Phylogenetic methods: the primary character matrix consists of 84 in-group taxa and two out-group taxa (Galeaspida and Osteostraci) coded for 262 characters. Character and taxon sampling sources and discussion are provided in the electronic supplementary material. Phylogenetic analyses used maximum-parsimony implemented in PAUP* 4.0.152 [35]. Nodal support was assessed via bootstrapping [36] and Bremer Decay Indices [37], carried out using AutoDecay [38] and PAUP*. Details of phylogenetic methods are provided in the electronic supplementary material. Character state transitions by node for the strict consensus cladogram of the MPTs were reconstructed in PAUP* assuming hard polytomies with DELTRAN [39] optimization (see Davis *et al.* [30], Coates *et al.* [16]).

A principal coordinate (PCO) analysis [40,41] was performed on the Hamming distance matrix [42] of the character data. Computed dissimilarity was restricted to characters coded for both taxa, and distances were normalized to the number of characters coded for both members in each taxon pair. For the PCO, all characters were treated as equally weighted and unordered.

3. Results

(a) Specimen description, including (b) results of computed tomography, anatomical reconstruction and thin section histology

Head length including the gill skeleton (figure 1*a,b*) is approximately 21 cm, and head plus trunk length as preserved with the caudal region mostly absent is approximately 60 cm (electronic supplementary material, figure S1), implying a total body length of approximately 80 cm.

Although considered one of the few ‘unambiguous sharks’ of the Lower and Middle Devonian [32], details of *Gladbachus* anatomy do not conform in a straightforward manner with contemporary models of early chondrichthyan anatomy. The internal skeleton consists of calcified cartilage with no perichondral bone, yet the cartilage surface lacks the tightly connected tesserae that is a hallmark of chondrichthyan skeletal anatomy [15,43]. Rather, most cartilage surfaces bear a mesh of continuously calcified ridges (electronic supplementary material, figure S2), broadly resembling the ‘wood-like’ [44] texture observed in some Mesozoic elasmobranchs. Discrete tesserae are visible only in the walls of the semicircular canals, but these are irregularly sized and shaped, with broad inter-tesseral spaces. Thin section histology and synchrotron microtomography show that poorly delineated tesserae are distributed elsewhere in the skeleton, but concealed beneath the continuously mineralized cartilage surface.

The dermal skeleton includes no large plates. Head scales (figure 1*d*) are mostly larger than trunk scales (figure 1*f*), and the lateral line runs between scales. However, scale shape, composition and histology are remarkable, as they resemble conditions observed in ‘placoderms’ [33,45], and differ markedly from polyodontode scales like those of *Doliodus* [4,46] and mongolepids [47,48]. In *Gladbachus*, scale and branchial denticle crowns consist of overlapping, mono-layered, cellular dentine tubercles (electronic supplementary material, figure S3), lacking neck and basal canals. The standard, total-group chondrichthyan scale growth pattern of areally apposed odontodes [32] is absent, as are growing monodontode scales [49],

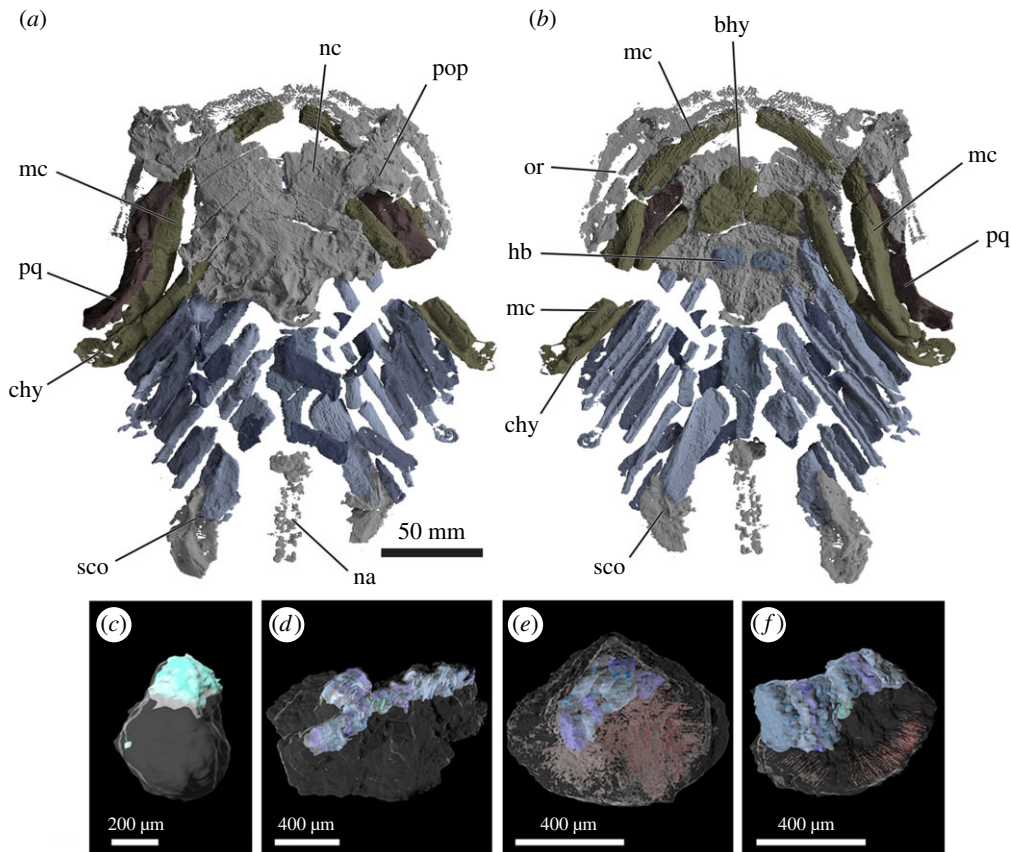


Figure 1. *Gladbachus adentatus* Heidtke & Krätschmer [31]. (a) Rendering of cranial and pectoral girdle remains in dorsal view and (b) ventral view; (c) mandibular tooth; (d) cranial roof scale; (e) branchial denticle; (f) trunk scale. All denticles and scales are rendered semi-transparent from micro-computed tomography scans. bhy, basihyal; chy, ceratohyal; hb, hypobranchial; mc, Meckel's cartilage; na, neural arches; nc, neurocranium; or, orbital ring; pop, postorbital process; pq, palatoquadrate; sco, scapulocoracoid.

and the non-growing placoid scales characteristic of modern chondrichthyans. Instead, the reconstructed growth pattern of *Gladbachus* scales is linear and bidirectional. Most unusually for a chondrichthyan, the cranial scales are asymmetric, with irregular and inconsistent shapes. Fin spines, and spines associated with girdles and the flank region, are completely absent.

The anterior section of the braincase is not preserved (figure 1*a,b*), thus evidence of a precerebral fontanelle is unknown, *contra* Heidtke & Kratschmer [31]. The right postorbital process includes traces of a jugular canal, and a groove on the posterior surface, probably for articulation with the upper jaw (electronic supplementary material, figure S4). The basi-cranium is compressed against the subjacent visceral arches, and too poorly preserved to demonstrate the presence or absence of a ventral cranial fissure, or canals for all or part of the dorsal aorta network. Reconstructions of the vestibular, semicircular canals and ampullary spaces (electronic supplementary material, figure S4*c*) demonstrate that the otic capsules were large and widely separated across the midline. In extant gnathostomes, this degree of lateral separation is manifest only in embryonic forms, and resemble adult conditions observed in 'placoderms' [50–53]. A pair of ring-shaped structures flanking the dorsal ridge, next to the anterior lip of the persistent otico-occipital fissure probably represents endolymphatic duct openings. This location for the endolymphatic ducts is consistent with the absence of an endolymphatic fossa or single, median endolymphatic foramen, which characterizes all Recent and fossil conventional chondrichthyans.

The jaws, hyoid arch and gill skeleton are exceptionally complete (figures 1*a,b* and 2; electronic supplementary material,

figure S5), providing ready comparison with recently described in-group [15,54] and out-group [55] examples. The mandibular arch morphology (electronic supplementary material, figure S6) is more conventional than previously understood. In contrast with previous descriptions [31,56], there is no palatal symphysis. The difference in length between the upper and lower jaws is considerable (figure 2*e*), and comparable to conditions in *Acanthodes* [30,57], implying that a significant portion of the upper dentition was borne on the underside of the neurocranium; presumably on the internasal plate (cf. *Ptomacanthus* [29]; *Doliodus* [5]). Notably, the scales and teeth (mixed) bordering the gape are preserved as continuous, subparallel bands spanning the inter-orbital space (figure 1*a,b*). The palatoquadrate is generally comparable to that of an early, conventional chondrichthyan (e.g. *Orthacanthus* [58]). The well-developed otic process bears a broad posterodorsal rim; the palatine process is broad and short, but there is no evidence of a flange or process contributing to a palatobasal articulation (figure 2*a*). Preserved most completely on the left side of the specimen, the anterior of the palate is thrust beneath the postorbital process (figure 1*a*). The section of jaw visible in front of the preserved portion of the braincase is the anterior extremity of Meckel's cartilage. The posterior portion of Meckel's cartilage is also exposed on the dorsal surface of the specimen, but rotated through 90°, such that the dorsal surface is compressed against the mesial surface of the palatoquadrate.

The hyoid arch (figures 1*a,b* and 2*c,d*) is morphologically distinct from the gill arches. There is no interhyal, and both the large and well-mineralized ceratohyal and slender first ceratobranchial articulate with a broad basihyal. The five gill

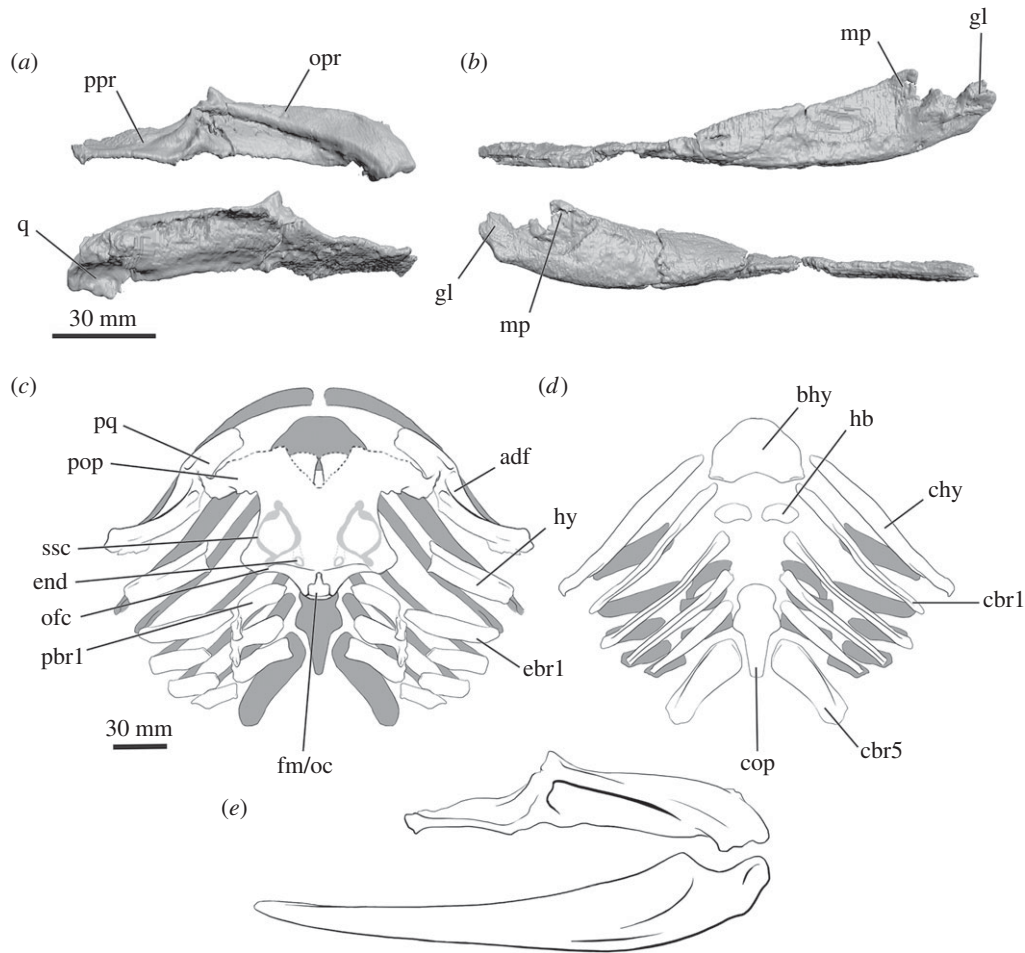


Figure 2. *Gladbachus adentatus* Heidtke & Krätschmer [31]. (a) Palatoquadrate; (b) Meckel's cartilage; (c) jaws, hyoid arch and gill arches restored, dorsal view; (d) gills reconstructed ventral view; (e) reconstruction of articulated mandibular arch, left lateral view. adf, adductor fossa; bhy, basihyal; cbr, ceratobranchial; chy, ceratohyal; cop, copula; ebr, epibranchial; end, endolymphatic duct; fm/oc, foramen magnum/occipital cotylus; gl, glenoid; hb, hypobranchial; hy, hyomandibula; mp, mesial process; opr, otic process; pbr, pharyngobranchial; pop, postorbital process; ppr, palatine process; pq, palatoquadrate; q, quadrate condyle, unmineralized site of; ssc, semicircular canal network; ofc, otico-occipital fissure.

arches (electronic supplementary material, figure S7) are positioned caudal to the braincase, as in non-holocephalan chondrichthyans. Epibranchials are present on the first four arches, with anteriorly directed simple pharyngobranchials (with no suprpharyngobranchials) present in the first three gill arches (figures 1a and 2c) as in osteichthyans and *Ozarcus* [15]. A pair of short, laterally directed cartilages medial to the base of the second gill provide the only evidence of hypobranchials. The fifth arch ceratobranchials are unusually broad, nearly rectangular and keeled along the anterior margin. Remarkably, and uniquely, these resemble the posteriormost ceratobranchials of *Paraplesiobatis*, a Lower Devonian 'placoderm' [55] (electronic supplementary material, figure S8). The ceratobranchials of *Gladbachus*' fourth and fifth gill arches articulate with a large basibranchial copula, which is separated from the basihyal process by a large gap. This revised description provides the first accurate association of dorsal to ventral parts of each arch.

Although reported and named as toothless, *Gladbachus* possesses a dentition of small, mono-, bi- and tri-cuspid teeth lining the jaws, with branchial denticles lining gill arches I–IV (figure 1a–c; electronic supplementary material, figure S3). The teeth are individually separate, and despite a suggestion of lingual to labial alignment, there is no trace of whorl-like families as in conventional, non-holocephalan, chondrichthyans.

(c) Phylogenetic analysis and principal coordinates analysis

Phylogenetic analysis of the dataset returned 249 600 most parsimonious trees (TL = 691, CI = 0.396, RI = 0.785, RCI = 0.311). The strict consensus cladogram of MPTs (figure 3a; electronic supplementary material, figure S11) strongly corroborates recent phylogenetic hypotheses of early gnathostomes [23–27], reconstructing all taxa usually referred to as acanthodians in a paraphyletic assemblage branching from the chondrichthyan stem. Here, *Gladbachus* is also recovered as a stem chondrichthyan, as the sister taxon to a poorly resolved set of climatiid acanthodians and conventional chondrichthyans (including crown clade Chondrichthyes). A monophyletic group uniting diplacanthid, ischnacanthid and acanthodid acanthodians forms a clade that is the sister group of all other total-group chondrichthyans, including *Gladbachus*.

The widely discussed Lower and Middle Devonian sharks *Doliodus* and *Pucapampella* branch from close to the apex of the chondrichthyan stem. *Pucapampella* is recovered in an uncertain position relative to several 'acanthodian' genera and the clade of conventional chondrichthyans. *Doliodus* is recovered as a sister taxon to conventional chondrichthyans.

Contra Qiao *et al.* [26] and Zhu *et al.* [27], *Ramirosuarezia* is not recovered among 'acanthodian' stem chondrichthyans,

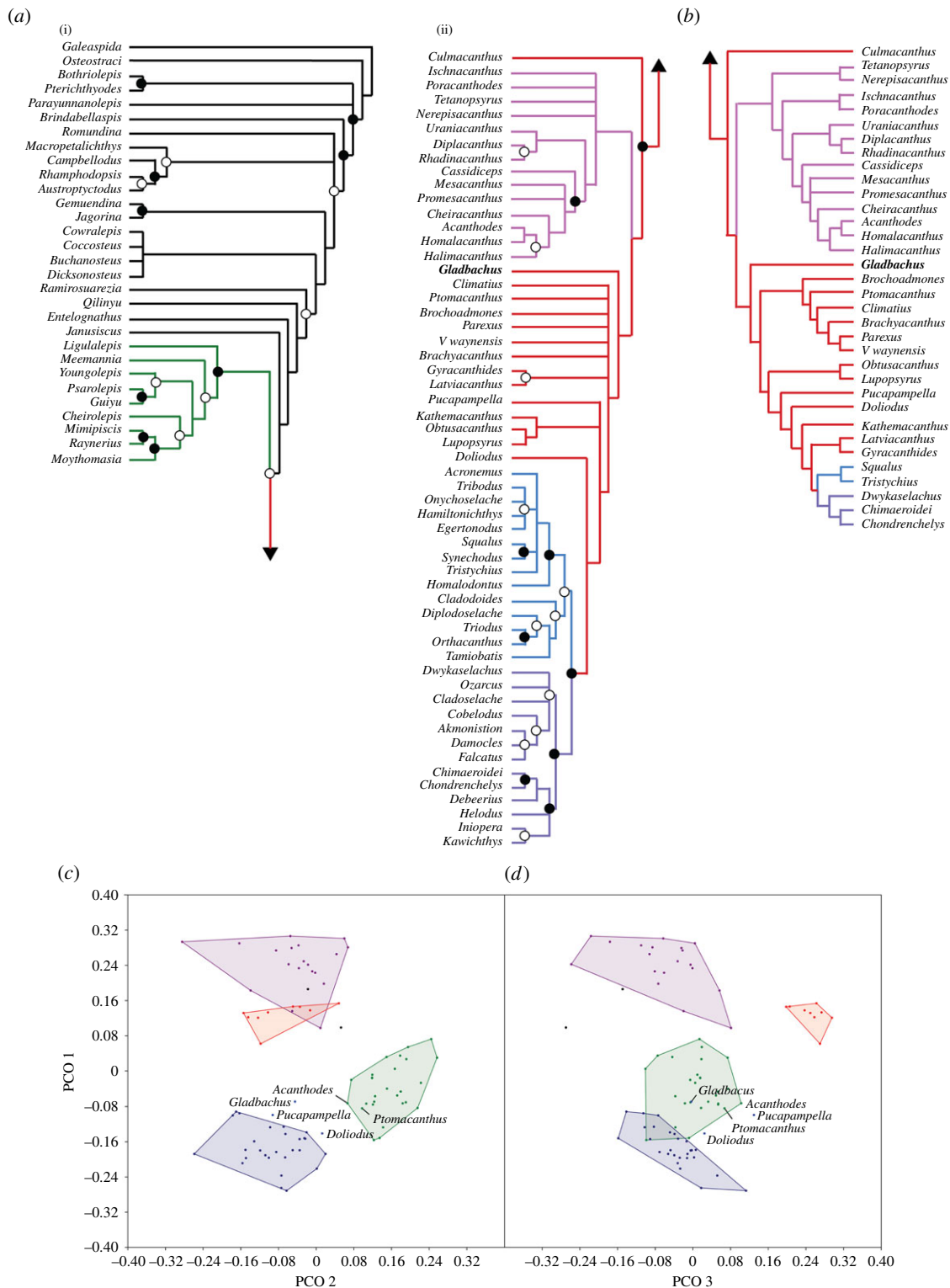


Figure 3. Phylogenetic placement of *Gladbachus adentatus* Heidtk & Krätschmer [31]. (a) parts (i) and (ii) join at arrowheads. Strict consensus, complete tree. (b) Strict consensus of chondrichthyan total-group obtained from reduced taxon set; arrowhead joins arrowhead of (a) part (i). Branch colours: black, stem-group gnathostomes; green, Osteichthyes; magenta, acanthodid stem Chondrichthyes; red, non-acanthodid stem Chondrichthyes; purple, Holocephali (crown Chondrichthyes); blue, Elasmobranchii (crown Chondrichthyes). Circles mark nodes with bootstrap support greater than 50% and/or decay values greater than 1; filled circles mark nodes with bootstrap support greater than 75% and/or decay values greater than 3. (c) Phenetic results: PCO 1 (18.1% explained variance) is plotted on the vertical axis and PCO 2 (9.6%) is plotted on the horizontal axis. (d) PCO 1 (vertical) versus PCO 3 on the horizontal axis (8.1%). Details of the PCO analysis are presented in the electronic supplementary material. The four traditionally named groups (placoderms in purple, acanthodians in green, chondrichthyans in blue, osteichthyans in red) cluster in distinct non-overlapping regions on the first three PCO dimensions. Relevant stem chondrichthyan taxa are indicated in each plot.

but rather, is nested among stem gnathostomes, with other taxa, such as *Qilinyu*, *Entelognathus* and *Janusiscus* branching the crownward of the paraphyletic placoderms.

Within the chondrichthyan crown group, xenacanth and ctenacanth (*sensu lato*) form a clade branching from the elasmobranch stem. A further, poorly resolved cluster,

including *Homalodontus*, *Tristychius*, *Acronemus* and hybodontids, branches from more crownward nodes, suggesting successive sister groups to the elasmobranch crown and close relatives. Holocephalans include the symmoriids, corroborating the arrangement found in Coates *et al.* [16].

A phylogenetic analysis on a reduced sample of chondrichthyans, focusing on the relationships among stem members (figure 3b), recovered 24 MPTS, with a mostly resolved set of relationships among acanthodians along the chondrichthyan stem. In this reduced analysis, *Gladbachus* again branches from within the ‘acanthodians’, suggesting that the position of *Gladbachus* within this paraphyletic assemblage is not the result of noise introduced into the dataset by the large chondrichthyan sample.

PCO analysis of the character data recovers all four of the traditional gnathostome divisions (‘placoderms’, ‘acanthodians’, osteichthyans and chondrichthyans) as discrete clusters in the space defined by the first three PCO axes (figure 3c,d). Notably, *Gladbachus* clusters with chondrichthyans in the PCO, despite its phylogenetic position among ‘acanthodians’. *Gladbachus*, *Doliodus* and *Pucapampella* each occupy positions in PCO space between conventionally defined chondrichthyans and ‘acanthodians’; however, these three genera are all significantly closer in PCO space to chondrichthyan taxa than to ‘acanthodians’ (*t*-tests of the inter-taxon distances in PCO space for *Gladbachus*, *Doliodus* and *Pucapampella* yield *p*-values of 1.39×10^{-6} , 0.01 and 8.65×10^{-8} , respectively).

4. Discussion

(a) Tree shapes and implications for evolutionary timescale

Owing principally to its plesiomorphic scale conditions and the absence of a dentition consisting of toothwhorls, *Gladbachus* is reconstructed close to the base of chondrichthyan total-group (figure 3a,b), removed from *Doliodus* and *Pucapampella*, which have traditionally been ascribed to the Chondrichthyes, but interleaved among taxa normally referred to as ‘acanthodians’. Accordingly, despite a phenetic similarity to conventionally defined chondrichthyans, phylogenetically, *Gladbachus* is an acanthodian-grade stem chondrichthyan.

Support for the acanthodian branching pattern is weak (electronic supplementary material, figure S11), but consistent with recent analyses [23–27]. Recent reconstructions have recovered traditional acanthodian family-level sets: acanthodids, ischnacanthids, diplacanthids and climatiids (electronic supplementary material, figure S9). In all of these trees, the climatiids group with conventional chondrichthyans, echoing results of Brazeau [29] and Davis *et al.* [30]. Diplacanthids, ischnacanthids and acanthodids fall into one of two arrangements: (i) as successive sister groups to more crownward taxa [25,27], or (ii) as in the present analysis, a monophyletic clade [23,24]. Here, we propose resurrecting the term Acanthodii to define the diplacanthid–ischnacanthid–acanthodid clade.

Support for the chondrichthyan crown clade is strong (figure 3a), introducing new data for the elasmobranch branch and corroborating the topology found in Coates *et al.* [16]. A time-calibrated phylogeny using the strict consensus tree (figure 4) places the origin of the crown group at least as early as the end-Middle Devonian. The initial evolutionary radiation

of crown chondrichthyans is primarily post-Devonian, forming a significant component of the vertebrate recovery after the end-Devonian Hangenberg extinction [60,61], which is evident from faunas recorded at Lower Carboniferous localities such as Glencartholm [62], Bearsden [62] and Bear Gulch [63,64].

Conventional chondrichthyan conditions, exemplified by *Doliodus* [4], are present by the middle-Lower Devonian (Pragian: approx. 410 Ma), and a minimum date for the origin of the chondrichthyan total-group is currently tethered to the late Silurian (Ludlow: approx. 423 Ma) by the earliest well-preserved osteichthyan (*Guiyu*) [65]. However, the earliest ‘acanthodian’ stem-chondrichthyan body fossils (*Nerepisacanthus*) are only slightly younger (Pridoli: approx. 419 Ma) [66], and a wide variety of ‘acanthodians’ are known from the Lower Devonian (e.g. *Ptomacanthus*, *Brochoadmones*, *Cassidiceps* and *Promesacanthus* [29,67–70]). Such diversity, first apparent in the Lochkovian (figure 4) supported by a taphonomically biased record of articulated specimens, implies either a sudden radiation in the early Lower Devonian or a severely under-sampled history of Silurian stem sharks. The latter hypothesis is supported by isolated scales scattered through the Middle Ordovician to Silurian [48,49], including strikingly characteristic, classically defined ‘acanthodian’ scales from the Rhuddanian (Llandovery approx. 440 Ma) of the Siberian Platform [71]. In the present phylogenetic context, we prefer to combine the micro- and macro-/articulated fossil records, which strongly suggest that the chondrichthyan total-group, and, therefore, the gnathostome crown node, dates to at least the earliest Silurian, approximately 440 Ma. Thus, the early history of chondrichthyans consists of two phases (figure 4): a Silurian–Devonian evolutionary radiation of micromeric, acanthodian-like taxa, and a subsequent Carboniferous radiation of the crown clade, initially dominated by holocephalans [16,64].

(b) Palaeobiological inferences

Gladbachus adds to an increasingly populated chondrichthyan stem lineage that also includes *Acanthodes* [24,30], *Ptomacanthus* [29,67], *Pucapampella* [8–10] and *Doliodus* [4–7]. The resultant data on early chondrichthyan morphological diversity captures endoskeletal details comparable to the content of early osteichthyans, contributing to a more balanced interpretation of the initial gnathostome radiation. However, there is no straightforward emerging sequence of character acquisition for the chondrichthyan crown group (crown clade apomorphies are listed in electronic supplementary material, figure S10). The current analysis highlights conflicting patterns of character-state distributions, implying repeated and convergent evolution of chondrichthyan-like specializations among the earliest total-group members. For *Gladbachus*, PCO analysis clearly identifies the chondrichthyan-like nature of its body plan (figure 3c), but this stands in marked contrast to its reconstruction as representative of a previously unrecognized ‘acanthodian’ lineage (figures 3a,b and 4). *Gladbachus* approaches a quantifiably defined shark space, but does so from a phylogenetically distinct origin (electronic supplementary material, figure S10).

The character combination observed in *Gladbachus*, alongside the array of contrasting conditions observed in Early Devonian acanthodians (figure 4), defies conventional hypotheses of morphologically segregated acanthodian and chondrichthyan morphotypes, reinforcing the hypothesis that pre-Devonian stem-chondrichthyan diversity is fundamentally under-sampled. Reasons for the absence of substantial Silurian

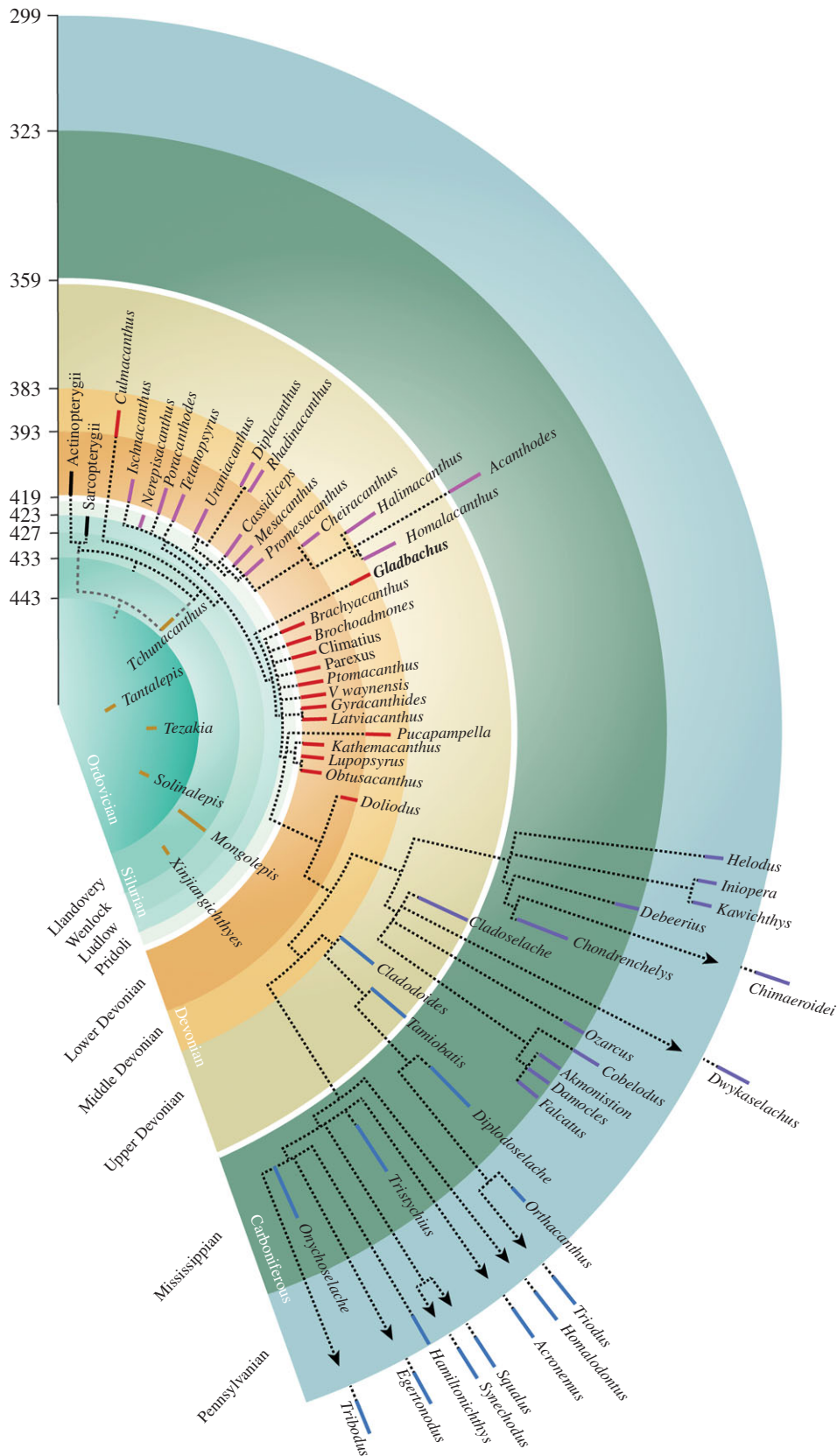


Figure 4. Early chondrichthyan phylogeny: simplified strict consensus of phylogenetic analysis results calibrated against Ordovician–Carboniferous chronostratigraphic chart. Consensus computed from matrix with 86 taxa and 262 characters. Taxon bar colour: black, non-chondrichthyan; magenta, acanthodid stem chondrichthyan; red, non-acanthodid stem chondrichthyan; purple, holocephalan crown chondrichthyan; blue, elasmobranch crown chondrichthyan. Bar length corresponds to earliest occurrence stage duration. Brown bar signifies the total range of chondrichthyan-like scale-based taxon. Timescale (Ma) from Cohen *et al.* [59]. Complete cladogram shown in figure 3a.

remains of crown gnathostomes are unclear, although restricted environmental specificity has been conjectured [72]. *Gladbachus* is a morphotypic outlier, in the sense that although phylogenetically placed within the acanthodian grade, it lacks fin spines, its

scales lack synapomorphies shared with any acanthodian subgroup and its estimated body length (electronic supplementary material, figure S1) is two to three times greater than contemporary or earlier ‘acanthodians’, with the notable

exception of gyracanthids [61]. Furthermore, several features of the skeletal morphology suggest that *Gladbachus* was a continuous ram suspension feeder [73], somewhat like modern basking sharks (*Cetorhinus*). The head, including the gill skeleton, accounts for approximately 25% of estimated total body length, the reconstructed oral aperture is likely to have been in a near-perpendicular plane to the direction of forward movement, the dentition is minimal, and the lower jaw is long and slender (figure 2*b,c*). To the best of our knowledge, this is the earliest combination of such features known in any jawed vertebrate, adding to an emerging picture of total-group chondrichthyans as early, nektonic specialists, in contrast with the reconstructed demersal habits of their heavily skeletonized osteichthyan and ‘placoderm’ contemporaries [74]. Aspects of this character suite occur repeatedly among stem chondrichthyans, suggesting that the familiar gill slit condition of sharks might originate from such early, and apparently multiple, natural experiments in suspension feeding.

5. Conclusion

Gladbachus offers a glimpse of early chondrichthyan diversity yet to be discovered. Significantly, *Gladbachus* scales, if discovered as isolated specimens, would be unrecognizable as chondrichthyan in the new, total-group sense, unlike an increasing variety of Silurian and Ordovician [47–49,75] scale-based taxa assigned with increasing confidence to the chondrichthyan total-group. Insights offered by *Gladbachus* and other early chondrichthyans suggest that the morphological disparity in the early members of the chondrichthyan total-group was probably substantially greater than that which is

observed in the more-or-less stable shark morphotype which has persisted from the Middle Devonian through to the present. Accordingly, the importance of *Gladbachus* lies in its apparent morphological incongruence with its phylogenetic position, hinting at multiple paths leading to the modern shark-like body plan.

Data accessibility. Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.84mh3> [76].

Authors' contributions. M.I.C. and J.A.F. conceived the idea and designed the research. K.E.C. provided additional input. I.J.S. and P.S.A. provided all thin section histological analyses, related figure preparations and comparative scale data. K.E.C. and M.I.C. completed initial CT renderings. M.K.T. generated present CT renderings and produced the figures. K.E.C. provided comparative developmental data. M.L.R. and P.J.L.R. conducted the synchrotron CT scanning. J.A.F. and M.I.C. conducted phylogenetic analyses. J.A.F. conducted PCO analysis. The manuscript was drafted by M.I.C. with significant input from J.A.F., I.J.S. and K.E.C.

Competing interests. The authors declare no competing interests.

Funding. This work was supported by grants DEB-0917922 and DEB 1541491 from the National Science Foundation (USA) (to M.I.C.). GeoSoilEnviroCARS is supported by the National Science Foundation—Earth Sciences (EAR-1128799) and Department of Energy-GeoSciences (DE-FG02-94ER14466). The Advanced Photon Source, a U.S. Department of Energy (DOE) Office of Science User Facility, is operated for the DOE Office of Science by Argonne National Laboratory under contract no. DE-AC02-06CH11357.

Acknowledgements. We thank J.A. Clack and M. Lowe for specimen loan, U. Heidtke for provision of materials recording early preparation of specimen and K. A. Hardy for assistance with CT renderings. We thank the GeoSoilEnviroCARS (Sector 13), Advanced Photon Source (APS), Argonne National Laboratory for access and support to complete significant portions of this work.

References

- Zangerl R. 1981 Chondrichthyes I. In *Handbook of paleoichthyology 3A* (ed. H-P Schultze), 115 p. New York, NY: Gustav Fischer Verlag.
- Janvier P. 1996 *Early vertebrates*. Oxford, UK: Oxford University Press.
- Stahl BJ. 1999 Chondrichthyes III. In *Holocephali. Handbook of paleoichthyology 4* (ed. H-P Schultze), 164 p. München, Germany: Verlag Dr. Friedrich Pfeil.
- Miller RF, Cloutier R, Turner S. 2003 The oldest articulated chondrichthyan from the Early Devonian period. *Nature* **425**, 501–504. (doi:10.1038/nature02001)
- Maisey JG, Miller R, Turner S. 2009 The braincase of the chondrichthyan *Doliodus* from the Lower Devonian Campbellton Formation of New Brunswick, Canada. *Acta Zool.-Stockholm Suppl.* **90**, 109–122. (doi:10.1111/j.1463-6395.2008.00330.x)
- Maisey JG, Turner S, Naylor GJP, Miller RF. 2013 Dental patterning in the earliest sharks: implications for tooth evolution. *J. Morphol.* **275**, 586–596. (doi:10.1002/jmor.20242)
- Maisey JG, Miller R, Pradel A, Denton JSS, Bronson A, Janvier P. 2017 Pectoral morphology in *Doliodus*: bridging the ‘acanthodian’–chondrichthyan divide. *Am. Mus. Novit.* **3875**, 1–15. (doi:10.1206/3875.1)
- Maisey JG. 2001 A primitive chondrichthyan braincase from the middle Devonian of Bolivia. In *Major events in early vertebrate evolution* (ed. PE Ahlberg), pp. 263–288. London, UK: Taylor & Francis.
- Maisey JG, Anderson ME. 2001 A primitive chondrichthyan braincase from the Early Devonian of South Africa. *J. Vertebr. Paleontol.* **21**, 702–713. (doi:10.1671/0272-4634(2001)021[0702:APCBFT]2.0.CO;2)
- Janvier P, Maisey JG. 2010 The Devonian vertebrates of South America and their biogeographical relationships. In *Morphology, phylogeny and paleobiogeography of fossil fishes* (eds DK Elliot, JG Maisey, X Yu, D Miao), pp. 431–459. München, Germany: Verlag, Dr. Freidrich Pfeil.
- Maisey JG. 2005 Braincase of the Upper Devonian shark *Cladodoides wildungensis* (Chondrichthyes, Elasmobranchii), with observations on the braincase in early chondrichthyans. *Bull. Am. Mus. Nat. Hist.* **288**, 1–103. (doi:10.1206/0003-0090(2005)288<0001:BOTUDS>2.0.CO;2)
- Maisey JG. 2007 The braincase in Paleozoic symmoriform and cladoselachian sharks. *Bull. Am. Mus. Nat. Hist.* **307**, 1–122. (doi:10.1206/0003-0090(2007)307[1:TBIPSA]2.0.CO;2)
- Pradel A. 2010 Skull and brain anatomy of Late Carboniferous Sibirhynchidae (Chondrichthyes, Iniopterygia) from Kansas and Oklahoma (USA). *Geodiversitas* **32**, 595–566. (doi:10.5252/g2010n4a2)
- Pradel A, Tafforeau P, Maisey JG, Janvier P. 2011 A new Paleozoic Symmoriformes (Chondrichthyes) from the Late Carboniferous of Kansas (USA) and Cladistic Analysis of Early Chondrichthyans. *PLoS ONE* **6**, e24938. (doi:10.1371/journal.pone.0024938)
- Pradel A, Maisey JG, Tafforeau P, Mapes RH, Mallatt JA. 2014 A Palaeozoic shark with osteichthyan-like branchial arches. *Nature* **509**, 608–611. (doi:10.1038/nature13195)
- Coates MI, Gess RW, Finarelli JA, Criswell KE, Tietjen K. 2017 A symmoriform chondrichthyan braincase and the origin of chimaeroid fishes. *Nature* **541**, 208–211. (doi:10.1038/nature20806)
- Coates MI, Tietjen K. in press. The neurocranium of the Lower Carboniferous shark *Tristychius arcuatus* (Agassiz, 1837). *Earth Environ. Sci. Trans. R. Soc. Edinb.*
- Schaeffer B. 1981 The xenacanth shark neurocranium, with comments on elasmobranch monophyly. *Bull. Am. Mus. Nat. Hist.* **169**, 1–66.
- Coates MI, Sequeira SEK. 1998 The braincase of a primitive shark. *Trans. R. Soc. Edinb. (Earth Sci.)* **89**, 63–85. (doi:10.1017/S026359330000701X)
- Coates MI, Sequeira SEK. 2001 A new stethacanthid chondrichthyan from the Lower Carboniferous of

- Bearnsden, Scotland. *J. Vertebr. Paleontol.* **21**, 438–459. (doi:10.1671/0272-4634(2001)021[0438:ANSCTF]2.0.CO;2)
21. Coates MI, Sequeira SEK. 2001 Early sharks and primitive gnathostome interrelationships. In *Major events in early vertebrate evolution* (ed. PE Ahlberg), pp. 241–262. London, UK: Taylor & Francis.
 22. Zhu M, Yu X, Ahlberg PE, Choo B, Lu J, Qiao QL, Zhao J, Blom H, Zhu Y. 2013 A Silurian placoderm with osteichthyan-like marginal jaw bones. *Nature* **502**, 188–193. (doi:10.1038/nature12617)
 23. Lu J, Giles S, Friedman M, den Blaauwen JL, Zhu M. 2016 The oldest actinopterygian highlights the cryptic early history of the hyperdiverse ray-finned fishes. *Curr. Biol.* **26**, 1602–1608. (doi:10.1016/j.cub.2016.04.045)
 24. Brazeau MD, de Winter V. 2015 The hyoid arch and braincase anatomy of *Acanthodes* support chondrichthyan affinity of ‘acanthodians’. *Proc. R. Soc. B* **282**, 20152210. (doi:10.1098/rspb.2015.2210)
 25. King B, Qiao T, Lee MSY, Zhu M, Long JA. 2016 Bayesian morphological clock methods resurrect placoderm monophyly and reveal rapid early evolution in jawed vertebrates. *Syst. Biol.* **66**, 499–516. (doi:10.1093/sysbio/syw107)
 26. Qiao T, King B, Long JA, Ahlberg PE, Zhu M. 2016 Early gnathostome phylogeny revisited: multiple method consensus. *PLoS ONE* **11**, e0163157. (doi:10.1371/journal.pone.0163157)
 27. Zhu M, Ahlberg P, Pan Z, Zhu Y, Qiao T, Zhao W, Jia L, Lu J. 2016 A Silurian maxillate placoderm illuminates jaw evolution. *Science* **354**, 334–336. (doi:10.1126/science.aah3764)
 28. Denison R. 1979 Acanthodii. In *Handbook of paleoichthyology 3D* (ed. H-P Schultze) 62 p. New York, NY: Gustav Fischer Verlag.
 29. Brazeau MD. 2009 The braincase and jaws of a Devonian ‘acanthodian’ and modern gnathostome origins. *Nature* **457**, 305–308. (doi:10.1038/nature07436)
 30. Davis SP, Finarelli JA, Coates MI. 2012 *Acanthodes* and shark-like conditions in the last common ancestor of modern gnathostomes. *Nature* **486**, 247–250. (doi:10.1038/nature11080)
 31. Heidtke UHJ, Krätschmer K. 2001 *Glabdachus adentatus* nov. gen. et sp., ein primitiver Hai aus dem Oberen Givetium (Oberes Mitteldevon) der Bergisch Gladbach – Paffrath-Mulde (Rheinisches Schiefergebirge). *Mainzer geowiss. Mitt.* **30**, 105–122.
 32. Brazeau MD, Friedman M. 2014 The characters of Palaeozoic jawed vertebrates. *Zool. J. Linn. Soc.* **170**, 779–821. (doi:10.1111/zooj.12111)
 33. Burrow CJ, Turner S. 2013 Scale structure of the putative chondrichthyan *Glabdachus adentatus* Heidtke & Krätschmer, 2001 from the Middle Devonian Rheinisches Schiefergebirge, Germany. *Hist. Biol.* **25**, 385–390. (doi:10.1080/08912963.2012.722761)
 34. Burrow CJ, den Blaauwen J, Newman M, Davidson R. 2016 The diplacanthid fishes (Acanthodii, Diplacanthiformes, Diplacanthidae) from the Middle Devonian of Scotland. *Palaeontol. Electronica.* **19**, 1–83.
 35. Swofford DL. 2003 *PAUP*: phylogenetic analysis using parsimony (*and other methods)*, version 4.0a147. Sunderland, MA: Sinauer Associates.
 36. Felsenstein J. 1985 Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**, 783–791. (doi:10.1111/j.1558-5646.1985.tb00420.x)
 37. Bremer K. 1988 The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* **42**, 795–803. (doi:10.1111/j.1558-5646.1988.tb02497.x)
 38. Eriksson T. 2001 *AutoDecay*, version 5.0.
 39. Swofford DL, Maddison WP. 1987 Reconstructing ancestral character states under Wagner parsimony. *Math. Biosci.* **87**, 199–229. (doi:10.1016/0025-5564(87)90074-5)
 40. Wills MA. 1998 Crustacean disparity through the Phanerozoic: comparing morphological and stratigraphic data. *Biol. J. Linn. Soc.* **65**, 455–500. (doi:10.1111/j.1095-8312.1998.tb01149.x)
 41. Davis JC. 1986 *Statistics and data analysis in geology*. New York, NY: John Wiley & Sons.
 42. Creanza N, Schwarz JS, Cohen JE. 2010 Intraseasonal dynamics and dominant sequences in H3N2 influenza. *PLoS ONE* **5**, e8544. (doi:10.1371/journal.pone.0008544)
 43. Seidel R, Lyons K, Blumer M, Zalansky P, Fratzi P, Weaver JC, Dean MN. 2016 Ultrastructural and developmental features of the tessellated endoskeleton of elasmobranchs (sharks and rays). *J. Anat.* **229**, 681–702. (doi:10.1111/joa.12508)
 44. Maisey JG. 2013 The diversity of tessellated calcification in modern and extinct chondrichthyans. *Rev. Paléobiol.* **32**, 355–371.
 45. Burrow CJ, Turner S. 1999 A review of placoderm scales, and their significance in placoderm phylogeny. *J. Vertebr. Paleontol.* **19**, 204–219. (doi:10.1080/02724634.1999.10011135)
 46. Ginter M, Hampe O, Duffin C. 2010 Paleozoic elasmobranchii: teeth. In *Handbook of paleoichthyology 3D* (ed. H-P Schultze) 168 p. München, Germany: Verlag Dr. Friedrich Pfeil.
 47. Karatajūtė-Talimaa V. 1998 Determination methods for the exoskeletal remains of early vertebrates. *Fossil Record* **1**, 21–51. (doi:10.5194/fr-1-21-1998)
 48. Andreev PS, Coates MI, Shelton RM, Cooper RM, Smith MP, Sansom IJ. 2015 Upper Ordovician chondrichthyan-like scales from North America. *Palaeontology* **58**, 691–704. (doi:10.1111/pala.12167)
 49. Andreev PS, Coates MI, Karatajūtė-Talimaa V, Shelton RM, Cooper PR, Sansom IJ. 2017 *Elegestolepis* and its kin, the earliest monodontode chondrichthyans. *J. Vertebr. Paleontol.* **37**, e1245664. (doi:10.1080/02724634.2017.1245664)
 50. Stensiö EA. 1963 Anatomical studies on the arthrodiran head (part I). *K. Sv. Vet. Akad. Handl. Ser. 4.* **9**, 1–419.
 51. Young, GC. 1980 A new early Devonian placoderm from New South Wales, Australia, with a discussion of placoderm phylogeny. *Palaeontographica* **A167**, 10–76.
 52. Goujet D. 1984 *Les poissons placodermes du Spitsberg*. Paris, France: CNRS.
 53. Hu Y, Lu J, Young GC. 2017 New findings in a 400 million-year-old Devonian placoderm shed light on jaw structure and function in basal gnathostomes. *Sci. Rep.* **7**, 7813. (doi:10.1038/s41598-017-07674-y)
 54. Heidtke UHJ, Schwind C, Krätschmer K. 2004 Über die Organisation des Skelettes und die verwandtschaftlichen Beziehungen der Gattung *Triodus* Jordan 1849 (Elasmobranchii: Xenacanthida). *Mainzer Geowiss. Mitt.* **32**, 9–54.
 55. Brazeau MD, Friedman M, Jerve A, Atwood RC. 2017 A three-dimensional placoderm (stem-group gnathostome) pharyngeal skeleton and its implications for primitive gnathostome pharyngeal structure. *J. Morphol.* **278**, 1220–1228. (doi:10.1002/jmor.20706)
 56. Heidtke UHJ. 2009 *Glabdachus adentatus*, die Geschichte des weltweit ältesten Hais—untersucht und beschrieben aus dem AK Geowissenschaften. *Pollichia Kurrier.* **25**, 24–26.
 57. Miles RS. 1973 Relationships of acanthodians. In *Interrelationships of fishes* (eds PH Greenwood, RS Miles, C Patterson), pp. 63–103. London, UK: Academic Press.
 58. Hotton N. 1952 Jaws and teeth of American xenacanth sharks. *J. Paleontol.* **26**, 489–500.
 59. Cohen KM, Finney SC, Gibbard PL, Fan J-X. 2017 The ICS International Chronostratigraphic Chart (2013; updated). *Episodes* **36**, 199–204.
 60. Sallan LC, Coates MI. 2010 End Devonian extinction and a bottleneck in the early evolution of modern jawed vertebrates. *Proc. Natl Acad. Sci. USA* **107**, 10 131–10 135. (doi:10.1073/pnas.0914000107)
 61. Sallan LC, Galimberti AK. 2015 Body-size reduction in vertebrates following the end-Devonian mass extinction. *Science* **35**, 812–815. (doi:10.1126/science.aac7373)
 62. Dineley DL, Metcalf SJ. 1999 Fossil fishes of Great Britain. In *Geological conservation review series 16* (ed. D Palmer) 675 pp. Peterborough, UK: Joint Nature Conservation Committee.
 63. Lund R, Poplin C. 1999 Fish diversity of the Bear Gulch Limestone, Namurian, Lower Carboniferous of Montana, USA. *Geobios* **32**, 285–295. (doi:10.1016/S0016-6995(99)80042-4)
 64. Grogan ED, Lund R, Greenfest-Allen E. 2012 The origin and relationships of early chondrichthyans. In *Biology of sharks and their relatives* (eds JC Carrier, JA Musick, MR Heithaus), pp. 3–29. Boca Raton, FL: CRC Press.
 65. Zhu M, Zhao W, Jia L, Lu J, Qiao T, Qu Q. 2009 The oldest articulated osteichthyan reveals a mosaic of gnathostome characters. *Nature* **458**, 469–474. (doi:10.1038/nature07855)
 66. Burrow CJ, Rudkin D. 2014 Oldest near-complete acanthodian: the first vertebrate from the Silurian Bertie Formation konservat-Lagerstätte, Ontario. *PLoS ONE* **9**, e104171. (doi:10.1371/journal.pone.0104171)

67. Brazeau MD. 2012. A revision of the anatomy of the early Devonian jawed vertebrate *Ptomacanthus anglicus* Miles. *Palaeontology* **55**, 355–367. (doi:10.1111/j.1475-4983.2012.01130.x)
68. Hanke GF, Wilson MVH. 2006 Anatomy of the Early Devonian acanthodian *Brochoadmones milesi* based on nearly complete body fossils, with comments on the evolution and development of paired fins. *J. Vertebr. Paleontol.* **26**, 526–537. (doi:10.1671/0272-4634(2006)26[526:AOTEDA]2.0.CO;2)
69. Gagnier, P-Y, Wilson MVH. 1996 Early Devonian acanthodians from northern Canada. *Palaeontology* **39**, 241–258.
70. Hanke GF. 2008 *Promesacanthus eppleri* n. gen., n. sp., a mesacanthid (Acanthodii, Acanthodiformes) from the Lower Devonian of northern Canada. *Geodiversitas* **30**, 287–302.
71. Karatajūtė-Talimaa V, Smith MM. 2003 Early acanthodians from the Lower Silurian of Asia. *Trans. R. Soc. Edinb. (Earth Sci.)* **92**, 277–299.
72. Sansom IJ, Andreev P. In press. The Ordovician enigma: fish, first appearances and phylogenetic controversies. In *Evolution and development of fishes* (eds Z Johanson, M Richter, C Underwood). Cambridge, UK: Cambridge University Press.
73. Sanderson SL, Wassersug R. 1993 Convergent and alternative designs for vertebrate suspension feeding. In *The skull volume 3: functional and evolutionary mechanisms* (eds J Hanken, BK Hall), pp. 37–112. Chicago, IL: University of Chicago Press.
74. Blicek A. 2011 From adaptive radiations to biotic crises in Palaeozoic vertebrates: a geobiological approach. *Geol. Belg.* **14**, 203–227. (doi:10.1007/s12549-016-0260-1)
75. Sansom IJ, Davies NS, Coates MI, Nicoll RS, Ritchie A. 2012 Chondrichthyan-like scales from the Middle Ordovician of Australia. *Palaeontology* **55**, 243–247. (doi:10.1111/j.1475-4983.2012.01127.x)
76. Coates MI, Finarelli JA, Sansom IJ, Andreev PA, Criswell KE, Tietjen K, Rivers ML, La Riviere PJ. 2017 Data from: An early chondrichthyan and the evolutionary assembly of a shark body plan. Dryad Digital Repository. (<https://doi.org/10.5061/dryad.84mh3>)