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1 **Endocast and bony labyrinth of a Devonian ‘placoderm’ challenges stem gnathostome**
2 **phylogeny**

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24

25 **Summary:**

26 Our understanding of the earliest evolution of jawed vertebrates depends on a credible
27 phylogenetic framework for the jawed stem gnathostomes collectively known as ‘placoderms’.
28 However, their relationships, and even whether ‘placoderms’ represent a single radiation or a
29 paraphyletic array, remain contentious. Here we describe the endocranial cavity and bony
30 labyrinth of *Brindabellaspis stensioi*, commonly recovered as a taxon of uncertain affinity
31 branching near the base of ‘placoderms’. While some features of its braincase and endocast
32 resemble those of jawless vertebrates, its inner ear displays a repertoire of crown gnathostome
33 characters. Both parsimony and Bayesian analyses suggest that prevailing hypotheses of
34 ‘placoderm’ relationships are unstable, with newly-revealed anatomy pointing to a radical
35 revision of early gnathostome evolution. Our results call into question the appropriateness of
36 arthrodire-like ‘placoderms’ as models of primitive gnathostome anatomy and raise questions of
37 homology relating to key cranial features.

38 **Results**

39 One of the major transitions in vertebrate history was the evolution of gnathostomes, or jawed
40 vertebrates, from jawless ancestors. The major morphological gap apparent when considering
41 only living vertebrate diversity—extant jawless fishes comprise just hagfish and lamprey—is
42 largely filled in by the fossil record [1]. ‘Placoderms’, the most crownward assemblage on the
43 gnathostome stem, occupy a pivotal place in this discussion. Traditional hypotheses of
44 relationships posit a monophyletic Placodermi [2–4], whereas most recent analyses recover
45 ‘placoderms’ as a paraphyletic array from which crown gnathostomes arose over 420 million
46 years ago [5–12]; but see ref [13]. In either scenario, antiarchs are typically recovered near the
47 base of the ‘placoderm’ assemblage, sharing some anatomical similarities with fossil agnathan
48 outgroups such as galeaspids and osteostracans, with arthrodires recovered proximate to the
49 gnathostome crown [1, 5–7, 9–11]; but see ref [12]. Uncertainty surrounding the relationships

50 between different ‘placoderm’ groups, as well as their broader taxonomic status, are compounded
51 by an uneven understanding of anatomy across the radiation, particularly of the phylogenetically
52 informative braincase and brain cavity—endocast (see Supplementary Materials).

53 *Brindabellaspis stensioi* [14] is a ‘placoderm’-grade stem gnathostome from the Early
54 Devonian of New South Wales, Australia. Although almost exclusively recovered among the
55 earliest diverging ‘placoderms’ [5–9, 11,12, 15–17], it has variably been allied with rhenanids [13]
56 acanthothoracids [4] and antiarchs [13], some of which are of dubious monophyly. Comparisons
57 with fossil jawless fishes have frequently been drawn on the basis of gross external and braincase
58 anatomy [14] and general proportions of the endocast [1, 18]. Other distinctive features, such as a
59 large endolymphatic cavity, have been interpreted as autapomorphies [14, 19]. Here, we provide
60 high-resolution CT data of two more recently discovered specimens (Figure 1), detailing
61 unexplored parts of the endocast and offering a reinterpretation of previously described regions of
62 the braincase and skull roof.

63 Tomographic data reveals the position of dermal bone sutures, clarifying the structure of
64 the skull roof. Unlike in previous interpretations [14, 20], we identify an independent median
65 pineal plate sitting posterior to the rostral plate, rather than a single rostopineal (Figures 1, 2).
66 We also confirm the presence of four bones contributing to the lateral margin of the skull roof,
67 contra refs [14, 20]. *Brindabellaspis* possesses an elongate ossification (postmarginal) flanking
68 the serial lateral line-bearing bones, resembling maxillate ‘placoderms’ [6, 11] and early
69 osteichthyans [21]; in most other ‘placoderms, the postmarginal is either lost or present only as
70 the tip of the lateral corner of the skull roof [3].

71 Broadly speaking, our results affirm past descriptions of the endocavity [14], although
72 with key additions and clarifications. The extremely short telencephalic region (see comparison to
73 other taxa in Figure S3) of the endocast has a flat anterior face with no bulge anterior to the
74 olfactory and terminal nerves, contra ref [14] (Figure 1c and e;). We also confirm that the
75 hypophysis is oriented anteroventrally [14] (Figure 1e). Although an anteriorly or anteroventrally

76 directed hypophysis has sometimes been considered restricted to fossil agnathans (e.g. *Shuyu* [22],
77 *Mimetaspis* [23]: Figure S3) and ‘placoderms’ [19], it is also reported in crown gnathostomes [17,
78 24–26]. *Brindabellaspis* has a laterally expansive cerebellum, which is wider than both the
79 forebrain and hindbrain, and an anteroposteriorly elongate vagus complex, which is several times
80 wider than the spino-occipital nerve foramina posterior to it (Figures 1d and f, and S2). These
81 were previously suggested as being shared between extinct jawless fishes and *Brindabellaspis*,
82 but are now known to be widespread in other stem and crown gnathostomes [17, 19, 25] (Figures
83 3 and S2), and are presumably plesiomorphic for the gnathostome crown. As described by Young
84 [14], the olfactory tracts are elongate, and diverge anteriorly towards the widely separated and
85 laterally positioned nasal capsules (Figures 1c, 3, and S2). Divergent olfactory tracts are
86 otherwise only known in crown gnathostomes [17, 25–27]; in other ‘placoderms’ and the
87 galeaspid *Shuyu* [22] the olfactory tracts are parallel and typically short (Figure 3), although it is
88 possible that this arrangement is a reflection of the orbital position of the nostrils in
89 *Brindabellaspis*. The myelencephalic region of the endocast anterior to the vagus nerve in
90 *Brindabellaspis* accounts for some some 16% of the total length of the brain cavity, which is
91 inconsistent with the proportions in most ‘placoderms’ (20-30%, Figures 3 and S3) but within the
92 range of extinct agnathans and crown gnathostomes (between 8-20%, Figures 3 and S3).

93 Our CT data reveal important new anatomical details of the bony labyrinth and
94 endolymphatic complex. In addition to features identified in the endocast, the bony labyrinth of
95 *Brindabellaspis* (Figures 1c-f, 3, and S2) bears important similarities to those of crown
96 gnathostomes, with considerable difference to those of other ‘placoderms’. The labyrinth is
97 anteroposteriorly short, and all three semicircular canals have large diameters. The anterior
98 semicircular canal is much shorter than its posterior counterpart, and in dorsal view the two
99 diverge at a much smaller angle than in other ‘placoderms’ such as the rhenanid *Jagorina* and
100 arthrodire *Kujdanowiaspis* (Figures 1c-f and 4, and S2). Most strikingly, CT data demonstrate
101 that the anterior and posterior semicircular canals of *Brindabellaspis* join in a crus commune,

102 with a dorsoventrally long sinus superior developed ventrally. This configuration is typical of
103 crown gnathostomes [17, 25–27], and the combination is unknown in other ‘placoderms’ (Figure
104 4). There is no significant preampullary portion of the posterior semicircular canal, and the
105 utriculus does not separate the anterior and external semicircular canals (both contra the condition
106 in all known ‘placoderms’ except *Romundina* [19]). While incomplete ventrally, the curvature of
107 the sacculus suggests that it is significantly smaller than in other ‘placoderms’, barely protruding
108 laterally (Figures 3 and 4). It is also restricted ventral to the plane of the external semicircular
109 canal, a condition seen elsewhere only in crown gnathostomes (Figures 3 and 4). Despite the lack
110 of an external semicircular canal or utricular chamber in agnathans [22], a number of labyrinth
111 characters can be polarised across the jawless-jawed vertebrate transition. Osteostracans possess
112 small angles between anterior and posterior semicircular canals, and a crus commune but no
113 developed sinus superior (Figure 4). Quantitative analyses of the endocast and bony labyrinth in
114 stem and early gnathostomes is challenging: these features have been described using computed
115 tomography for a single jawless fish [22] and just two ‘placoderms’ [19, 28]; other comparisons
116 are known only from historical interpretive drawings or wax models [23, 29–32]. As such, it is
117 difficult to determine the extent to which morphological features of the bony labyrinth reflect the
118 external geometry of the skull. Detailed three-dimensional data for a range of extinct jawless and
119 jawed fishes will be crucial to probing these relationships in the future.

120 Although previously considered autapomorphic [14], our data allow similarities to be drawn
121 between the endolymphatic systems of *Brindabellaspis* and crown gnathostomes. The complex in
122 *Brindabellaspis* can be divided into three distinct sections: a large, well-developed endolymphatic
123 sac; an ascending duct connecting the vestibular chamber to the endolymphatic sac; and a distal
124 duct extending from the sac, through the dermal bone, and opening externally (Figures 1d-f, 3, 4,
125 and S2). There is no “second sac”, contra ref [19]. In both jawless and jawed stem gnathostomes,
126 the endolymphatic complex is a simple tube-like structure that extends unidirectionally, and is
127 positioned close to the labyrinth [18–19, 22–23]. In contrast, the crown gnathostome system is

128 more complex and divided into three distinct regions [33], much as in *Brindabellaspis*, and
129 located mesially, closer to the brain cavity than the labyrinth [34–35] (Figures 3 and 4). Although
130 incompletely known, the endocavities of the antiarchs *Minicrania* [36] and *Phymolepis* [37] hint
131 at the presence of a mesially-directed endolymphatic duct and an endolymphatic sac, as well as a
132 relatively short hindbrain.

133 **Discussion**

134 A revised and expanded morphological matrix, analysed under both parsimony and Bayesian
135 frameworks, provides novel—and conflicting—insights into early gnathostome evolution. Under
136 parsimony analysis, jaw-bearing gnathostomes fall into one of two monophyletic groups (Figures
137 4 and S4). The more stemward of these contains the bulk of traditionally-recognised ‘placoderms’,
138 albeit with arthodires representing a nested radiation within this clade. *Brindabellaspis* is
139 recovered as the earliest diverging member of a clade comprising, successively: antiarchs,
140 maxillate ‘placoderms’, and crown gnathostomes. The position of *Brindabellaspis* and antiarchs
141 as proximate to the gnathostome crown, with arthodires representing a nested radiation within a
142 clade of ‘placoderms’, is unexpected [1, 5–7, 9–11]; (but see ref [13]) and indicates the
143 importance of endocranial data and previous biases towards external morphology. The placement
144 of *Brindabellaspis* is supported by features of the bony labyrinth and endolymphatic complex,
145 and of antiarchs by characters including absence of opercular suspension on the braincase, a
146 posteriorly open cucullaris fossa, and a long obstantic margin. However, results under Bayesian
147 analyses differ from our parsimony analysis and recall more common hypotheses of placoderm
148 paraphyly [5–7, 9–11, 17], with antiarchs recovered as the earliest-diverging ‘placoderm’ clade
149 and arthodires as sister taxa to maxillate ‘placoderms’ and the gnathostome crown. Outside of
150 these nodes, however, other ‘placoderms’—including *Brindabellaspis*—fall in a polytomy, and
151 arthodires are recovered as paraphyletic. Support values for early gnathostome relationships
152 across our parsimony tree are low, and the proximity of antiarchs to the gnathostome crown node

153 raises several questions of homology. The transition from posteriorly-positioned to anteriorly-
154 positioned nasal capsules, as well as changes to jaw suspension, are now optimised as evolving
155 twice: once within the clade comprising *Romundina*, rhenanids, ptyctodonts, petalichthyids and
156 arthrodires; and once within the clade comprising maxillate ‘placoderms’ and crown
157 gnathostomes. The recovery of arthrodires as removed from maxillate ‘placoderms’ plus crown
158 gnathostomes also requires a number of homoplasies in the skull roof and trunk armour.
159 Resolving these joint conflicts of phylogenetic relationships and anatomical evolution represents
160 a fundamental challenge of early gnathostome evolution, and is one that cannot be resolved
161 without detailed CT-based reassessment of the anatomy of key ‘placoderm’ taxa.

162 Our work adds considerably to knowledge of labyrinth and endocast variation across stem
163 gnathostomes, highlighting the major impact that CT-based descriptions and re-examination of
164 key taxa can have on both phylogenetic resolution and schemes of morphological evolution. The
165 unexpected character combination in *Brindabellaspis* suggests that endocranial characters
166 previously considered exclusive to crown gnathostome are likely widely distributed amongst a
167 diversity of stem jawed vertebrates. However, outstanding questions remain about the homology
168 of features common to both arthrodires and crown gnathostomes, notably in the skull roof and
169 nasal capsules. The conflicting phylogenetic hypotheses of relationships presented here highlight
170 major uncertainties on the gnathostome stem, calling into question long-standing assumptions
171 about patterns of character evolution. Recent work on the diversity of ‘acanthothoracid’
172 dentitions, also revealed by CT data, suggests a more complex picture of dental character
173 evolution and provides independent evidence that at least some ‘acanthothoracids’ may branch
174 closer to the gnathostome crown node than previously thought [12]. Notably, the position of
175 arthrodires as removed from maxillate ‘placoderms’ plus crown gnathostomes challenges
176 previous understanding of arthrodire-like taxa as representative of the primitive gnathostome
177 condition [11, 28, 38].

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188 Y.H. carried out the reconstruction of datasets and digital segmentation; Y.Z., S.G. and J. L.
189 performed the phylogenetic analysis and constructed figures; M.B. and S.G. performed principal
190 component analyses; Y.Z., J.L., S.G., and M.B. wrote the manuscript; and all authors reviewed
191 and revised the manuscript. Y.Z. and S.G. contributed equally.

192 **Declaration of Interests:** The authors declare no competing interests.

193 **Figure Legends**

194 **Figure 1** The skull of the ‘placoderm’ *Brindabellaspis stensioi*, based on high-resolution CT.

- 195 (A) Ventral view of endocranium (ANU 49493)
- 196 (B) Dorsal view of skull roof (AM F81911)
- 197 (C) Dorsal view of endocranial cavity (ANU 49493)
- 198 (D) Left lateral view of endocranium (ANU 49493)
- 199 (E) Right lateral view of endocranial cavity (ANU 49493)
- 200 (F) Enlarged bony labyrinth and endolymphatic sac region
- 201 (G) Mesial view of the skeletal labyrinth (ANU 49493)

202 (H) Ventral view of the skeletal labyrinth (ANU 49493)

203 Abbreviations: a.ps, efferent pseudobranchial artery; asc, anterior semicircular canal; asc.amp,
204 ampullae of anterior semicircular canal; c.c, crus commune; conj.asc+esc, conjunction of
205 anterior and external semicircular canals; die, diencephalon; e.endd, exit of endolymphatic
206 duct; ends, endolymphatic sac; esc, external semicircular canal; esc.amp, ampullae of external
207 semicircular canal; fo.hy, hypophysial fossa; hy.v, hypophysial vein; mes, mesencephalon;
208 met, metencephalon; mye, myelencephalon; nc, nasal capsule; olf.t, olfactory tract; pit.v,
209 pituitary vein; psc, posterior semicircular canal; psc.amp, ampullae of posterior semicircular
210 canal; rec.p, pineal recess; rec.pap, parapineal recess; rec.utr, utricular recess; sac, sacculus;
211 spio, spino-occipital nerves; s.su, sinus superior; tel, telencephalon; 0, terminal nerve; II,
212 optic nerve, III, oculomotor nerve; IV, trochlear nerves; Vpro, profundus branch of trigeminal
213 nerve; Vtg, maxillary and mandibular branches of trigeminal nerve; VI, abducens nerve; VII,
214 facial nerve; VIII, otic nerve; IX, glossopharyngeal nerve; X, vagus nerve; Xa, anterior
215 branch of vagus nerve. Scale bars, 1 cm.

216 **Figure 2. Braincase of *Brindabellaspis stensioi* (AM F81911), based on high-resolution CT.**

217 (A) Dorsal view, showing the dermal skull roof.

218 (B) Ventral view, showing the segmented skull roof and neurocranium.

219 (C) Left lateral view of whole skull.

220 (D) Left lateral view of neurocranium only. Segmenting could not be completed in the otic
221 region of the braincase due to very low contrast between the braincase and surrounded
222 limestone matrix, which was only partially acid-etched. Digital transverse sections
223 showing the dermal bone sutures.

224 Abbreviations: Ce, central; Mg, marginal; Nu, nuchal; Pi, pineal; Pm, postmarginal; Pn,
225 postnasal; Pna, anterior paranuchal; Pnu, paranuchal; Prm, premedian; Pro, preorbital; Pto,
226 postorbital; Ro, rostral.

227 Scale bar, 1 cm.

228 **Figure 3. Comparative morphology of crania in selected early vertebrates, aligned and**
229 **scaled to match skeletal labyrinth dimensions (grey bar). Cranial outlines (light grey) and**
230 **endocast outlines (yellow) in dorsal (left) and ventral (right) views.** Data sources for each
231 genus are provided in Supplementary Information.

232 **Figure 4. Phylogeny showing the evolution of the inner ear and endolymphatic complex, and**
233 **endocasts in early vertebrates.**

234 (A) The inner ear and endolymphatic complex of selected crown gnathostomes in lateral and
235 dorsal view, showing the shared characters between those in *Brindabellaspis* and the
236 crown gnathostomes (boxed area). The phylogeny is a simplified version of the
237 parsimony strict consensus tree (Figure S4)

238 (B) Brain cavity of selected gnathostomes in lateral view, mapped in the full version of the
239 parsimony strict consensus tree (Figure S4)

240 **STAR Methods**

241 **KEY RESOURCES TABLE**

242 **Note for the specimens listed in the Key Resources Table**

243 Young assigned six specimens to *Brindabellaspis stensioi*, three of which are skulls [14]. Five
244 additional specimens, which also provide information on skull morphology, were described in
245 2018 [20]. The similar size, proportion, condition of the nasal opening inside the dermal orbit,
246 distinctive dermal ornament of flat-topped tubercles, and the proximity of all specimens
247 supports their referral to *Brindabellaspis stensioi*. The endocranial morphology of
248 *Brindabellaspis* redescribed here is based mainly on X-ray computed microtomography of two
249 specimens, AM F81911 and ANU 49493, from ref [20]. We list in the key resources table six
250 specimens from the original paper and the five additional specimens. Additional ‘CPC’ numbers,
251 used by Young [14] for some ANU specimens, are given in parentheses for completeness. All but

252 the last two specimens are held in the Department of Applied Mathematics, Research School of
253 Physics, ANU.

254 **Anatomical notes on new skull roof interpretation**

255 The original identification of skull roof bones in *Brindabellaspis* [14] has been revised
256 twice [3, 20] on the basis of external examination. Tomographic data reveals newly recognized
257 sutures, allowing a revised interpretation of the skull roof pattern. This differs significantly from
258 previous reconstructions in the following details:

259 Firstly, previous interpretations have reconstructed a large rostromeatal plate with a posterior
260 convex margin, resembling the plate in the acanthothoracid *Romundina* and arthrodiroids such as
261 *Buchanosteus*. In our new interpretation, however, this posterior extension is in fact a separate
262 pineal plate. The rostral has a sinuous posterior margin, which interdigitates with the narrow,
263 rectangular pineal and the large, quadrate preorbital (Figure 2a).

264 Secondly, previous interpretations do not agree on the bones around the posterolateral
265 boundary of the orbit and the lateral edge of the skull roof. Our new interpretation resembles that
266 of Young [3], with a series of four bones (contra the five in refs. 14,20) forming the lateral edge
267 of the skull roof: a postnasal; a bar-shaped bone forming the ventral margin of the orbit and
268 tentatively identified as a postorbital plate; a postmarginal; and a paranuchal (Figure 2a). The
269 postmarginal canal runs through the postmarginal, rather than through the presumed postorbital
270 plate (as reconstructed by refs. 14,20).

271 The skull roof of *Brindabellaspis* is highly apomorphic, particularly with regard to the
272 anteriorly elongated bill-like premedian and accompanying lateral postnasals. Interestingly, its
273 skull roof pattern shows some resemblance to the recently discovered Silurian maxillate
274 placoderms, *Entelognathus* and *Qilinyu* [6, 11]. In both *Brindabellaspis* and maxillate placoderms,
275 a large postmarginal is present and forms a substantial portion of the lateral margin of the skull
276 roof, outflanking the serial bones bearing the lateral line canal (carried by the postorbital,
277 marginal and anterior and posterior paranuchals). In most other placoderms, the postmarginal is

278 either much reduced, forming only the tip of the lateral corner of the skull roof, as in many
279 arthrodiros, or completely lost, as in *Romundina*, petalichthyids and ptyctodonts. Notably, some
280 of the earliest-diverging osteichthyans such as *Guiyu* primitively have large ossifications flanking
281 the bones bearing the lateral line canals. These bones form a considerable part of posterolateral
282 margin of the skull roof [21], although the exact homology of these two bones (named
283 extratemporal and accessory extratemporal in *Guiyu*) to the postmarginal of placoderms is
284 difficult to establish. Finally, in *Brindabellaspis* the lateral-line-bearing marginal and anterior
285 paranuchals are a series of rounded bones like in *Entelognathus* and *Qilinyu*, rather than the large
286 polygon or irregularly shaped bones in most other placoderms.

287

288 **Notes on endocast and labyrinth morphology in stem gnathostomes**

289 The endocranial cavity morphology seen in ‘placoderms’ highlights the extreme diversity
290 present across the assemblage, and with reference to outgroups allows us to reconstruct character
291 polarity.

292 The two groups of jawless stem gnathostomes (or “ostracoderms”) that have well-preserved
293 endocranial cavities, namely osteostracans and galeaspids, display considerable variation in
294 morphology. The close affinity of osteostracans to jawed vertebrates is supported by features of
295 the inner ear, in particular its drum-shaped vestibular cavity (sacculus), and anteroposterior
296 asymmetry [23,30,32]. In contrast, the galeaspid *Shuyu*, despite possessing separated nasal sacs
297 and olfactory tracts as in jawed vertebrates, lacks vestibular structures; the ventral part of the
298 labyrinth, or *pars inferior*, is simply a continuation of the anterior and posterior semicircular
299 canals as in living cyclostomes [22]. The whole profile of the inner ear in *Shuyu* also resembles
300 living cyclostomes in being anteroposteriorly symmetrical. Both *Shuyu* and osteostracans possess
301 a distinct crus commune, but the crus commune of osteostracans does not appear to extend into a
302 developed sinus superior. The ventral extension of the crus commune seems variable in the
303 osteostracans with inner ear morphology known. It is somewhat more pronounced in *Kiaeraspis*

304 *auchenaspidooides* (Figure 4; ref.30:text-Figure 19) than in *Mimetaspis hoeli* (ref. 23:text-Figure
305 18) and *Norselaspis glacialis* (ref. 32: Figure 30), but is still more similar to the condition in
306 *Romundina* than the distinct sinus superior in *Brindabellaspis* and crown gnathostomes. A better
307 understanding of the crus commune in osteostracan inner ears is hampered by the lack of updated
308 digital data, the availability of which would allow dissection of individual structures in strictly
309 directional views.

310 Arthrodires represent some of the first described and “stereotypical” placoderms [2,29,38-
311 40]. In recent phylogenetic analyses, arthrodires are typically resolved close to the crown
312 gnathostome node [5,6,11,15,16], but in our parsimony analysis are nested within a monophyletic
313 group containing many conventional ‘placoderms’. The endocranial cavity, especially the
314 labyrinth morphology, is well-known in *Kujdanowiaspis* [29, 41, 42] and *Buchanosteus* [31],
315 both of which display derived (or apomorphic) features when compared to agnathan outgroups.
316 These features include a very long hindbrain; elongated general profile of the labyrinth; absence
317 of crus commune, and laterally directed endolymphatic duct (Figure 4). In agnathans and most
318 ‘placoderms’ the endolymphatic duct runs parallel in dorsal view (Figs. 2 and 3). The
319 telencephalic and diencephalic regions of the arthrodire endocast resemble *Romundina* in having
320 a bulged dorsal “forehead” and a ventral pre-hypophysial “step” anterior to the hypophysial fossa
321 (Figure S3). The olfactory tracts proximally join the robust and long optic nerve canals that are
322 perpendicular to the axis of the endocast. The condition in which the olfactory tracts proximally
323 join the robust and long optic nerve canal is shared in *Shuyu*, other ‘placoderms’ such as *Jagorina*
324 [43], and *Brindabellaspis* (Figures. 1d, 2, 3, and S2), suggesting it is the primitive gnathostome
325 condition. Of special interest is the incompletely known endocast in the derived arthrodire
326 *Tapinosteus* [29]. *Tapinosteus* belongs to the arthrodire subgroup Eubrachythoraci [44] and was
327 supposedly adapted to free-swimming lifestyle with a fusiform body, resembling crown
328 gnathostomes. However, the preserved part of the inner ear resembles that of other arthrodires in
329 the low general profile and the absence of crus commune. The olfactory tracts are also parallel.

330 Although data are limited, this indicated that endocast and inner ear morphology are unlikely to
331 broadly reflect ecological mode.

332 Together with arthrodiros, antiarchs were among the first ‘placoderms’ to be described [39].
333 Antiarchs are typically resolved at the base of the ‘placoderm’ position close to *Brindabellaspis*
334 in recent phylogenetic analyses. Notably, antiarchs possess various features difficult to compare
335 to other ‘placoderm’ subgroups, such as a unique skull roofing pattern and “lateral plate”, a cheek
336 bone bearing the dental and occlusal surface, a pectoral appendage clad in macromeric dermal
337 plates, and a long, box-like trunk armour with multiple median dorsal plates. It is unclear whether
338 these features represent derived or primitive gnathostome conditions—or indeed apomorphies—
339 partly due to the lack of neurocranial evidence in the group. Endocavity anatomy is known in
340 most detail for *Minicrania* [36], a primitive antiarch from the Early Devonian of Yunnan, China.
341 External observation of the specimen suggests the presence of a bulbous endolymphatic sac not
342 unlike the one in *Brindabellaspis*. The putative endocavity in *Minicrania* shows a short hindbrain
343 section, and, based on the imprint of the braincase on the visceral surface of the skull roof, it is
344 likely that most antiarchs display this condition. The distal part of the endolymphatic duct in the
345 yunnanolepiform antiarch *Phymolepis* [37] is mesially directed as in *Brindabellaspis*, providing
346 potential further support for a close relationship between antiarchs, *Brindabellaspis* and the
347 gnathostome crown. In addition, antiarchs appear to have an anteroposteriorly compact labyrinth,
348 with the anterior and posterior semicircular canals in dorsal view forming an angle close to that in
349 *Brindabellaspis* and most crown gnathostomes, and smaller than that in petalichthyids and
350 arthrodiros. It is worth noting that these observations are not included in the current data matrix
351 due to the limited data available for *Minicrania* and *Phymolepis*. Detailed descriptions based on
352 tomographic data of this and other taxa is likely to yield more support for the systematic position
353 of antiarchs, providing more insights into the primitive gnathostome characters in the future.

354 Petalichthyids include morphologically diverse taxa such as *Diandongpetalichthys*,
355 *Eurycaraspis* and macropetalichthyids, but are traditionally united in one group. To date, the

356 endocranial cavity is only reported in the macropetalichthyids *Macropetalichthys* and
357 *Shearsbyaspis*. The former is more completely preserved [42]. *Shearsbyaspis* is digitally
358 reconstructed based on tomographic data, but the posterior part of cranium in the examined
359 specimen is lost [45]. The olfactory tracts in both taxa are unusually long, but are anteriorly
360 directed and parallel, as in most other ‘placoderms’, and the endocast in *Macropetalichthys* also
361 displays an elongate hindbrain region contributed by both the otic and the cranio-spinal sections.
362 In both taxa, the large and bulbous sacculus, thin semicircular canals and pre-ampullary portions
363 of the anterior and external semicircular canals resemble those of arthrodires and rhenanids.
364 *Macropetalichthys* is unique in having the distal part of the endolymphatic duct vertically ascends
365 and flares. This cavity was labelled “fosse endolymphatique” by Stensiö [42], following
366 chondrichthyan terminology. However, unlike the chondrichthyan condition, the endolymphatic
367 duct first extends posteriorly for most of its length, and this flared section is far more distal than
368 the endolymphatic sac in *Brindabellaspis*, resulting in unclear homology. However, the three-
369 dimensional morphology of endolymphatic complex in *Macropetalichthys* is poorly known, and
370 more information is needed to determine whether the flared condition is independent from those
371 in *Brindabellaspis* and crown gnathostomes or not.

372 Rhenanids are ‘placoderm fishes’ with flat, disc-shaped bodies like those of stingray, and the
373 dermal skeleton deviates considerably from the typical ‘placoderm’ bauplan. As in
374 *Macropetalichthys*, the endocranial cavity of the rhenanid *Jagorina* lacks an updated three-
375 dimensional description, despite good preservation of the neurocranium [42, 43, 46]. The inner
376 ear of *Jagorina* resembles arthrodires in displaying a bulbous utricular and sacculus chamber,
377 anterior and external semicircular canals separated by the utricular recess, and a simple tube-like
378 endolymphatic duct. The olfactory tracts are coded as “diverged” in current matrix based on
379 drawings by Stensiö [43], the otic section of the hindbrain is long as in most other ‘placoderms’,
380 and the craniospinal section is very short as in crown gnathostomes.

381 *Brindabellaspis* was previously assigned into Acanthothoraci, a poorly known and loosely
382 defined placoderm group showing considerable morphological disparity, and which is probably
383 paraphyletic. The labyrinth of the acanthothoracid *Romundina* displays an interesting
384 combination of inner ear and endolymphatic features [19], representing a possible intermediate
385 between *Brindabellaspis* and arthrodire / rhenanid conditions. The general profile is not elongated,
386 but is not as longitudinally compressed as in *Brindabellaspis* and the crown group. The angle
387 between the anterior and posterior semicircular canals in dorsal view is sharper than the condition
388 in rhenanids and arthodires, but is larger than that in agnathans, crown-group, and
389 *Brindabellaspis*. The crus commune is present but the sinus superior is not developed, more-or-
390 less resembling the condition in osteostracans. The posterior semicircular canal does not have an
391 extensive preampullary section; the sacculus is large, dorsally positioned in relation to the
392 external semicircular plane, and is flat inclined in anterior view; and the auditory nerve bifurcates
393 before entering the labyrinth cavity, all as in other placoderms. However, the sacculus is
394 irregularly shaped, and the utricular does not separate the ampullary ends of anterior and external
395 semicircular canals, which joins before entering the utricular chamber, as in *Brindabellaspis* and
396 crown gnathostomes (Figs. 2 and 3).

397 **CONTACT FOR REAGENT AND RESOURCE SHARING**

398 Further information and requests for resources and reagents may be directed to and will be
399 fulfilled by the lead contact, Jing Lu (lujing@ivpp.ac.cn).

400 **METHOD DETAILS**

401 **X-ray computed microtomography** Both specimens were scanned with the HeliScan CT
402 Scanner (ANU1) in the CT Lab, Department of Applied Mathematics, Research School of
403 Physics, Australian National University. ANU 49493 was scanned in 2017 with a 3 mm
404 aluminium filter (resolution: 30 microns). The specimen was placed 161 mm from the source,
405 with detector position 625 mm from the source, and was probed separately with a polychromatic
406 X-ray beam (Bremsstrahlung radiation) with accelerating voltage of 120kV and a current of

407 120 μ A. AM F81911 was first scanned in 2017 with a 3 mm aluminium filter (resolution: 34
408 microns), with the specimen placed 180 mm from the 120kv accelerating voltage and 120 μ A
409 current polychromatic X-ray beam source; the detector was placed 786 mm from the source. AM
410 F81911 was re-scanned in 2018 to obtain a more focused view of the inner ear area, using the
411 same filter as the 2017 scan (resolution: 35 microns). The specimen was positioned 187 mm from
412 the source, and detector position positioned 599 mm from the source; it was probed separately
413 with 100kv accelerating voltage and 150 μ A current polychromatic X-ray beam (Bremsstrahlung
414 radiation). All reconstructions of these scans were based on 3600 radiographic projections on a
415 2872 \times 2840 Pixium Flat Panel camera. Tomograms were segmented in Mimics
416 (biomedical.materialise.com/mimics; Materialise, Leuven, Belgium) and the completed models
417 exported as .ply files to Blender (blender.org) for rendering.

418 **Phylogenetic analysis** Parsimony analysis was performed in PAUP v. 4.0a158 [47] with the
419 following settings: 500 random addition sequences, five trees held at each step, maxtrees set to
420 automatically increase, nchuck =10 000, chuckscore =1, tree bisection and reconstruction strategy
421 enabled. The data matrix is based on refs 9,11, 17 and 34. We added or amended 14 characters
422 (see character list for full details), revised a number of codings and removed redundant characters
423 to give a total of 118 taxa and 360 characters. We also added two taxa: *Minicrania* and
424 *Phymolepis*. The four taxa in Vařkaninová et al. [12] were not included due to the low proportion
425 of characters that can be coded on the basis of published data; all four act as wildcard taxa.
426 Osteostraci and Galeaspida were set as the outgroup. All characters are unweighted, and six
427 characters (c.62, c.123, c.160, c.256, c.258, c.262) were ordered. The full character list is given
428 below. Bremer support values were calculated in TNT, with only Bremer Indices higher than one
429 retained in the strict consensus tree nodes. An optimization tree, showing all ambiguous character
430 changes, was generated in MacClade [49] (see Supplementary Data 5). The Bayesian analysis was
431 run in MrBayes v.3.2.6 [50] under the Mkv model, with Galeaspida set as the outgroup. The

432 analysis was run until the standard deviation of split frequencies reached less than 0.01, indicating
433 convergence had been reached, and this was confirmed in Tracer [51]. The first half of each run
434 was discarded as burn-in.

435 The results of both the parsimony and Bayesian analyses are summarized in Supplementary
436 Figure 6. The parsimony analysis resulted in 818628 most parsimonious trees of 1106 steps; the
437 large number of trees is mostly due to very poor resolution within total group chondrichthyans.
438 The complete strict consensus tree with node support is summarised in Supplementary Figure 4a.
439 RI = 0.793; CI = 0.35; HI=0.649; RC=0.278. The Bayesian analysis is summarized in
440 Supplemental Figure 4b.

441 **Notes on homoplasies invoked by our parsimony analysis**

442 Although supported by our parsimony analysis, the phylogenetic distance between
443 arthrodires and maxillate ‘placoderms’ plus the gnathostome crown demands a number of
444 homoplasies. These broadly fall into three categories: jaw suspension (c.92, c.93, c.328), pectoral
445 fin articulation (c.194), and the posterior nose – anterior nose transition. In previous hypotheses
446 of relationships, the posterior nose to anterior nose transition (an anatomical complex of several
447 characters: c.112, c.115, c.127, c.134 c.157) happened only once: at the node subtending
448 arthrodires, maxillate ‘placoderms’ and crown gnathostomes. In the scenario of relationships
449 hypothesised in our parsimony analysis, early members of each of the two jawed vertebrate
450 clades are ‘posterior nosed’, with the transition to an anterior nose occurring independently within
451 them (once in maxillate ‘placoderm’ and crown gnathostomes, and in a stepwise manner in the
452 clade comprising *Romundina*, rhenanids, ptyctodonts, petalichthyids and arthrodires). There are
453 also three homoplasies between the skull roof and trunk armour of arthrodires and maxillate
454 ‘placoderms’ (c.92, c.313, c.323, c.328).

455 **DATA AND SOFTWARE AVAILABILITY**

456 Data availability: The CT data that support the findings of this study, as well as 3D surface files
457 of described material, are deposited on figshare: <https://figshare.com/s/d040d38b2e0ae3501f65>.
458 All other data files are included in the Supplementary Materials.

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460 **References:**

- 461 1. Janvier, P. (1996). *Early Vertebrates* (Oxford: Clarendon Press; Oxford University Press).
- 462 2. Young, G. C. (1986). The relationships of placoderm fishes. *Zool. J. Linn. Soc.* 88, 1–57.
- 463 3. Young, G. C. (2010). Placoderms (armored fish): dominant vertebrates of the Devonian
464 period. *Annu. Rev. Earth Planet. Sci.* 38, 523–550.
- 465 4. Goujet, D., and Young, G. C. (2004). Placoderm anatomy and phylogeny: new insights.
466 In *Recent Advances in the Origin and Early Radiation of Vertebrates*, G. Arratia, M. V. H.
467 Wilson, & R. Cloutier, ed. (München: Verlag Dr. Friedrich Pfeil), pp. 109–126.
- 468 5. Brazeau, M. D. (2009). The braincase and jaws of a Devonian ‘acanthodian’ and modern
469 gnathostome origins. *Nature* 457, 305–308.
- 470 6. Zhu, M., Yu, X., Ahlberg P. E., Choo B., Lu, J., Qiao, T., Qu, Q., Zhao, W., Jia, L., Blom,
471 H., and Zhu, Y. (2013). A Silurian placoderm with osteichthyan-like marginal jaw bones.
472 *Nature* 502, 188–193.
- 473 7. Dupret, V., Sanchez, S., Goujet, D., Tafforeau, P., and Ahlberg, P. E. (2014). A primitive
474 placoderm sheds light on the origin of the jawed vertebrate face. *Nature* 507, 500–503.
- 475 8. Brazeau, M. D., and Friedman, M. (2015). The origin and early phylogenetic history of
476 jawed vertebrates. *Nature* 520, 490–497.
- 477 9. Giles, S., Friedman, M., and Brazeau, M. D. (2015). Osteichthyan-like cranial conditions
478 in an Early Devonian stem gnathostome. *Nature* 520, 82–85.
- 479 10. Long, J. A., Mark-Kurik, E., Johanson, Z., Lee, M. S. Y., Young, G. C., Min, Z., Ahlberg,
480 P. E., Newman, M., Jones, R., den Blaauwen, J., Choo, B., and Trinajstić, K. (2015).

- 481 Copulation in antiarch placoderms and the origin of gnathostome internal fertilization.
482 Nature 517, 196–199.
- 483 11. Zhu, M., Ahlberg, P. E., Pan, Z., Zhu, Y., Qiao, T., Zhao, W., Jia, L., and Lu, J. (2016). A
484 Silurian maxillate placoderm illuminates jaw evolution. Science 354, 334–336.
- 485 12. Vaškaninová, V., Chen, D., Tafforeau, P., Johanson, Z., Ekrt, B., Blom, H., and Ahlberg,
486 P. E. (2020). Marginal dentition and multiple dermal jawbones as the ancestral condition
487 of jawed vertebrates. Science 369, 211–216.
- 488 13. King, B., Qiao, T., Lee, M. S. Y., Zhu, M., and Long J. A. (2016). Bayesian
489 morphological clock methods resurrect placoderm monophyly and reveal rapid early
490 evolution in jawed vertebrates. Syst. Biol. 66, 599–516.
- 491 14. Young, G. C. (1980). A new Early Devonian placoderm from New South Wales,
492 Australia, with a discussion of placoderm phylogeny. Palaeontogr. Abt. A 167, 10–76.
- 493 15. Davis, S. P., Finarelli, J. A., and Coates, M. I. (2012). *Acanthodes* and shark-like
494 conditions in the last common ancestor of modern gnathostomes. Nature 486, 247–250.
- 495 16. Qiao, T., King, B., Long, J. A., Ahlberg, P. E., and Zhu, M. (2016) Early gnathostome
496 phylogeny revisited: multiple method consensus. PLoS One 11, e0163157.
- 497 17. Clement, A. M., King, B., Giles S., Choo, B., Ahlberg P. E., Young, G. C, and Long, J. A.
498 (2018). Neurocranial anatomy of an enigmatic Early Devonian fish sheds light on early
499 osteichthyan evolution. eLife 7, e34349.
- 500 18. Janvier, P. (1984). The relationships of the Osteostraci and Galeaspida. J. Vertebr.
501 Paleontol.4, 344–358.
- 502 19. Dupret, V., Sanchez, S., Goujet, D., and Ahlberg, P. E. (2017). The internal cranial
503 anatomy of *Romundina stellina* Orvig, 1975 (Vertebrata, Placodermi, Acanthothoraci)
504 and the origin of jawed vertebrates-Anatomical atlas of a primitive gnathostome. PLoS
505 One 12, e0171241.

- 506 20. King B., Young, G., C., and Long, J. A. (2018). New information on *Brindabellaspis*
507 *stensioides* Young, 1980, highlights morphological disparity in Early Devonian placoderms.
508 R. Soc. Open Sci. 5, 180094.
- 509 21. Zhu, M., Zhao, W., Jia, L., Lu, J., Qiao, T., and Qu, Q. (2009). The oldest articulated
510 osteichthyan reveals mosaic gnathostome characters. Nature. 458, 469–474.
- 511 22. Gai, Z., Donoghue, P. C. J., Zhu, M., Janvier, P., and Stampanoni, M. (2011). Fossil
512 jawless fish from China foreshadows early jawed vertebrate anatomy. Nature 476, 324–
513 327.
- 514 23. Stensiö, E. A. (1964). Les Cyclostomes fossiles ou Ostracodermes. In Traité de
515 Paléontologie, 4, part 1, J. Piveteau, ed. (Paris: Masson), pp. 96–82.
- 516 24. Coates, M. I. (1999). Endocranial preservation of a Carboniferous actinopterygian from
517 Lancashire, U.K., and the interrelationships of primitive actinopterygians. Philos. Trans.
518 R. Soc. Lond. B. Biol. Sci. 354, 435–462.
- 519 25. Giles, S., and Friedman, M. (2014). Virtual reconstruction of endocast anatomy in early
520 ray-finned fishes (Osteichthyes, Actinopterygii), J. Paleontol. 88, 636–651.
- 521 26. Clément, G., and Ahlberg, P. E. (2010). The endocranial anatomy of the early
522 sarcopterygian *Powichthys* from Spitsbergen, based on CT scanning, In Morphology,
523 Phylogeny and Paleobiogeography of Fossil Fishes. D. K. Elliott, J. G. Maisey, X. Yu
524 and D. Miao, ed. (München: Verlag Dr. Friedrich Pfeil), pp. 363–377.
- 525 27. Maisey, J. G. (2005). Braincase of the Upper Devonian shark *Cladodoides wildungensis*
526 (Chondrichthyes, Elasmobranchii), with observations on the braincase in early
527 chondrichthyans. Bull. Am. Mus. Nat. Hist. 288, 1–103.
- 528 28. Castiello, M., Jerve, A., Burton, M.G., Friedman, M., and Brazeau, M. D. (2020).
529 Endocranial morphology of the petalichthyid placoderm *Ellopetalichthys scheii* from the

- 530 Middle Devonian of Arctic Canada, with remarks on the inner ear and neck joint
531 morphology of placoderms. *Canadian Journal of Earth Sciences*. 999, 1–12.
- 532 29. Stensiö, E. A. (1963a). Anatomical studies on the arthrodiran head. Part 1. Preface,
533 geological and geographical distribution, the organization of the head in the
534 Dolichothoraci, Coccosteomorphi and Pachyosteomorphi. Taxonomic appendix. Kgl.
535 Svenska. Vetenskapsakad. Handl. 9, 1–419.
- 536 30. Stensiö, E. A. (1927). The Downtonian and Devonian vertebrates of Spitsbergen. Part 1.
537 Family Cephalaspidae. *Skrifter om Svalbard og Nordishavet 12*: 1–391.
- 538 31. Young, G. C. (1979). New information on the structure and relationships of
539 *Buchanosteus* (Placodermi: Euarthrodira) from the Early Devonian of New South Wales.
540 *Zool. J. Linnean. Soc.* 66, 309–352.
- 541 32. Janvier, P. (1985). Les Céphalaspides du Spitsberg: anatomie, phylogénie et systématique
542 des Ostéostracés siluro-dévoniens; revisions des Ostéostracés de la Formation de Wood
543 Bay (Dévonien inférieur du Spitsberg). (Paris: Cahiers de Paléontologie, Centre national
544 de la Recherche scientifique).
- 545 33. Gardiner, J. M., Hueter, R. E., Maruska, K. P., Sisneros, J. A., Casper, B. M., Mann, D.
546 A., and Demski, L. S. (2004). Sensory physiology and behavior of elasmobranchs. In
547 *Biology Of Sharks And Their Relatives*, J. A. Musick, J. C. Carrier, and M. R. Heithaus,
548 ed. (Boca Raton: CRC Press), pp. 325–368.
- 549 34. Coates, M. I., Gess, R. W., Finarelli, J.A., Criswell, K. E., and Tietjen, K. (2017). A
550 symmoriiform chondrichthyan braincase and the origin of chimaeroid fishes. *Nature* 541,
551 208–211.
- 552 35. Lu, J., Giles, S., Friedman, M., and Zhu, M. (2017). A new stem sarcopterygian
553 illuminates patterns of character evolution in early bony fishes. *Nat. Commun.* 8, 1932 .

- 554 36. Zhu, M., and Janvier, P. (1996). A small antiarch, *Minicrania lirouyii* gen. et sp. nov.,
555 from the Early Devonian of Qujing, Yunnan (China), with remarks on antiarch phylogeny.
556 *J. Vert. Paleont.* *16*, 1–15.
- 557 37. Wang, Y, and Zhu, M. (2018). Redescription of *Phymolepis cui Fengshanensis* (Antiarcha:
558 Yunnanolepididae) using high-resolution computed tomography and new insights into
559 anatomical details of the endocranium in antiarchs. *PeerJ* *6*, e4808.
- 560 38. Rücklin, M., Donoghue, P. C. J., Johanson, Z., Trinajstić, K., Marone, F., and
561 Stampanoni, M. (2012). Development of teeth and jaws in the earliest jawed vertebrates.
562 *Nature* *491*, 748–751.
- 563 39. Andrews, S. M. (1982). The discovery of fossil fishes in Scotland up to 1845, with a
564 checklist of Agassiz's figured specimens. (Edinburgh: Royal Scottish Museum).
- 565 40. Miles, R. S. (1969). Features of placoderm diversification and the evolution of the
566 arthrodire feeding mechanism. *Trans. R. Soc. Edinburgh.* **68**, 123–170.
- 567 41. Stensiö, E. A. (1963b). The brain and the cranial nerves in fossil lower craniate
568 vertebrates. *Skr. norske VidenskAkad. Oslo, Mat.-naturv. Kl.* *1963*, 1–120.
- 569 42. Stensiö, E. A. (1969). Elasmobranchiomorphi Placodermata Arthrodires. In *Traité de*
570 *Paléontologie*, J., Piveteau, ed. (Paris: Masson), pp. 71–692.
- 571 43. Stensiö, E. A. (1950). La cavité labyinthique, l'ossification sclerotique et l'orbite de
572 *Jagorina*. In *Paeontologie et transformisme*, A., George, ed., (Paris: Albin Michel). pp. 9–
573 43.
- 574 44. Zhu, Y., Zhu, M., and Wang, J. (2016). Redescription of *Yinostius major* (Arthrodira:
575 Heterostiidae) from the Lower Devonian of China, and the interrelationships of
576 Brachythoraci. *J. Zool. Lond.* *176*, 806–834.
- 577 45. Castiello, M. and Brazeau, M. D. (2018). Neurocranial anatomy of the petalichthyid
578 placoderm *Shearsbyaspis oepiki* Young revealed by X-ray computed microtomography.
579 *Palaeontology* *61*, 369–389.

- 580 46. Lelièvre, H., Janvier, P., Janjou, D., and Halawani, M. (1995). *Nefudina qalibahensis* nov.
581 gen., nov. sp. un rhenanide (Vertebrata, Placodermi) du Dévonien inférieur de la
582 formation Jauf (Emsien) d'Arabie Saoudite. *Geobios M. S.* 18, 109–115.
- 583 47. Swofford, D. L. (2003) PAUP*: Phylogenetic analysis using parsimony (* and other
584 methods), version 4.0b 10. (Sinauer Associates).
- 585 48. Zhu, Y., Lu, J., and Zhu, M. (2019). Reappraisal of the Silurian placoderm *Silurolepis*
586 and insights into the dermal neck joint evolution. *R. Soc. Open Sci.* 6, 191181.
- 587 49. Maddison, D. R. and W. P. Maddison, (2005). MacClade 4: Analysis of phylogeny and
588 character evolution. Version 4.08a. <http://macclade.org>.
- 589 50. Huelsenbeck, J. P. (2001). Bayesian inference of phylogeny and its impact on
590 evolutionary biology. *Science* 294, 2310–2314.
- 591 51. Rambaut, A., Suchard, M.A., Xie, D. & Drummond, A. J. (2014). Tracer v1.6.
592 <http://tree.bio.ed.ac.uk/software/tracer/>
593