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

3

4

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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).

82 Scales, denticles, teeth, and calcified cartilage were examined using synchrotron μ 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; 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;
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 1.39×10^{-6} , 0.01, and 8.65×10^{-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 Glencarholm [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

342

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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.

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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.

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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.

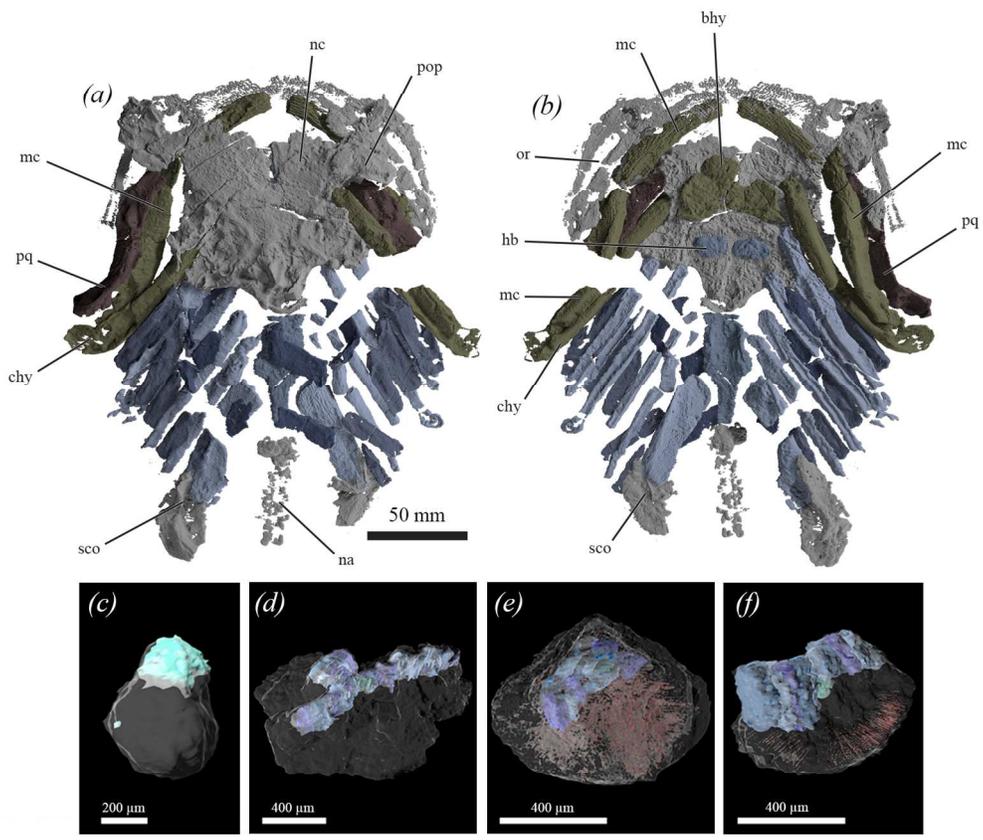


Figure 1

146x128mm (300 x 300 DPI)

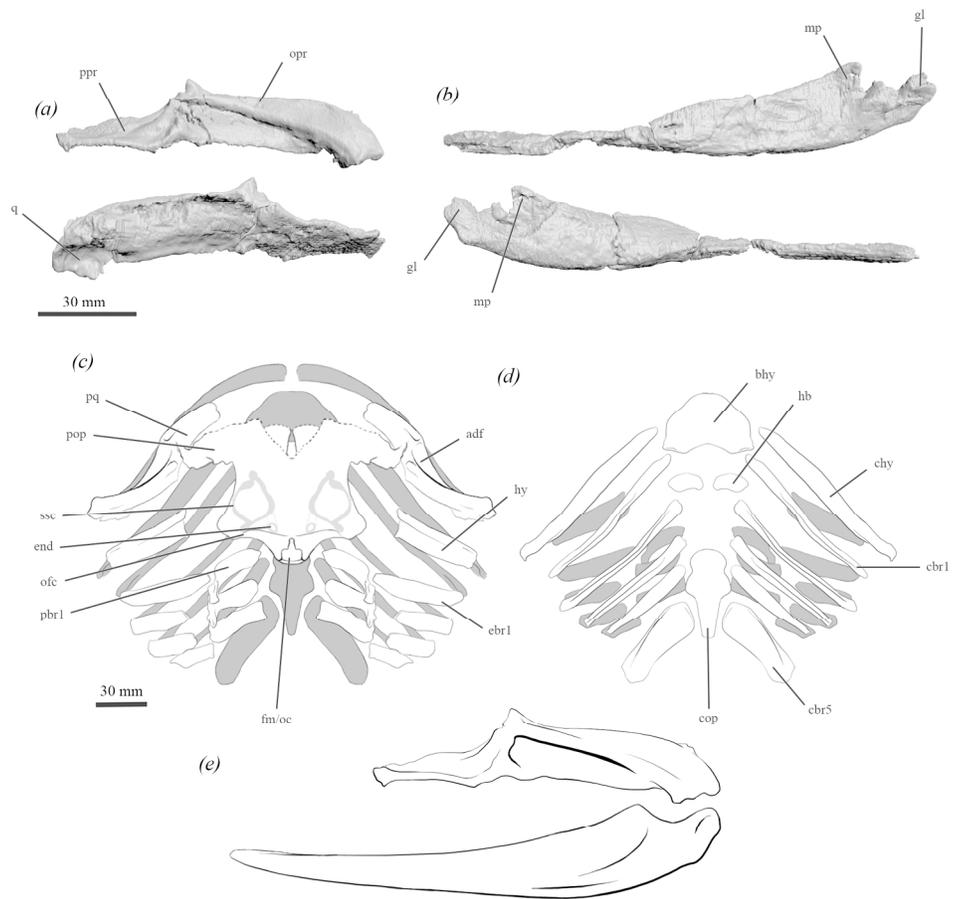


Figure 2

184x174mm (300 x 300 DPI)

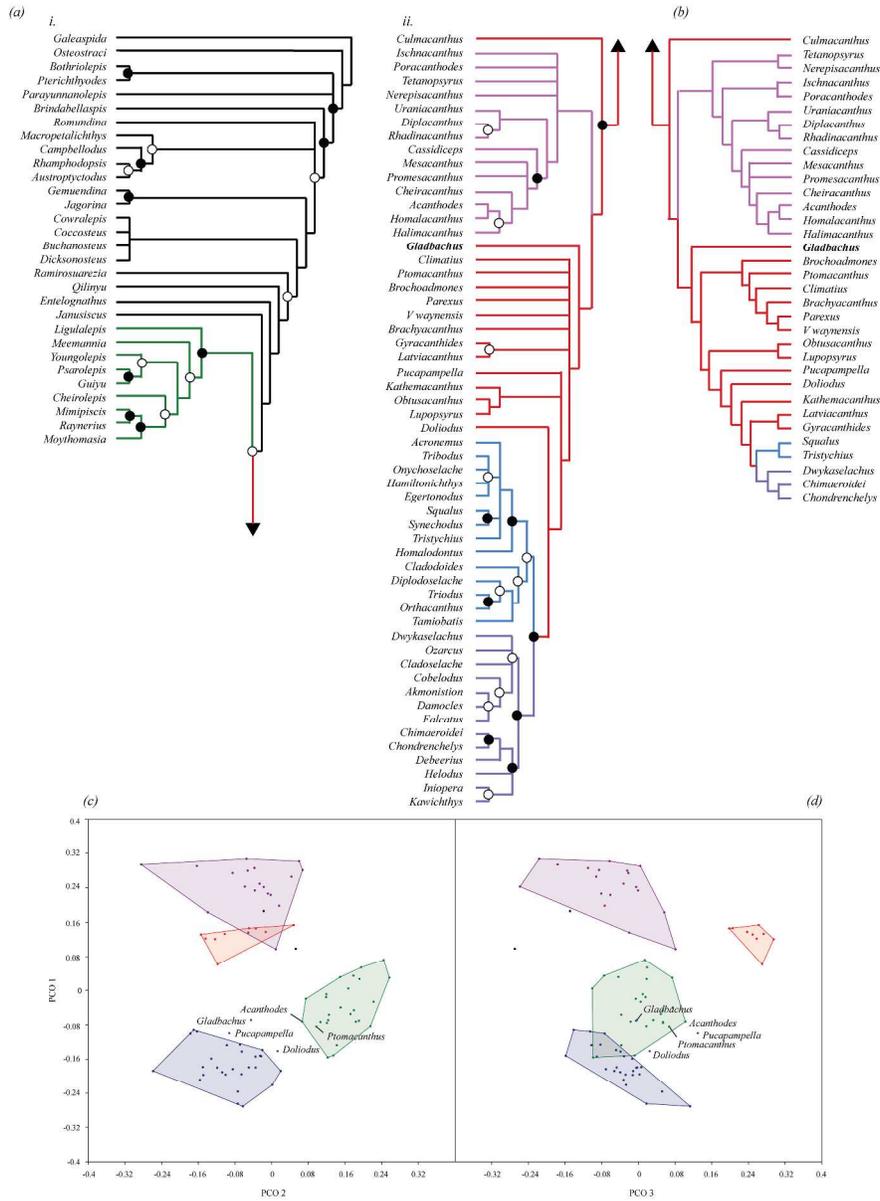


Figure 3

303x416mm (300 x 300 DPI)

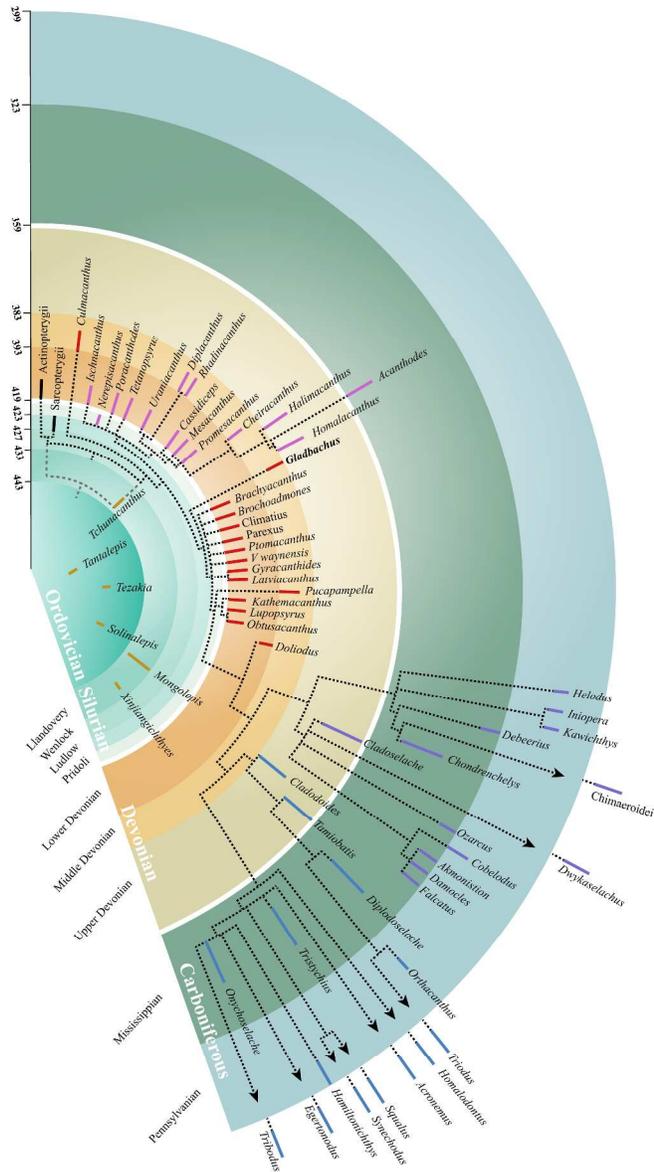


Figure 4

293x426mm (300 x 300 DPI)