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

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

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

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19

20

21 **Abstract**

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

38

39

40 **Keywords:**

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

42

43

## 44 1. Introduction

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

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

69

70

71 **2. Materials and methods**72 **(a) Specimens**

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

78

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

80 Whole specimen scans: large scale scans were completed by the High Resolution X-ray Computed  
81 Tomography facility at the University of Texas at Austin (UTCT, [www.digimorph.org](http://www.digimorph.org)).

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

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

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

95

96 **(c) Phylogenetic and phenetic analysis**

97 The phylogenetic data matrix is developed from sources including iterations of the early gnathostome data  
98 matrix by Brazeau [29], Davis *et al.* [30] and Zhu *et al.* [22]; most recently updated by Lu *et al.* [23],  
99 Qiao *et al.* [26], Zhu *et al.* [27] and Burrow *et al.* [34]. Chondrichthyan content includes substantial  
100 additions of new data drawn from Pradel *et al.* [14,15], Coates *et al.* [16], Coates & Tietjen [17], and  
101 observation of original specimens (electronic supplementary material).

102 Phylogenetic Methods: The primary character matrix consists of 84 ingroup taxa and 2 outgroup  
103 taxa (Galeaspida and Osteostraci) coded for 262 characters. Character and taxon sampling sources and  
104 discussion are provided in electronic supplementary material. Phylogenetic analyses used maximum  
105 parsimony implemented in PAUP\*4.0.152 [35]. Nodal support was assessed via bootstrapping [36] and  
106 Bremer Decay Indices [37], carried out using AutoDecay [38] and PAUP\*. Details of phylogenetic  
107 methods are provided in the electronic supplementary material. Character state transitions by node for the  
108 strict consensus cladogram of the MPTs were reconstructed in PAUP\* assuming hard polytomies with  
109 DELTRAN [39] optimization (see Davis *et al.* [30], Coates *et al.* [16]).

110 A Principle Coordinate analysis (PCO) [40,41] was performed on the Hamming distance matrix  
111 [42] of the character data. Computed dissimilarity was restricted to characters coded for both taxa, and  
112 distances were normalized to the number of characters coded for both members in each taxon pair. For the  
113 PCO, all characters were treated as equally weighted and unordered.

114

115

116 **3. Results**

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

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

122           Although considered one of the few 'unambiguous sharks' of the Lower and Middle Devonian  
123 [32], details of *Gladbachus* anatomy do not conform in a straightforward manner with contemporary  
124 models of early chondrichthyan anatomy. The internal skeleton consists of calcified cartilage with no  
125 perichondral bone, yet the cartilage surface lacks the tightly connected tesserae that is a hallmark of  
126 chondrichthyan skeletal anatomy [15,43]. Rather, most cartilage surfaces bear a mesh of continuously  
127 calcified ridges (electronic supplementary material, figure S2), broadly resembling the 'wood-like' [44]  
128 texture observed in some Mesozoic elasmobranchs. Discrete tesserae are visible only in the walls of the  
129 semicircular canals, but these are irregularly sized and shaped, with broad intertesseral spaces. Thin  
130 section histology and synchrotron microtomography show that poorly delineated tesserae are distributed  
131 elsewhere in the skeleton, but concealed beneath the continuously mineralized cartilage surface.

132           The dermal skeleton includes no large plates. Head scales (figure 1*d*) are mostly larger than trunk  
133 scales (figure 1*f*) and the lateral line runs between scales. However, scale shape, composition and  
134 histology are remarkable, as they resemble conditions observed in 'placoderms' [45,33], and differ  
135 markedly from polyodontode scales like those of *Doliodus* [4,46] and mongolepids [47,48]. In  
136 *Gladbachus*, scale and branchial denticle crowns consist of overlapping, mono-layered, cellular dentine  
137 tubercles (electronic supplementary material, figure S3), lacking neck and basal canals. The standard,  
138 total-group chondrichthyan scale growth pattern of areally apposed odontodes [32] is absent, as are  
139 growing monodontode scales [49], and the non-growing placoid scales characteristic of modern  
140 chondrichthyans. Instead, the reconstructed growth pattern of *Gladbachus* scales is linear and  
141 bidirectional. Most unusually for a chondrichthyan, the cranial scales are asymmetric, with irregular and  
142 inconsistent shapes. Fin spines, and spines associated with girdles and the flank region, are completely  
143 absent.

144           The anterior section of the braincase is not preserved (figure 1*a,b*), thus evidence of a precerebral  
145 fontanelle is unknown, *contra* Heidtke and Kratschmer [31]. The right postorbital process includes traces of a  
146 jugular canal, and a groove on the posterior surface, likely for articulation with the upper jaw (electronic  
147 supplementary material, figure S4). The basicranium is compressed against the subjacent visceral arches, and



148 too poorly preserved to demonstrate presence or absence of a ventral cranial fissure, or canals for all or part of  
149 the dorsal aorta network. Reconstructions of the vestibular, semicircular canals and ampullary spaces  
150 (electronic supplementary material, figure S4c) demonstrate that the otic capsules were large and widely  
151 separated across the midline. In extant gnathostomes, this degree of lateral separation is manifest only in  
152 embryonic forms, and resemble adult conditions observed in 'placoderms' [50-53]. A pair of ring-shaped  
153 structures flanking the dorsal ridge, next to the anterior lip of the persistent otico-occipital fissure probably  
154 represents endolymphatic duct openings. This location for the endolymphatic ducts is consistent with the  
155 absence of an endolymphatic fossa or single, median endolymphatic foramen, which characterizes all Recent  
156 and fossil conventional chondrichthyans.

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

174 The hyoid arch (figures 1*a,b* and 2*c,d*) is morphologically distinct from the gill arches. There is  
175 no interhyal, and both the large and well-mineralized ceratohyal and slender first ceratobranchial  
176 articulate with a broad basihyal. The five gill arches (electronic supplementary material, figure S7) are  
177 positioned caudal to the braincase, as in non-holocephalan chondrichthyans. Epibranchials are present on  
178 the first four arches, with anteriorly-directed simple pharyngobranchials (with no  
179 suprapharyngobranchials) present in the first three gill arches (figures 1*a* and 2*c*) as in osteichthyans and  
180 *Ozarcus* [15]. A pair of short, laterally directed cartilages medial to the base of the second gill provide the  
181 only evidence of hypobranchials. The fifth arch ceratobranchials are unusually broad, nearly rectangular,  
182 and keeled along the anterior margin. Remarkably, and uniquely, these resemble the posteriormost  
183 ceratobranchials of *Paraplesiobatis*, a Lower Devonian 'placoderm' [55] (electronic supplementary  
184 material, figure S8). The ceratobranchials of *Gladbachus* fourth and fifth gill arches articulate with a large  
185 basibranchial copula, which is separated from the basihyal by a large gap. This revised description  
186 provides the first accurate association of dorsal to ventral parts of each arch.

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

192

### 193 **(c) Phylogenetic analysis and principal coordinates analysis.**

194 Phylogenetic analysis of the data set returned 249,600 most parsimonious trees (TL = 691, CI = 0.396, RI  
195 = 0.785, RCI = 0.311). The strict consensus cladogram of MPTs (figure 3*a*, electronic supplementary  
196 material, figure S11) strongly corroborates recent phylogenetic hypotheses of early gnathostomes [23-27],  
197 reconstructing all taxa usually referred to as acanthodians in a paraphyletic assemblage branching from  
198 the chondrichthyan stem. Here, *Gladbachus* is also recovered as a stem-chondrichthyan, as the sister  
199 taxon to a poorly resolved set of climatiid acanthodians and conventional chondrichthyans (including

200 crown clade Chondrichthyes). A monophyletic group uniting diplacanthid, ischnacanthid and acanthodid  
201 acanthodians forms a clade that is the sister group of all other total-group chondrichthyans, including  
202 *Gladbachus*.

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

207 *Contra* Qiao *et al.* [26] and Zhu *et al.* [27], *Ramirosuarezia* is not recovered among 'acanthodian'  
208 stem chondrichthyans, but rather, is nested among stem-gnathostomes, with other taxa, such as *Qilinyu*,  
209 *Entelognathus* and *Janusiscus* branching crownward of the paraphyletic placoderms.

210 Within the chondrichthyan crown-group, xenacanth and ctenacanth (*sensu lato*) form a clade  
211 branching from the elasmobranch stem. A further, poorly resolved cluster, including *Homalodontus*,  
212 *Tristychius*, *Acronemus* and hybodontids branches from more crownward nodes, suggesting successive  
213 sister groups to the elasmobranch crown and close relatives. Holocephalans include the symmoriids,  
214 corroborating the arrangement found in Coates *et al.* [16].

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

220 Principal coordinates (PCO) analysis of the character data recovers all four of the traditional  
221 gnathostome divisions ('placoderms', 'acanthodians', osteichthyans and chondrichthyans) as discrete  
222 clusters in the space defined by the first three PCO axes (figure 3c,d). Notably, *Gladbachus* clusters with  
223 chondrichthyans in the PCO, despite its phylogenetic position among 'acanthodians'. *Gladbachus*,  
224 *Doliodus* and *Pucapampella* each occupy positions in PCO space between conventionally defined  
225 chondrichthyans and 'acanthodians', however, these three genera are all significantly closer in PCO space

226 to chondrichthyan taxa than to 'acanthodians' (t-tests of the intertaxon distances in PCO space for  
227 *Gladbachus*, *Doliodus*, and *Pucapampella* yield p-values of  $1.39 \times 10^{-6}$ , 0.01, and  $8.65 \times 10^{-8}$ , respectively).

228

229

#### 230 **4. Discussion**

##### 231 **(a) Tree shapes and implications for evolutionary timescale.**

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

238 Support for the acanthodian branching pattern is weak (electronic supplementary material, figure  
239 S11), but consistent with recent analyses [23-27]. Recent reconstructions have recovered traditional  
240 acanthodian family-level sets: acanthodids, ischnacanthids, diplacanthids and climatiids (electronic  
241 supplementary material, figure S9). In all of these trees, the climatiids group with conventional  
242 chondrichthyans, echoing results of Brazeau [29] and Davis *et al.* [30]. Diplacanthids, ischnacanthids and  
243 acanthodids fall into one of two arrangements, 1) as successive sister groups to more crownward taxa  
244 [25,27], or 2) as in the present analysis, a monophyletic clade [23,24]. Here, we propose resurrecting the  
245 term Acanthodii to define the diplacanthid-ischnacanthid-acanthodid clade.

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

251 Hangenberg extinction [59,60], which is evident from faunas recorded at Lower Carboniferous localities  
252 such as Glencartholm [61], Bearsden [61], and Bear Gulch [62,63].

253         Conventional chondrichthyan conditions, exemplified by *Doliodus* [4], are present by the middle-  
254 Lower Devonian (Pragian: ~410mya), and a minimum date for the origin of the chondrichthyan total-  
255 group is currently tethered to the late Silurian (Ludlow: ~423 mya) by the earliest well-preserved  
256 osteichthyan (*Guiyu*) [64]. However, the earliest 'acanthodian' stem-chondrichthyan body fossils  
257 (*Nerepisacanthus*) are only slightly younger (Pridoli: ~419 mya) [65], and a wide variety of 'acanthodians'  
258 are known from the Lower Devonian (e.g. *Ptomacanthus*, *Brochoadmones*, *Cassidiceps* and  
259 *Promesacanthus* [29,66-69]). Such diversity, first apparent in the Lochkovian (figure 4) supported by a  
260 taphonomically biased record of articulated specimens, implies either a sudden radiation in the early  
261 Lower Devonian or a severely under-sampled history of Silurian stem-sharks. The latter hypothesis is  
262 supported by isolated scales scattered through the Middle Ordovician to Silurian [48,49], including  
263 strikingly characteristic, classically defined 'acanthodian' scales from the Rhuddanian (Llandovery  
264 ~440mya) of the Siberian Platform [70]. In the present phylogenetic context, we prefer to combine the  
265 micro- and macro-/articulated fossil records, which strongly suggest that the chondrichthyan total group,  
266 and, therefore, the gnathostome crown node, dates to at least the earliest Silurian, ~440 million-years-ago.  
267 Thus, the early history of chondrichthyans consists of two phases (figure 4): a Silurian-Devonian  
268 evolutionary radiation of micromeric, acanthodian-like taxa, and a subsequent Carboniferous radiation of  
269 the crown clade, initially dominated by holocephalans [16,63].

270

#### 271 **(b) Palaeobiological inferences**

272         *Gladbachus* adds to an increasingly populated chondrichthyan stem lineage that also includes  
273 *Acanthodes* [24,30], *Ptomacanthus* [29,66], *Pucapampella* [8-10] and *Doliodus* [4-7]. The resultant data  
274 on early chondrichthyan morphological diversity captures endoskeletal detail comparable to the content of  
275 early osteichthyans, contributing to a more balanced interpretation of the initial gnathostome radiation.  
276 However, there is no straightforward emerging sequence of character acquisition for the chondrichthyan

277 crown group (crown clade apomorphies are listed in electronic supplementary material, figure S10). The  
278 current analysis highlights conflicting patterns of character-state distributions, implying repeated and  
279 convergent evolution of chondrichthyan-like specializations among the earliest total-group members. For  
280 *Gladbachus*, PCO analysis clearly identifies the chondrichthyan-like nature of its body plan (figure 3c),  
281 but this stands in marked contrast to its reconstruction as representative of a previously unrecognized  
282 'acanthodian' lineage (figures 3a,b and 4). *Gladbachus* approaches a quantifiably defined shark space, but  
283 does so from a phylogenetically distinct origin (electronic supplementary material, figure S10).

284         The character combination observed in *Gladbachus*, alongside the array of contrasting conditions  
285 observed in Early Devonian acanthodians (figure 4), defies conventional hypotheses of morphologically  
286 segregated acanthodian and chondrichthyan morphotypes, reinforcing the hypothesis that pre-Devonian  
287 stem-chondrichthyan diversity is fundamentally under-sampled. Reasons for the absence of substantial  
288 Silurian remains of crown gnathostomes are unclear, although restricted environmental specificity has  
289 been conjectured [71]. *Gladbachus* is a morphotypic outlier, in the sense that although phylogenetically  
290 placed within the acanthodian grade, it lacks fin spines, its scales lack synapomorphies shared with any  
291 acanthodian subgroup, and its estimated body length (electronic supplementary material, figure S1) is two  
292 to three times greater than contemporary or earlier 'acanthodians', with the notable exception of  
293 gyracanthids [60]. Furthermore, several features of the skeletal morphology suggest that *Gladbachus* was  
294 a continuous ram suspension feeder [72], somewhat like modern basking sharks (*Cetorhinus*). The head,  
295 including the gill skeleton, accounts for ~25% of estimated total body length, the reconstructed oral  
296 aperture is likely to have been in a near-perpendicular plane to the direction of forward movement, the  
297 dentition is minimal, and the lower jaw is long and slender (figure 2b,c). To the best of our knowledge,  
298 this is the earliest combination of such features known in any jawed vertebrate, adding to an emerging  
299 picture of total-group chondrichthyans as early, nektonic specialists, in contrast to the reconstructed  
300 demersal habits of their heavily skeletonized osteichthyan and 'placoderm' contemporaries [73]. Aspects  
301 of this character-suite occur repeatedly among stem chondrichthyans, suggesting that the familiar gill slit

302 condition of sharks might originate from such early, and apparently multiple, natural experiments in  
303 suspension feeding.

304

305

## 306 **5. Conclusion**

307 *Gladbachus* offers a glimpse of early chondrichthyan diversity yet to be discovered. Significantly,  
308 *Gladbachus* scales, if discovered as isolated specimens, would be unrecognizable as chondrichthyan in  
309 the new, total-group sense, unlike an increasing variety of Silurian and Ordovician [47-49,74] scale-based  
310 taxa assigned with increasing confidence to the chondrichthyan total-group. Insights offered by  
311 *Gladbachus* and other early chondrichthyans suggest that the morphological disparity in the early  
312 members of the chondrichthyan total group was likely substantially greater than that which is observed in  
313 the more-or-less stable shark-morphotype which has persisted from the Middle Devonian through to the  
314 present. Accordingly, the importance of *Gladbachus* lies in its apparent morphological incongruence with  
315 its phylogenetic position, hinting at multiple paths leading to the modern shark-like body plan.

316

317 **Data accessibility.** Data available from the Dryad Digital Repository:

318 <https://doi.org/10.5061/dryad.84mh3>

319

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

327

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329

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341

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### 343 **References**

- 344 1. Zangerl R. 1981 Chondrichthyes I. *Handbook of Paleoichthyology 3A* (ed. H-P Schultze) 115 pp.  
345 New York, USA: Gustav Fischer Verlag.
- 346
- 347 2. Janvier P. 1996 *Early Vertebrates*. Oxford, UK: Oxford University Press.
- 348
- 349 3. Stahl BJ. 1999 Chondrichthyes III: Holocephali. *Handbook of Paleoichthyology 4* (ed. H-P Schultze)  
350 164 pp. München, Germany: Verlag Dr. Friedrich Pfeil.

351



- 352 4. Miller RF, Cloutier R, Turner S. 2003 The oldest articulated chondrichthyan from the Early Devonian  
353 period. *Nature*. **425**, 501–504. (doi:10.1038/nature02001)  
354
- 355 5. Maisey JG, Miller R, Turner S. 2009 The braincase of the chondrichthyan *Doliodus* from the  
356 Lower Devonian Campbellton Formation of New Brunswick, Canada. *Acta Zool.-Stockholm*  
357 *Suppl.* **90**, 109-122. (doi:10.1111/j.1463-6395.2008.00330.x)  
358
- 359 6. Maisey JG, Turner S., Naylor GJP, Miller RF. 2013 Dental patterning in the earliest sharks:  
360 implications for tooth evolution. *J. Morphol.* **2013**, 1-11. (doi:10.1002/jmor.20242)  
361
- 362 7. Maisey JG, Miller R, Pradel A, Denton JSS, Bronson A, Janvier P. 2017 Pectoral morphology in  
363 *Doliodus*: bridging the 'acanthodian'-chondrichthyan divide. *Am. Mus. Novit.* **3875**, 1-15.  
364 (doi:10.1206/3875.1)  
365
- 366 8. Maisey JG. 2001 A primitive chondrichthyan braincase from the middle Devonian of Bolivia. In  
367 *Major Events in Early Vertebrate Evolution* (ed. PE Ahlberg), pp. 263–288 London, UK: Taylor  
368 & Francis.  
369
- 370 9. Maisey JG, Anderson ME. 2001 A primitive chondrichthyan braincase from the Early Devonian  
371 of South Africa. *J. Vertebr. Paleontol.* **21**, 702-713. (doi:10.1671/0272-  
372 4634(2001)021[0702:APCBFT]2.0.CO;2)  
373
- 374 10. Janvier P, Maisey JG. 2010 The Devonian vertebrates of South America and their biogeographical  
375 relationships. In *Morphology, Phylogeny and Paleobiogeography of Fossil Fishes* (eds DK Elliot, JG  
376 Maisey, X Yu, D Miao), pp. 431-459. München, Germany: Verlag, Dr. Freidrich Pfeil.  
377

- 378 11. Maisey JG. 2005 Braincase of the Upper Devonian shark *Cladodoidea wildungensis*  
379 (Chondrichthyes, Elasmobranchii), with observations on the braincase in early chondrichthyans.  
380 *Bull. Am. Mus. Nat. Hist.* **288**, 1–103. (doi:10.1206/0003-  
381 0090(2005)288<0001:BOTUDS>2.0.CO;2)  
382
- 383 12. Maisey JG. 2007 The braincase in Paleozoic symmoriiform and cladoselachian sharks. *Bull. Am.*  
384 *Mus. Nat. Hist.* **307**,1-122.  
385
- 386 13. Pradel A. 2010 Skull and brain anatomy of Late Carboniferous Sibirhynchidae (Chondrichthyes,  
387 Iniopterygia) from Kansas and Oklahoma (USA). *Geodiversitas* **32**, 595–66.  
388 (doi:10.5252/g2010n4a2)  
389
- 390 14. Pradel A, Tafforeau P, Maisey JG, Janvier P. 2011 A new Paleozoic Symmoriiformes  
391 (Chondrichthyes) from the Late Carboniferous of Kansas (USA) and Cladistic Analysis of Early  
392 Chondrichthyans. *PLoS ONE*. **6**, e24938. (doi:10.1371/journal.pone.0024938)  
393
- 394 15. Pradel A, Maisey JG, Tafforeau P, Mapes RH, Mallatt JA. 2014 A Palaeozoic shark with  
395 osteichthyan-like branchial arches. *Nature*. **509**, 608-611. (doi:10.1038/nature13195)  
396
- 397 16. Coates MI, Gess RW, Finarelli JA, Criswell KE, Tietjen K. 2017 A symmoriiform chondrichthyan  
398 braincase and the origin of chimaeroid fishes. *Nature*. **541**, 208-211. (doi:10.1038/nature20806)  
399
- 400 17. Coates MI, Tietjen K. in press. The neurocranium of the Lower Carboniferous shark *Tristychius*  
401 *arcuatus* (Agassiz, 1837). *Earth Environ. Sci. Trans. R. Soc. Edinb.*  
402

- 403 18. Schaeffer B. 1981 The xenacanth shark neurocranium, with comments on elasmobranch monophyly.  
404 *Bull. Am. Mus. Nat. Hist.* **169**, 1-66.  
405
- 406 19. Coates MI, Sequeira SEK. 1998 The braincase of a primitive shark. *Trans. R. Soc. Edinb. (Earth*  
407 *Sci.)* **89**, 63–85. (doi:10.1017/S026359330000701X)  
408
- 409 20. Coates MI, Sequeira SEK. 2001a A new stethacanthid chondrichthyan from the Lower  
410 Carboniferous of Bearsden, Scotland. *J. Vertebr. Paleontol.* **21**, 438–459 (2001a).  
411 (doi:10.1671/0272-4634(2001)021[0438:ANSCFT]2.0.CO;2)  
412
- 413 21. Coates MI, Sequeira SEK. 2001b Early sharks and primitive gnathostome interrelationships. In  
414 *Major Events in Early Vertebrate Evolution* (ed. PE Ahlberg), pp. 241–262 London, UK: Taylor  
415 & Francis.  
416
- 417 22. Zhu M, Yu X, Ahlberg PE, Choo B, Lu J, Qiao QL, Zhao J, Blom H, Zhu Y. 2013 A Silurian  
418 placoderm with osteichthyan-like marginal jaw bones. *Nature.* **502**, 188-193.  
419 (doi:10.1038/nature12617)  
420
- 421 23. Lu J, Giles S, Friedman M, den Blaawen JL, Zhu M. 2016 The oldest actinopterygian highlights  
422 the cryptic early history of the hyperdiverse ray-finned fishes. *Curr. Biol.* **26**, 1-7.  
423 (doi:10.1016/j.cub.2016.04.045)  
424
- 425 24. Brazeau MD, de Winter V. 2015 The hyoid arch and braincase anatomy of *Acanthodes* support  
426 chondrichthyan affinity of 'acanthodians'. *Proc. R. Soc. B* **282**: e20152210 (doi:10.1098/rspb.  
427 2015.2210)  
428

- 429 25. King B, Qiao T, Lee MSY, Zhu M, Long JA. 2016 Bayesian morphological clock methods  
430 resurrect placoderm monophyly and reveal rapid early evolution in jawed vertebrates. *Syst. Biol.*  
431 **2016**, syw107 (doi:10.1093/sysbio/syw107)  
432
- 433 26. Qiao T, King B, Long JA, Ahlberg PE, Zhu M. 2016 Early Gnathostome Phylogeny Revisited:  
434 Multiple Method Consensus. *PLoS ONE*. **11**, e0163157. (doi:10.1371/journal.pone.0163157).  
435
- 436 27. Zhu M, Ahlberg P, Pan Z, Zhu Y, Qiao T, Zhao W, Jia L., Lu J. 2016 A Silurian maxillate  
437 placoderm illuminates jaw evolution. *Science*. **354**, 334-336. (doi:10.1126/science.aaah3764)  
438
- 439 28. Denison R. 1979 Acanthodii. *Handbook of Paleoichthyology 3D* (ed. H-P Schultze) 62 pp. New  
440 York, USA: Gustav Fischer Verlag.  
441
- 442 29. Brazeau MD. 2009 The braincase and jaws of a Devonian ‘acanthodian’ and modern gnathostome  
443 origins. *Nature*. **457**, 305-308. (doi:10.1038/nature07436)  
444
- 445 30. Davis SP, Finarelli JA, Coates MI. 2012 *Acanthodes* and shark-like conditions in the last common  
446 ancestor of modern gnathostomes. *Nature*. **486**, 247-250. (doi:10.1038/nature11080)  
447
- 448 31. Heidtke UHJ, Krätschmer K. 2001 *Gladbachus adentatus* nov. gen. et sp., ein primitiver Hai aus dem  
449 Oberen Givetium (Oberes Mitteldevon) der Bergisch Gladbach – Paffrath-Mulde (Rheinisches  
450 Schiefergebirge). *Mainzer geowiss. Mitt.* **30**, 105-122.  
451
- 452 32. Brazeau MD, Friedman M. 2014 The characters of Palaeozoic jawed vertebrates. *Zool. J. Linn. Soc.*  
453 **170**, 779-821. (doi:10.1111/zoj.12111)

- 454
- 455 33. Burrow CJ, Turner S. 2013 Scale structure of the putative chondrichthyan *Gladbachus adentatus*  
456 Heidtke & Krätschmer, 2001 from the Middle Devonian Rheinisches Schiefergebirge, Germany. *Hist.*  
457 *Biol.* **25**, 385-390. (doi:10.1080/08912963.2012.722761)
- 458
- 459 34. Burrow CJ, den Blaauwen, J, Newman M, Davidson R. 2016 The diplacanthid fishes  
460 (Acanthodii, Diplacanthiformes, Diplacanthidae) from the Middle Devonian of Scotland.  
461 *Palaeontol. Electronica.* **19**, 1-83.
- 462
- 463 35. Swofford DL. 2003 PAUP\*. Phylogenetic analysis using parsimony (\*and other methods). Version  
464 4.0a147 Sunderland, MA: Sinauer Associates.
- 465
- 466 36. Felsenstein J. 1985 Confidence-limits on phylogenies - an approach using the bootstrap. *Evolution.*  
467 **39**, 783-791.
- 468
- 469 37. Bremer K. 1988 The limits of amino-acid sequence data in angiosperm phylogenetic reconstruction.  
470 *Evolution.* **42**, 795-803.
- 471
- 472 38. Eriksson T. 2001 *AutoDecay* Version 5.0.
- 473
- 474 39. Swofford DL, Maddison WP. 1987 Reconstructing ancestral character states under Wagner  
475 parsimony. *Math. Biosci.* **87**, 199-229.
- 476
- 477 40. Wills MA. 1998 Crustacean disparity through the Phanerozoic: comparing morphological and  
478 stratigraphic data. *Biol. J. Linn. Soc.* **65**, 455-500.
- 479

- 480 41. Davis JC. 1986 *Statistics and Data Analysis in Geology*. New York, USA: John Wiley & Sons.  
481
- 482 42. Creanza N, Schwarz JS, Cohen JE. 2010 Intraseasonal dynamics and dominant sequences in H3N2  
483 influenza. *PLoS ONE*. **5**, e8544 (doi:10.1371/journal.pone.0008544)  
484
- 485 43. Seidel R, Lyons K, Blumer M, Zalansky P, Fratzl P, Weaver JC, Dean MN. 2016 Ultrastructural  
486 and developmental features of the tessellated endoskeleton of elasmobranchs (sharks and rays). *J.*  
487 *Anat.* **2016**, 1-22 (doi:10.1111/joa.12508)  
488
- 489 44. Maisey JG. 2013 The diversity of tessellated calcification in modern and extinct chondrichthyans.  
490 *Rev. Paléobiol.* **32**, 355-371.  
491
- 492 45. Burrow CJ, Turner S. (1999) A review of placoderm scales, and their significance in placoderm  
493 phylogeny. *J. Vertebr. Paleontol.* **19**, 204-219 (doi:10.1080/02724634.1999.10011135)  
494
- 495 46. Ginter M, Hampe O, Duffin C. 2010 Paleozoic Elasmobranchii: Teeth. *Handbook of*  
496 *Paleoichthyology 3D* (ed. H-P Schultze) 168 pp. München, Germany: Verlag Dr. Friedrich Pfeil.  
497
- 498 47. Karatajūtė-Talimaa V. 1998 Determination methods for the exoskeletal remains of early vertebrates.  
499 *Fossil Record.* **1**, 21-51.  
500
- 501 48. Andreev PS, Coates MI, Shelton RM, Cooper RM, Smith MP, Sansom IJ. 2015 Upper  
502 Ordovician chondrichthyan-like scales from North America. *Palaeontology* **58**, 691-704.  
503 (doi:10.1111/pala.12167)  
504

- 505 49. Andreev PS, Coates MI, Karatajūtė-Talimaa V, Shelton RM, Cooper PR, Sansom IJ. 2017  
506 *Elegestolepis* and its kin, the earliest monodontode chondrichthyans. *J. Vertebr. Paleontol.* **37**,  
507 e1245664 (doi:10.1080/02724634.2017.1245664)  
508
- 509 50. Stensiö EA. 1963 Anatomical studies on the arthrodiran head (Part I). *K. Sv. Vet. Akad. Handl. Ser. 4.*  
510 **9**, 1-419.  
511
- 512 51. Young, GC. 1980 A new early Devonian placoderm from New South Wales, Australia, with a  
513 discussion of placoderm phylogeny. *Palaeontographica.* **A167**, 10–76.  
514
- 515 52. Goujet D. 1984 *Les Poissons Placodermes du Spitsberg*. Paris, France: CNRS.  
516
- 517 53. Hu Y, Lu J, Young GC. 2017 New findings in a 400 million-year-old Devonian placoderm shed  
518 light on jaw structure and function in basal gnathostomes. *Scientific Reports.* **7**: 7813.  
519 (doi:10.1038/s41598-017-07674-y)  
520
- 521 54. Heidtke UHJ, Schwind C, Krätschmer K. 2004 Über die Organisation des Skelettes und die  
522 verwandschaftlichen Beziehungen der Gattung *Triodus* Jordan 1849 (Elasmobranchii:  
523 *Xenacanthida*). *Mainzer geowiss. Mitt.* **32**, 9-54.  
524
- 525 55. Brazeau MD, Friedman M, Jerve A, Atwood RC. 2017 A three-dimensional placoderm (stem-group  
526 gnathostome) pharyngeal skeleton and its implications for primitive gnathostome pharyngeal  
527 structure. *J. Morphol.* **2017**, 1-9 (doi:10.1002/jmor.20706)  
528
- 529 56. Heidtke UHJ. 2009 *Gladbachus adentatus*, die Geschichte des weltweit ältesten Hais – untersucht  
530 und beschrieben aus dem AK Geowissenschaften. *Pollichia Kurrier.* **25**, 24-26.

- 531
- 532 57. Miles RS. 1973 Relationships of acanthodians. In *Interrelationships of Fishes* (eds PH  
533 Greenwood, RS Miles, C Patterson), pp. 63–103 London, UK: Academic.
- 534
- 535 58. Hotton N. 1952 Jaws and teeth of American xenacanth sharks. *J. Paleontol.* **26**, 489-500.
- 536
- 537 59. Sallan LC, Coates MI. 2010 End Devonian extinction and a bottleneck in the early evolution of  
538 modern jawed vertebrates. *Proc. Natl. Acad. Sci. USA.* **107**, 10131-10135.  
539 (doi:10.1073/pnas.0914000107)
- 540
- 541 60. Sallan LC, Galimberti AK. 2015 Body-size reduction in vertebrates following the end-Devonian mass  
542 extinction. *Science.* **35**, 812-815. (doi:10.1126/science.aac7373)
- 543
- 544 61. Dineley DL, Metcalf SJ. 1999. Fossil Fishes of Great Britain. *Geological Conservation Review*  
545 *Series 16* (ed. D Palmer) 675 pp. Peterborough, UK: Joint Nature Conservation Committee.
- 546
- 547 62. Lund R, Poplin C. 1999 Fish diversity of the Bear Gulch Limestone, Namurian, Lower Carboniferous  
548 of Montana, USA. *Geobios.* **32**, 285-295.
- 549
- 550 63. Grogan ED, Lund R, Greenfest-Allen E. 2012 The origin and relationships of early  
551 chondrichthyans. In *Biology of Sharks and Their Relatives* (eds JC Carrier, JA Musick, MR  
552 Heithaus), pp. 3-29 Boca Raton, USA: CRC Press.
- 553
- 554 64. Zhu M, Zhao W, Jia L, Lu J, Qiao T, Qu Q. 2009 The oldest articulated osteichthyan reveals a  
555 mosaic of gnathostome characters. *Nature.* **458**, 469-474. (doi:10.1038/nature07855)
- 556



- 557 65. Burrow CJ, Rudkin D. 2014 Oldest near-complete acanthodian: the first vertebrate from the  
558 Silurian Bertie Formation konservat-Lagerstätte, Ontario. *PLoS ONE*. **9**, e104171.  
559 (doi:10.1371/journal.pone.0104171)  
560
- 561 66. Brazeau MD. 2012. A revision of the anatomy of the early Devonian jawed vertebrate  
562 *Ptomacanthus anglicus* Miles. *Palaeontology*. **55**, 355-367. (doi:10.1111/j.1475-  
563 4983.2012.01130.x)  
564
- 565 67. Hanke GF, Wilson MVH. 2006 Anatomy of the Early Devonian acanthodian *Brochoadmones*  
566 *milesi* based on nearly complete body fossils, with comments on the evolution and development  
567 of paired fins. *J. Vertebr. Paleontol.* **26**, 526-537. (doi:10.1671/0272-  
568 4634(2006)26[526:AOTEDA]2.0.CO;2)  
569
- 570 68. Gagnier, P-Y, Wilson MVH. 1996 Early Devonian acanthodians from northern Canada.  
571 *Palaeontology*. **39**, 241–258.  
572
- 573 69. Hanke GF. 2008 *Promesacanthus epleri* n. gen., n. sp., a mesacanthid (Acanthodii,  
574 Acanthodiformes) from the Lower Devonian of northern Canada. *Geodiversitas*. **30**, 287–302.  
575
- 576 70. Karatajūtė-Talimaa V, Smith MM. 2003 Early acanthodians from the Lower Silurian of Asia. *Trans.*  
577 *R. Soc. Edinb. (Earth Sci.)* **92**, 277–299.  
578
- 579 71. Sansom IJ, Andreev P. in press The Ordovician enigma: fish, first appearances and phylogenetic  
580 controversies. In *Evolution and Development of Fishes* (eds Z. Johanson, M. Richter, C. Underwood).  
581 Cambridge, UK; Cambridge University Press.  
582

- 583 72. Sanderson SL, Wassersug R. 1993 Convergent and alternative designs for vertebrate suspension  
584 feeding. In *The Skull Volume 3: Functional and Evolutionary Mechanisms* (eds J Hanken, BK Hall).  
585 pp. 37-112 Chicago, USA: University of Chicago Press.  
586
- 587 73. Blicek A. 2011 From adaptive radiations to biotic crises in Palaeozoic vertebrates: a geobiological  
588 approach. *Geol. Belg.* **14**, 203-227. (doi:10.1007/s12549-016-0260-1)  
589
- 590 74. Sansom IJ, Davies NS, Coates MI, Nicoll RS, Ritchie A. 2012 Chondrichthyan-like scales from  
591 the Middle Ordovician of Australia. *Palaeontology* **55**, 243-247. (doi:10.1111/j.1475-  
592 4983.2012.01127.x)  
593
- 594 75. Cohen KM, Finney SC, Gibbard PL, Fan J-X. 2017 The ICS International Chronostratigraphic  
595 Chart (2013; updated) *Episodes* **36**, 199-204.  
596  
597

598 **FIGURES**

599  
600  
601 **Figure 1.** *Gladbachus adentatus* Heidtke and Krätschmer [31]. (a) Rendering of cranial and pectoral girdle  
602 remains in dorsal view and (b) ventral view. (c) mandibular tooth; (d) cranial roof scale; (e) branchial  
603 denticle; (f) trunk scale. All denticles and scales rendered semitransparent from micro-computed tomography  
604 scans. Abbreviations: bhy, basihyal; chy, ceratohyal; hb, hypobranchial; mc, Meckel's cartilage; na, neural  
605 arches; nc, neurocranium; or, orbital ring; pop, postorbital process; pq, palatoquadrate; sco, scapulocoracoid.

606  
607  
608 **Figure 2.** *Gladbachus adentatus* Heidtke and Krätschmer [31]. (a) Palatoquadrate; (b) Meckel's cartilage; (c)  
609 jaws, hyoid arch and gill arches restored, dorsal view; (d) gills reconstructed ventral view; (e) reconstruction  
610 of articulated mandibular arch, left lateral view. Abbreviations: adf, adductor fossa; bhy, basihyal; cbr,  
611 ceratobranchial; chy, ceratohyal; cop, copula; ebr, epibranchial; end, endolymphatic duct; fm/oc, foramen  
612 magnum/occipital cotylus; gl, glenoid; hb, hypobranchial; hy, hyomandibula; mp, mesial process; opr, otic  
613 process; pbr, pharyngobranchial; pop, postorbital process; ppr, palatine process; pq, palatoquadrate; q,  
614 quadrate condyle, unmineralized site of; ssc, semicircular canal network; ocf, otico-occipital fissure.

615  
616  
617 **Figure 3.** Phylogenetic placement of *Gladbachus adentatus* Heidtke and Krätschmer [31]. (a) parts *i* and  
618 *ii* join at arrow heads. Strict consensus, complete tree. (b) Strict consensus of chondrichthyan total group  
619 obtained from reduced taxon set; arrow head joins arrow head of (a) part *i*. Branch colours: black, stem  
620 group gnathostomes; green, Osteichthyes; magenta, acanthodid stem Chondrichthyes; red, non-acanthodid  
621 stem Chondrichthyes; purple, Holocephali (crown Chondrichthyes); blue, Elasmobranchii (crown  
622 Chondrichthyes). Circles mark nodes with bootstrap support greater than 50% and/or decay values greater  
623 than 1; filled circles mark nodes with bootstrap support greater than 75% and/or decay values greater than

624 3. (c) Phenetic results: PCO 1 (18.1% explained variance) is plotted on the vertical axis and PCO 2  
625 (9.6%) is plotted on the horizontal axis. (d) PCO 1(vertical) vs. PCO 3 on the horizontal axis (8.1%).  
626 Details of the PCO analysis are presented in the Supplementary Notes. The four traditionally named  
627 groups (placoderms in purple, acanthodians in green, chondrichthyans in blue, osteichthyans in red)  
628 cluster in distinct non-overlapping regions on the first three PCO dimensions. Relevant stem  
629 chondrichthyan taxa are indicated in each plot.

630  
631  
632 **Figure 4.** Early chondrichthyan phylogeny: simplified strict consensus of phylogenetic analysis results  
633 calibrated against Ordovician-Carboniferous chronostratigraphic chart. Consensus computed from matrix with  
634 86 taxa and 262 characters. Taxon bar colour: black, non-chondrichthyan; magenta, acanthodid stem  
635 chondrichthyan; red, non-acanthodid stem chondrichthyan; purple, holocephalan crown chondrichthyan; blue,  
636 elasmobranch crown chondrichthyan. Bar length corresponds to earliest occurrence stage-duration. Brown bar  
637 signifies total range of chondrichthyan-like scale-based taxon. Timescale (Ma) from Cohen *et al.* [75].  
638 Complete cladogram shown in figure 3a.

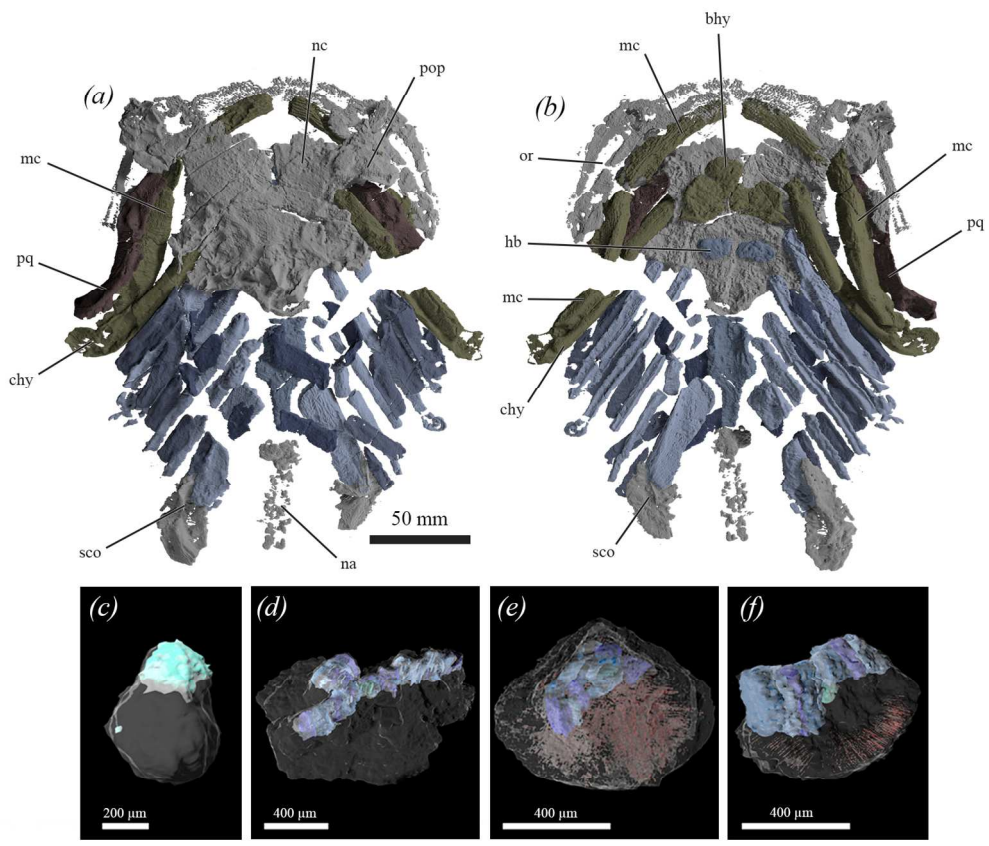


Figure 1

146x128mm (300 x 300 DPI)

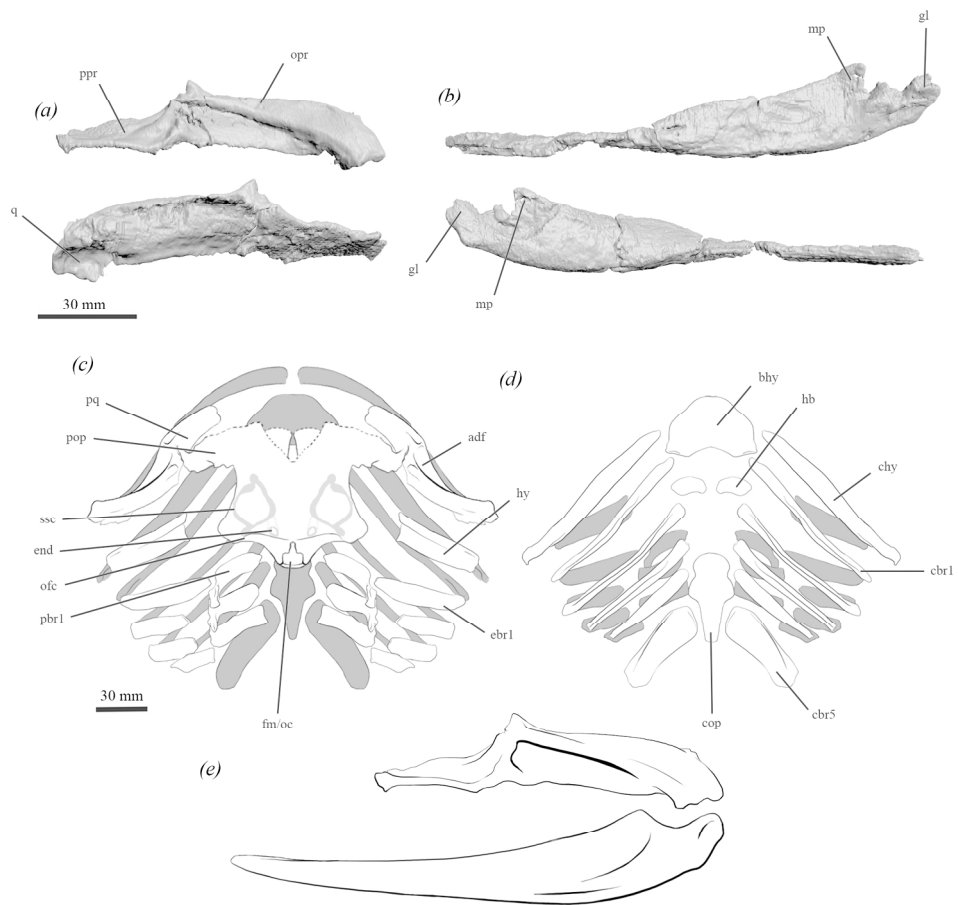


Figure 2

184x174mm (300 x 300 DPI)

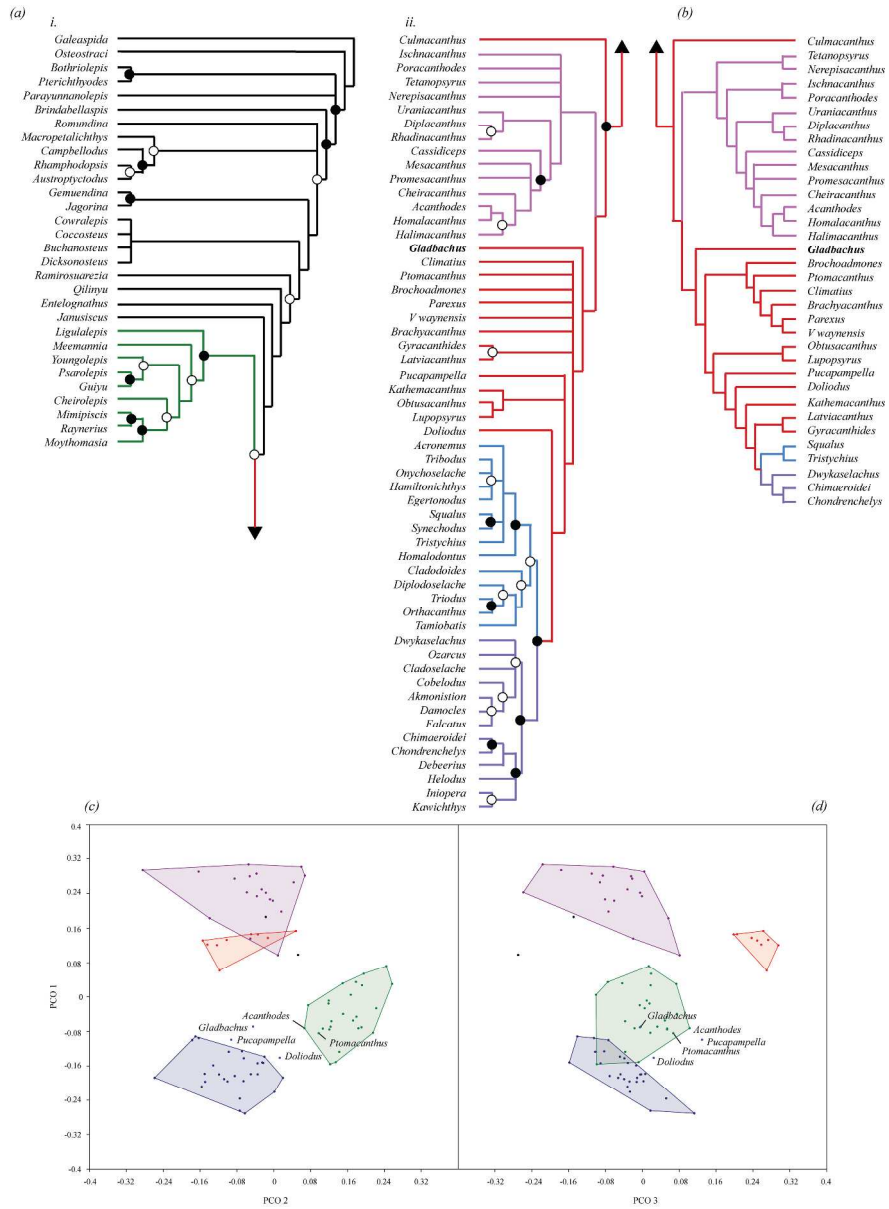


Figure 3

303x416mm (300 x 300 DPI)

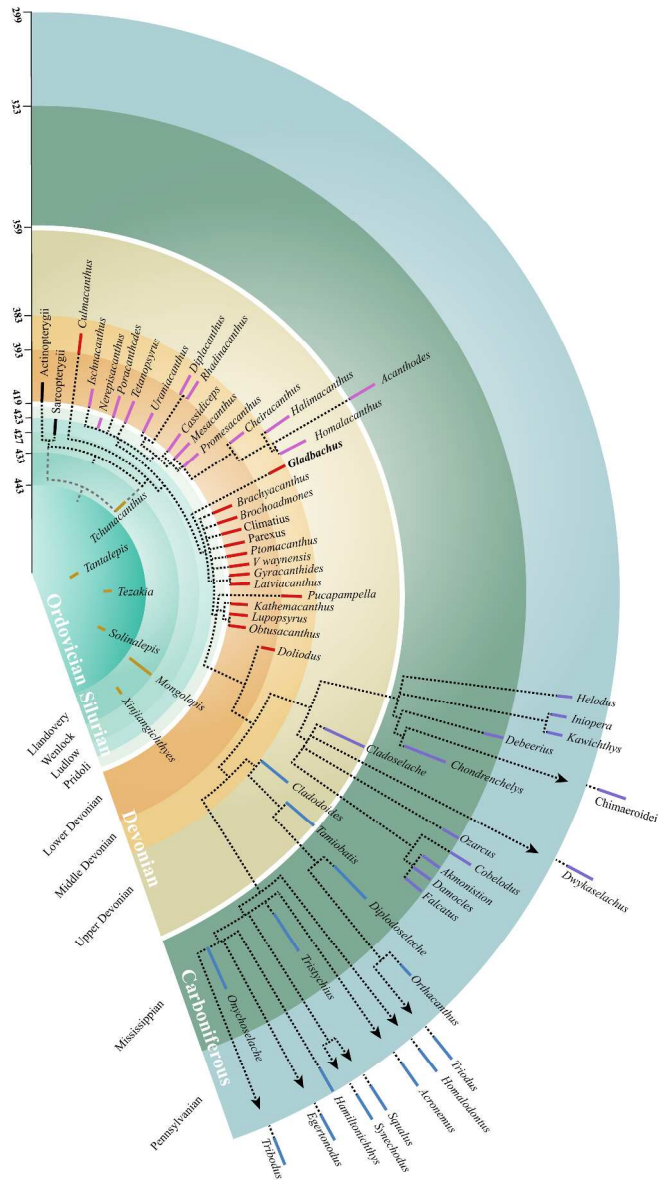


Figure 4

293x426mm (300 x 300 DPI)