

The nearshore cradle of early vertebrate diversification

Sallan, Lauren; Friedman, Matt; Sansom, Robert; Bird, Charlotte; Sansom, Ivan

DOI:

[10.1126/science.aar3689](https://doi.org/10.1126/science.aar3689)

License:

None: All rights reserved

Document Version

Peer reviewed version

Citation for published version (Harvard):

Sallan, L, Friedman, M, Sansom, R, Bird, C & Sansom, I 2018, 'The nearshore cradle of early vertebrate diversification', *Science*, vol. 362, no. 6413, pp. 460-464. <https://doi.org/10.1126/science.aar3689>

[Link to publication on Research at Birmingham portal](#)

Publisher Rights Statement:

This is the author's version of the work. It is posted here by permission of the AAAS for personal use, not for redistribution. The definitive version was published in *Science* on 26th October 2018.

DOI: [10.1126/science.aar3689](https://doi.org/10.1126/science.aar3689)

General rights

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

Take down policy

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact UBIRA@lists.bham.ac.uk providing details and we will remove access to the work immediately and investigate.

1 **Title: The nearshore cradle of early vertebrate diversification.**

2
3 **Authors:** Lauren Sallan^{1a*}, Matt Friedman², Robert S. Sansom³, Charlotte M. Bird⁴, Ivan
4 J. Sansom^{4a*}

5
6 **Affiliations:**

7
8 ¹Department of Earth and Environmental Science, University of Pennsylvania,
9 Philadelphia, Pennsylvania 19104.

10
11 ²Museum of Paleontology, University of Michigan, Ann Arbor, MI 48109.

12
13 ³School of Earth and Environmental Sciences, University of Manchester, Manchester,
14 M13 9PT UK.

15
16 ⁴School of Geography, Earth and Environmental Sciences, University of Birmingham,
17 Birmingham, B15 2TT UK.

18
19 ^aThese authors contributed equally.

20
21 *Correspondence to: lsallan@upenn.edu, i.j.sansom@bham.ac.uk

22
23 **Abstract:** Ancestral vertebrate habitats are subject to controversy, and obscured by
24 limited, often contradictory, paleontological data. We assembled fossil vertebrate
25 occurrence and habitat datasets spanning the mid-Paleozoic (480-360 Mya) and found
26 that early vertebrate clades, both jawed and jawless, originated in restricted, shallow
27 intertidal-subtidal environments. Nearshore divergences gave rise to body plans with
28 different dispersal abilities: robust fishes shifted more shoreward while gracile groups
29 moved seaward. Freshwaters were invaded repeatedly, but movement to deeper waters
30 was contingent upon form, and short-lived until the later Devonian. Our results contrast
31 with the onshore-offshore trends, reef-centered diversification, and mid-shelf clustering
32 observed in benthic invertebrates. Nearshore origins for vertebrates may be linked to the
33 demands of their mobility, and influenced the structure of their early fossil record and
34 diversification.

35
36 **One sentence summary:** Early vertebrates diversified in restricted, shallow marine
37 waters, with nearshore divergence in body form shaping their dispersal and fossil record.
38
39
40
41
42
43
44

45 The ancestral habitat of vertebrates has long been debated, with opinions ranging
46 from freshwater to open ocean (1-3). Inferences have been derived from either the
47 evolutionarily-distant modern fauna or qualitative narratives based on select fossils. Early
48 records of vertebrate divisions, such as jawed fishes and their relatives (total-group
49 gnathostomes), consist of long gaps between inferred origination and definitive
50 appearances (ghost lineages), punctuated by suggestive microfossils (4-7). Vertebrates,
51 apart from tooth-like conodont elements, were restricted in Ordovician ecosystems as
52 trivial components of the Great Ordovician Biodiversification Event (4, 5, 7). Ancestral
53 habitat is a critical factor in determining both pattern and mode of diversification,
54 potential mismatches between biodiversity and available habitat area, and the source of
55 apparent relationships with changing sea level (6). A lack of early vertebrate fossil data
56 and habitat information in compendia has limited quantitative approaches (4), preventing
57 resolution of this outstanding issue in vertebrate evolution.

58 We developed a database of total-group gnathostome occurrences (~480-360 My;
59 4, 5, 8) during their mid-Paleozoic diversification (n=1421; 9; Fig. S1). Data collection
60 focused on all occurrences from the interval encompassing the five oldest localities for
61 each major clade (n=188, Fig. 1, Figs. S1, S2) and phylogenetically-constrained genera
62 within jawless groups (n=785; Figs 2, 3; Figs. S1, S3, S4) for use with Bayesian ancestral
63 state reconstruction. We used environmental, lithological, and invertebrate community
64 information from the literature and available databases to assign occurrences to Benthic
65 Assemblage zones (10; Fig. 1). Benthic Assemblage zones are categorized and ordered as
66 freshwater (BA0), intertidal above typical wave base (BA1), shallow subtidal/lagoon
67 (BA2), deeper subtidal, including the start of tabulate coral-stromatoporoid reef systems

68 (BA3), mid- to outer-shelf zone (BA4 and BA5) and shelf margin towards the bathyal
69 region (BA6) and have been widely used in studies of mid-Paleozoic paleocommunities
70 (1, 10-12) (Fig. 1).

71 We applied Bayesian threshold models to phylogenies of occurrences using prior
72 probabilities of residence in each Benthic Assemblage zone. This allowed positive
73 inference of both ancestral habitats and amount of evolutionary change required to move
74 between zones (“liability” values; 13). All major clades, from the first skeletonizing
75 jawless fishes (astraspids, arandaspids) to jawed bony fishes (osteichthyans), originated
76 within nearshore intertidal and subtidal zones (~BA1-3), centered on BA2, over a period
77 of more than 100 million years (Fig. 1A, fig. S3). This area is relatively shallow, includes
78 lagoons in reefal systems, and is located entirely above storm wave base in the mid-
79 Paleozoic (11)(Fig. 1).

80 We appraised whether nearshore origination in gnathostomes resulted from
81 environmental bias in the record through comparison with habitat distributions for other
82 facets of the mid-Paleozoic captured in independent datasets, including fossiliferous
83 strata, regional paleocommunities, and global occurrences and richness (number of
84 genera) (Fig. 1B; figs. S11-S16) (10, 14). Analysis of mid-Paleozoic strata in the
85 Paleobiology Database (PBDB; 14), binned by distinct habitat categories (n=4437),
86 produced a distribution clustered on deep subtidal/reef environments (equivalent to
87 BA3/4 (10)) with many fewer records in freshwater-marginal marine (BA0-1) and the
88 basin/slope (~BA5/6) (Fig. 1B, figs. S11, S12). PBDB records of occurrences (n=111364)
89 or genera (n=24211) provide distributions that show even greater clustering on the mid-
90 shelf, but are highly correlated with sampled strata (linear regression: $r^2=0.96$, $p=0.0004$

91 and $r^2=0.94$; $p=0.0008$ respectively, fig. S12). Silurian and Lochkovian regional
92 paleocommunities (10) are also centered on BA3-4 (Fig. 1B, fig. S13). These records
93 suggest a global, mid-shelf center for sampling and diversity, and a null expectation of
94 originations in deep subtidal and reef environments (more so than expected from previous
95 studies focused on reef-bearing facies (15)). This is in stark contrast with shallower
96 gnathostome ancestral habitats (Fig. 1), which is thus unlikely to result from global
97 sampling bias.

98 Testing whether apparent nearshore origination resulted from preservational
99 biases in different habitats, we compared gnathostome distributions to Paleobiology
100 Database records for conodonts. Conodonts are the sister group of extant jawless
101 cyclostomes or the vertebrate total-group, largely known from phosphatic oral elements
102 (4) which serve as an independent preservational proxy. Conodonts are stratigraphic
103 index fossils and common along the marine depth gradient during the mid-Paleozoic (Fig.
104 1B, fig. S14). Conodont occurrences ($n=11915$) show a different distribution from other
105 Paleobiology Database records (Chi-squared $p<0.0001$), exhibiting a peak in BA2 and
106 more occurrences in BA5/6 (Figs. S14, S15). Conodont richness ($n=1308$) is more
107 clustered around BA3/4, particularly in the Silurian-Lochkovian ($n=505$)(Fig. 1B, figs.
108 S14, S15). This pattern argues against early gnathostome restriction resulting from
109 preservational bias, as does the plurality of vertebrate occurrences in deeper waters from
110 the early Silurian (Fig. 1C, fig. S1).

111 Jawed and jawless fish distributions are highly clustered in BA0-2 early in clade
112 history ($n=478$), in the Silurian and Lochkovian ($n=1035$), and over the mid-Paleozoic
113 ($n=2147$) (Fig. 1, figs. S1, S16-S18). We recover no significant or strong, positive

114 correlations between this gnathostome pattern and other fossil records (linear regression
115 r^2 range: -0.90-0.27, p-range: 0.41-0.9) (Fig. 1B, fig. S16).

116 Ancestral states show that gnathostomes originated preferentially nearshore, even
117 as diversity of species and body forms increased (Fig. 1A, fig. S2). Early occurrences are
118 significantly different from later records within groups (Chi-squared $p < 0.00001$) (Fig.
119 1C, fig. S18); gnathostomes as a whole, as well as jawed and jawless fishes specifically,
120 exhibit greater clustering in shallow marine settings (BA1-2) independent of exact time
121 of first appearance in the mid-Paleozoic (Fig. 1C, fig. S18). Shallow ancestral habitats are
122 always supported by our analyses despite variation in first appearances of jawed fishes
123 (e.g. inclusion of potential Ordovician “chondrichthyan” material; 15), placoderm
124 monophyly or paraphyly (8), and even increasing the minimum prior probability of
125 occurrences in all zones to a minimum of 5% or 10% to account for potential of false
126 absence, missing records or other sampling issues (Fig. 1A, figs. S2-S5; Table S1).
127 Gnathostomes continued to show a strong tendency to diverge in shallow marine waters
128 long after the invasion of deeper and freshwaters by older lineages, including after the
129 origin of jaws.

130 Threshold liability values suggest that shifts within the nearshore waters required
131 little evolutionary change and were common, as was invasion of freshwater (Table 1; Fig.
132 1C). Dispersal into deeper waters, including the forereef, shelf and open ocean (BA4-6),
133 was more restricted (Table 1), complicated by a short term tendency to return to the
134 ancestral shallows (Ornstein-Uhlenbeck, DIC weight=1; phylogenetic half-life in Table
135 1)(16). Yet, threshold values also suggest rapid dispersal across the offshore shelf (BA4-5)
136 once lineages managed to depart BA3, even though shifts into open waters (BA6) had

137 much higher requirements (Table 1). However, if sampling probabilities in all bins is
138 increased *a priori*, shallow-water restriction of early gnathostomes is explained by ever-
139 higher thresholds for continued movement offshore, starting at BA2 (Fig. 1A, figs. S2-S5;
140 Table S1).

141 Next, determined the association between body form and dispersal ability within
142 major groups. Clades were categorized into two body forms: 1) macromeric, which are
143 mostly robust and armored with large bony plates (e.g. heterostracans, osteostracans,
144 galeaspids)(17)(Fig. 2) or 2) micromeric, which are mostly gracile and either naked or
145 covered in small scales (e.g. thelodonts and anaspids)(17)(Fig. 3). These robust or gracile
146 forms can be approximated as having benthic or pelagic/nektonic lifestyles, respectively,
147 given gross similarity to living fishes (18, 19).

148 Analysis of all gnathostome early occurrences shows that both micromeric and
149 macromeric forms originated around shallow water BA2 (Fig. 1A, S2). However, group-
150 level analyses suggest that slight shifts shoreward or seaward preceded the later
151 diversification of these groups. Genus-level diversification of macromeric jawless
152 lineages was centered in the shallows (BA1-2) and freshwater (BA0) throughout their
153 multi-million-year existence (Fig. 2, figs. S6-S8, S19, S20). Later occurrences were
154 significantly more clustered in shallow and freshwater settings than the earliest members
155 of these clades (Chi-Squared $p < 0.0001$) (Fig. 2C, figs. S19, S20). Threshold values
156 indicate moving into deeper waters was more difficult for robust groups than
157 gnathostomes as a whole (Tables 1, S1, S2), and these featured a strong tendency to
158 return to the shallows (OU DIC weight range=0.99-1; phylogenetic half-life in Table 1).

159 The diversification of micromeric gnathostomes was centered in deeper subtidal
160 waters (BA3) following their origination in BA2 (Figs. 1A, 3, figs. S9, S10, S21, S22).
161 Early occurrences of these clades show a significantly greater concentration in BA1-2
162 than later forms (Chi-squared $p < 0.0001$) (Fig. S21, S22). A handful of early Silurian
163 thelodont taxa were already resident in deeper waters (BA3-5), following their Late
164 Ordovician appearances in BA1-2 (Fig. S21A). Early dispersal into deeper waters reflects
165 low threshold parameters (Table 1), and may be a general pattern for gracile clades.
166 Jawed fishes show a significant shift onto reefs and deeper settings in the later Devonian
167 (Chi-squared $p < 0.0001$) (Fig. 1C, figs. S1, S18), after the appearance of most subclades.
168 Robust jawless groups contain exceptions that may prove this rule; a few subclades with
169 fusiform bodies originated in BA3 and register deeper water occurrences than their
170 relatives by the mid-Silurian (e.g. tremataspid osteostracans) (Fig. 2, figs. S6-S8).

171 Dispersal in multiple directions appears to have been enabled by body form
172 evolution, rather than preceding the origin of new phenotypes in new habitats. These
173 shifts affected subsequent survival. Freshwater habitats were marked by the persistence
174 of robust clades like osteostracans and gracile forms like anaspids, without further
175 changes to gross body plan (Figs 2, 3). Sometimes identical deep-water lineages appear
176 short-lived and did not exhibit apparent further diversification, even on reefs (Fig. 1; 20).
177 Jawless gnathostomes show a significant shift in distribution (Chi-Squared $p < 0.00001$)
178 back into the ancestral nearshore habitats and adjacent estuarine areas following a peak in
179 distribution across the depth gradient in the Silurian to Early Devonian (Fig. 1C, figs. S1,
180 S18). This occurred just as jawed fishes moved out of nearshore habitats in the Devonian

181 (Fig. 1A, fig. S18)(4,21). This pattern is reflected in the greater representation of benthic
182 forms in later marine jawless fishes vs “nektonic” forms in jawed vertebrates (22).

183 Overall, results show that the nearshore served as the cradle of early vertebrate
184 taxonomic and gross morphological diversification (Figs 1-3). Specific body forms
185 evolved in coastal waters subsequently favoring expansion into shallower (e.g.
186 macromeric jawless fishes) or deeper areas (e.g. micromeric jawless fishes, jawed fishes).
187 This mirrors observations within living fishes of repeated splits into benthic and
188 pelagic/nektonic forms (18, 23), and the gross division of fish phenotype-environment
189 associations (19).

190 A persistent diversification center within the shallows may explain features of the
191 early vertebrate record (7, 24). Ordovician gnathostomes are primarily represented by
192 microfossils restricted to a small subset of nearshore facies (Fig. S1) subject to wave
193 action (11), despite worldwide distributions (4, 7, 17, 24). Ghost lineages for
194 gnathostomes might be caused by environmental endemism, low abundance, and/or a
195 relative lack of marginal marine strata (Figs. S1, S11-S13). Alternatively, a relationship
196 between Ordovician diversity and sea level (6) might have a common cause in changing
197 shallow habitat area; reduction in such environments would have delayed apparent
198 diversification and increased extinction risk (6, 25, 26).

199 Endemism in coastal waters may have later promoted origination of new clades.
200 Biogeographic patterns suggest that body-form divergence occurred in multiple shallow
201 settings, increasing overall diversity. Micromeric forms occur alongside macromeric
202 astraspids in the Ordovician of Laurentia, while robust galeaspids existed alongside
203 gracile chondrichthyans in the early Silurian of Gondwana (4-7,15, 17, 24, 27, 28).

204 Nektonic body plans developed in these hotspots enabled dispersal across deep early
205 Silurian oceans, away from local competition, leading to further diversification in
206 nearshore settings elsewhere (1, 15, 28). In contrast, benthic groups showed structured
207 geographic patterns (27), moving along coastlines and inshore, perhaps towards nutrient
208 inputs essential to their likely bottom-feeding and filtering lifestyles and away from
209 increased competition. Thus, continuous origination in shallow waters shaped the
210 evolution of vertebrates during, at least, their first phase of diversification.

211

212 **References and Notes**

213

214 1. A. J. Boucot, C. Janis, The environment of the early Paleozoic vertebrates. *Paleogeogr.*
215 *Paleoclimat. Palaeoecol.* **41**, 251-287 (1983).

216 2. T. C. Chamberlin, On the habitat of early vertebrates. *J. Geol.* **8**, 400- 412 (1900).

217 3. G. Carrete-Vega, J. J. Wiens, Why are there so few fish in the sea? *Proc. R. Soc. Lond.*
218 *B* **279**, 2323-2329 (2012).

219 4. M. Friedman, L. C. Sallan, Five hundred million years of extinction and recovery: a
220 Phanerozoic survey of large-scale diversity patterns in fishes. *Palaeontology* **55**,707-742
221 (2012).

222 5. I. J. Sansom, M. M. Smith, M. P. Smith, “The Ordovician radiation of vertebrates” in
223 *Major events in early vertebrate evolution*, P. E. Ahlberg, Ed. (Taylor & Francis, 2001),
224 pp. 156-171.

225

226 6. R. S. Sansom, E. Randle, P. C. J. Donoghue, Discriminating signal from noise in the
227 fossil record of early vertebrates reveals cryptic evolutionary history. *Proc. R. Soc. Lond.*
228 *B* **282**, 20142245 (2015).

229 7. N. S. Davies, I. J. Sansom, Ordovician vertebrate habitats: a Gondwanan perspective.
230 *Palaios* **24**, 717-722 (2009).

231 8. M. D. Brazeau, M. Friedman, The origin and early phylogenetic history of jawed
232 vertebrates. *Nature* **520**, 490-497 (2015).

233

234 9. Materials and methods are available as supplementary materials on *Science* online.

235 10. A. Boucot, J. Lawson, eds, *Paleocommunities: A Case Study from the Silurian and*
236 *Lower Devonian* Cambridge University: Cambridge (1999).

- 237
238 11. C. E. Brett, A. J. Boucot, B. Jones, Absolute depths of Silurian benthic assemblages.
239 *Lethaia* **26**, 25-40 (1993).
- 240 12. H. Armstrong, D. A. T. Harper, An earth system approach to understanding the end-
241 Ordovician (Hirnantian) mass extinction. *Geol. Soc. America Spec. Papers* **505**, 287-300
242 (2014)
- 243 13. L. K. Revell, Ancestral character estimation under the threshold model from
244 quantitative genetics. *Evolution* **68**, 743-759 (2014).
- 245 14. Data downloaded from the Paleobiology Database (Paleobiodb.org) June 6-12, 2018.
246
- 247 15. P. S. Andreev, et al. *Elegestolepis* and its kin, the earliest monodontode
248 chondrichthyans. *J. Vertebr. Paleontol.* **37**, e1245664 (2017).
249
- 250 16. T. F. Hansen, Stabilizing selection and the comparative analysis of adaptation.
251 *Evolution* **51**, 1341-1351 (1997).
- 252 17. P. Janvier, *Early Vertebrates* Oxford University (1996).
- 253 18. D. Schluter, *The Ecology of Adaptive Radiation* Oxford University (2000).
- 254 19. T. Claverie, P. C. Wainwright, A morphospace for reef fishes: elongation is the
255 dominant axis of body shape evolution. *PLoS ONE* **9**, e112732 (2014).
- 256 20. W. Kiessling, C. Simpson, M. Foote Reefs as cradles of evolution and sources of
257 biodiversity in the Phanerozoic. *Science* **327**, 196-198 (2010).
- 258 21. P. S. L. Anderson, M. Friedman, M. D. Brazeau, E. Rayfield, Initial radiation of jaws
259 demonstrated stability despite faunal and environmental change. *Nature* **476**, 206–209
260 (2011).
261
- 262 22. C. B. Klug, et al. The Devonian nekton revolution. *Lethaia* **43**, 465-477 (2010).
- 263 23. R. B. Langerhans, Predictability of phenotypic differentiation across flow regimes in
264 fishes. *Integr Comp Biol* **48**, 750-768 (2008).
- 265 24. M. P. Smith, P. C. J. Donoghue, I. J. Sansom, The spatial and temporal diversification
266 of Early Palaeozoic vertebrates. *Geol. Soc. London Spec. Publ.* **194**, 69-72 (2002).
- 267 25. B. Hannisdal, S. E. Peters, Phanerozoic Earth system evolution and marine
268 biodiversity. *Science* **334**, 1121-1124 (2011).
269
- 270 26. C. Pimiento, et al., The Pliocene marine megafaunal extinction and its impact on
271 functional diversity. *Nature Ecology and Evolution* **1**, 1100-1106 (2017).
272

- 273 27. R. S. Sansom, Endemicity and palaeobiogeography of the Osteostraci and Galeaspida:
274 a test of scenarios of gnathostome evolution. *Palaeontology* **52**, 1257-1273 (2009).
275
- 276 28. T. Märss, S. Turner, V. Karatajute-Talimaa, “Agnatha” II: Thelodonti in H. P.
277 Schultze Ed. *Handbook of Paleichthyology* **Vol. 1B** Dr. Friedrich Pfeil: 1-143 (2007).
- 278 29. F. M. Gradstein, J. G. Ogg, M. Schmitz, G. Ogg, *The Geologic Time Scale 2012*
279 (Elsevier, 2012).
280
- 281 30. A. J. Boucot, *Evolution and extinction rate controls* (Elsevier, 1975).
282
- 283 31. R. Plotnick, “Llandoveryan-Lochkovian eurypterid communities,” in
284 *Paleocommunities: A Case Study from the Silurian and Lower Devonian*, A. Boucot, J.
285 Lawson, Eds. (Cambridge Univ. Press, 1999), pp. 106-131.
286
- 287 32. W. P. Maddison, D. R. Maddison, Mesquite: a modular system for evolutionary
288 analysis. Version 3, <http://mesquiteproject.org> (2017)
289
- 290 33. R. S. Sansom, K. Freedman, S. E. Gabbott, R. A. Aldridge, M. A. Purnell,
291 Taphonomy and affinity of an enigmatic Silurian vertebrate *Jamoytius kerwoodi* White.
292 *Palaeontology* **53**, 1393-1409 (2010).
- 293 34. M. Zhu, X. B. Yu, P. E. Ahlberg, B. Choo, J. Lu, T. Qiao, Q. M. Qu, W. J. Zhao, L. T.
294 Jia, H. Blom, Y. A. Zhu, A Silurian placoderm with osteichthyan-like marginal jaw bones.
295 *Nature* **502**, 188-193 (2013).
- 296 35. J. N. Keating, P. C. J. Donoghue, Histology and affinity of anaspids, and the early
297 evolution of the vertebrate dermal skeleton. *Proc. R. Soc. Lond. B* **283**, 20152917 (2016).
298
- 299 36. J. Lu, S. Giles, M. Friedman, M. Zhu, A new stem-sarcopterygian illuminates patterns
300 of character evolution in early bony fishes. *Nature Communications* **8**, 1932 (2017)
301
- 302 37. B. L. King, Bayesian morphological clock methods resurrect placoderm monophyly
303 and reveal rapid early evolution in jawed vertebrates. *Syst. Biol.* **66**, 499–516 (2017).
304
- 305 38. R. S. Sansom, S. A. Rodygin, P. C. J. Donoghue, The anatomy, affinity and
306 phylogenetic significance of *Ilemoraspis kirkinskayae* (Osteostraci) from the Devonian of
307 Siberia. *J. Vert. Paleont.* **28**, 613-625 (2008).
- 308 39. R. S. Sansom, Phylogeny, classification and character polarity of the Osteostraci
309 (Vertebrata). *J. Syst. Paleont.* **7**, 95-115 (2009).
- 310 40. M. V. H. Wilson, T. Märss, Thelodont phylogeny revisited, with inclusion of key
311 scale-based taxa. *Eston. J. Earth Sci.* **58**, 297-310 (2009).

- 312 41. E. Randle, R. S. Sansom, Phylogenetic relationships of the ‘higher heterostracans’
313 (Heterostraci: Pteraspidoformes and Cyathaspididae), extinct jawless vertebrates. *Zool. J.*
314 *Linn. Soc.* **zlx025** (2017).
315
- 316 42. M. Zhu, Z. Gai, Phylogenetic relationships of galeaspids (Agnatha). *Front. Biol.*
317 *China* **2**, 1–19 (2007).
318
- 319 43. H. Blom, New birkeniid anaspid from the Lower Devonian of Scotland and its
320 phylogenetic implications. *Palaeontology* **55**, 641-652 (2012).
321
- 322 44. P. C. J. Donoghue, M. A. Purnell, R. J. Aldridge, S. Zhang, The interrelationships of
323 ‘complex’ conodonts (Vertebrata). *J. Syst. Palaeontol.* **6**, 119-153 (2008).
324
- 325 45. M. A. Bell, G. T. Lloyd, Strap: An R package for plotting phylogenies against
326 stratigraphy and assessing their stratigraphic congruence, *Palaeontology* **58**, 379-389
327 (2015).
328
- 329 46. J. C. Uyeda, T. F. Hansen, S. J. Arnold, J. Pienaar, The million year wait for
330 macroevolutionary bursts. *Proc. Natl. Acad. Sci. USA* **108**, 15908-15913 (2011).
331
- 332 47. L. J. Revell, phytools: an R package for phylogenetic comparative biology (and other
333 things). *Methods Ecol. Evol.* **3**, 217-233 (2012).
334
- 335 48. G. E. Uhlenbeck, L. S. Ornstein, On the theory of Brownian Motion *Phys. Rev.* **36**,
336 823-841 (1930)
337
- 338 49. R. Lande, 1976. Natural selection and random drift in phenotypic evolution.
339 *Evolution* **30**, 314-334 (1976).
340
- 341 50. M. Pagel, Inferring the historical patterns of biological evolution. *Nature* **401**, 877-
342 884 (1999).
343
- 344 51. D. Spiegelhalter, N. G. Best, B. P. Carlin, A. van der Linde, Bayesian measures of
345 model complexity and fit (with discussion). *J. Roy. Stat. Soc. B* **64**, 583-639 (2002).
346
- 347 52. K. P. Burnham, D. R. Anderson, *Model Selection and Multimodel Inference: A*
348 *Practical Information-Theoretic Approach* (Springer, 2002).
- 349 53. D.-G. Shu, *et al.*, Lower Cambrian vertebrates from south China. *Nature* **402**, 42–46
350 (1999)
- 351 54. I. J. Sansom, M. P. Smith, M. M. Smith, Scales of thelodont and shark-like fishes
352 from the Ordovician. *Nature* **379**, 628-620 (1996).
353
- 354 55. I. J. Sansom, N. S. Davies, M. I. Coates, M. I., R. S. Nicoll, A. Ritchie,
355 Chondrichthyan- like scales from the Middle Ordovician of Australia. *Palaeontology* **55**,
356 243–247 (2012)),

357
358 56. Z. Gai, P. C. J. Donoghue, M. Zhu, P. Janvier, M. Stampanoni, Fossil jawless fish
359 from China foreshadows early jawed vertebrate anatomy. *Nature* **476**, 324-327 (2011).
360
361 57. I. J. Sansom, D. K. Elliott, A thelodont from the Ordovician of Canada. *J. Vert.*
362 *Paleont.* **22**, 867-870 (2002).
363
364 58. R. J. Aldridge, S. E. Gabbott, J. N. Theron, “The Soom Shale,” in: *Palaeobiology II*
365 D. E. G. Briggs, P. R. Crowther, Eds (Blackwell, 2001), pp. 340-342.
366
367 59. D. J. E. Murdock, X.-P. Dong, J. E. Repetski, F. Marone, M. Stampanoni, P. C. J.
368 Donoghue, The origin of conodonts and of vertebrate mineralized skeletons. *Nature* **502**,
369 546–549 (2013)).

370 60. J. R. Wheelley, P. E. Jardine, R. J. Raine, I. Boomer, M. P. Smith, Paleoecologic and
371 paleoceanographic interpretation of $\delta^{18}\text{O}$ variability in Lower Ordovician conodont
372 species. *Geology* **46**, 467-470 (2018)

373 **Acknowledgements:** We thank Z. Min, for assistance with galeaspid occurrences; L.
374 Revell, G. Lloyd, J. Mitchell for advice on phylogenetic methods, S. Wang for assistance
375 with statistical tests, N. Tamura for providing the reconstructions used in Figures 1-3, and
376 D. Fraser and two anonymous reviewers for comments. **Funding:** University of
377 Pennsylvania (L.S.), Palaeontological Association Undergraduate Research Bursary
378 (C.M.B), University of Birmingham (I.J.S). **Author Contributions:** L.S. and I.J.S.
379 designed the study, assembled the figures, interpreted results, and drafted the manuscript.
380 L.S., R.S.S., C.M.B., and I.J.S. contributed data. L.S. performed analyses. L.S., M.F.,
381 R.S.S., C.M.B., and I.J.S. participated in designing analyses, discussion of results, and
382 editing of the manuscript. **Competing Interests:** None Declared. **Data and Materials**
383 **Availability:** All data are available in the supplementary materials and on Dryad at
384 doi:10.5061/dryad.g08m87q.

385 **Table 1. Best-Fit Model Parameters for Ancestral Habitats in Figures 1-3.**
386 *AncThresh* (13) holds the threshold for exiting BA0 constant at 0 and BA6 as Infinity.

387 Values for parameters are means after excluding “burn-in.” See Figs. S2-S10 and

388 Database S1 for ancestral states.

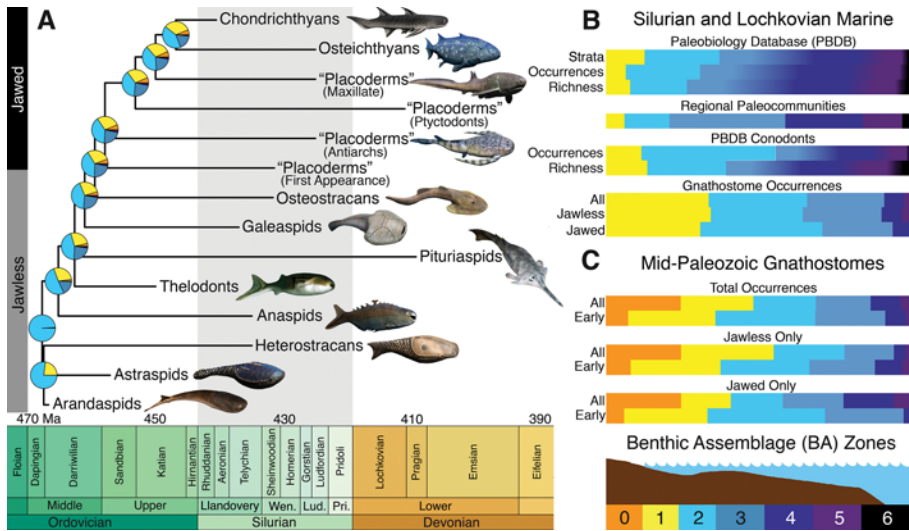
Clade	Mean Threshold Liabilities (20 mil. gen., 20% burn-in)							Log	<i>Alpha</i>	Half-life
	BA0	BA1	BA2	BA3	BA4	BA5	BA6	Likelihood		(My)
Gnathostomes	0	2.09	3.98	6.24	6.81	97.48	Inf	-657.77	0.13	5.33
Heterostracans	0	2.92	3.86	7.74	38.20	200.13	Inf	-979.86	0.12	5.78
Galeaspids	0	3.31	5.91	15.53	83.03	200.55	Inf	-446.63	0.01	138.63
Osteostracans	0	1.13	2.90	26.27	51.66	94.34	Inf	-433.09	0.08	8.66
Anaspids	0	0.19	0.34	1.35	1.40	103.24	Inf	-142.24	1.95	0.36
Thelodonts	0	0.61	0.93	2.05	2.15	110.77	Inf	-220.20	0.59	1.17

389

390

391

392 **Figure Legends:**



393

394 **Figure 1. Mid-Paleozoic vertebrates preferentially originated in shallow marine**

395 **habitats.** A) Intertidal (BA1) to subtidal (BA2-3) ancestral habitats for total-group

396 gnathostome clades (n=188) assuming placoderm paraphyly and Silurian first occurrence

397 for chondrichthyans. Full results shown in Figs. S2-S5. B) Silurian and Lochkovian

398 marine distributions for Paleobiology Database fossiliferous strata (n=858), richness

399 (n=6980) and occurrences (n=30004), conodont richness (n=505) and occurrences

400 (n=7447), paleocommunities, (n=2401) and gnathostome occurrences (n=1035) show

401 mid-Paleozoic records peaking on the mid-shelf (BA3-4) with few records in marginal

402 marine settings, in contrast to the shallow water preferences of early gnathostomes. C)

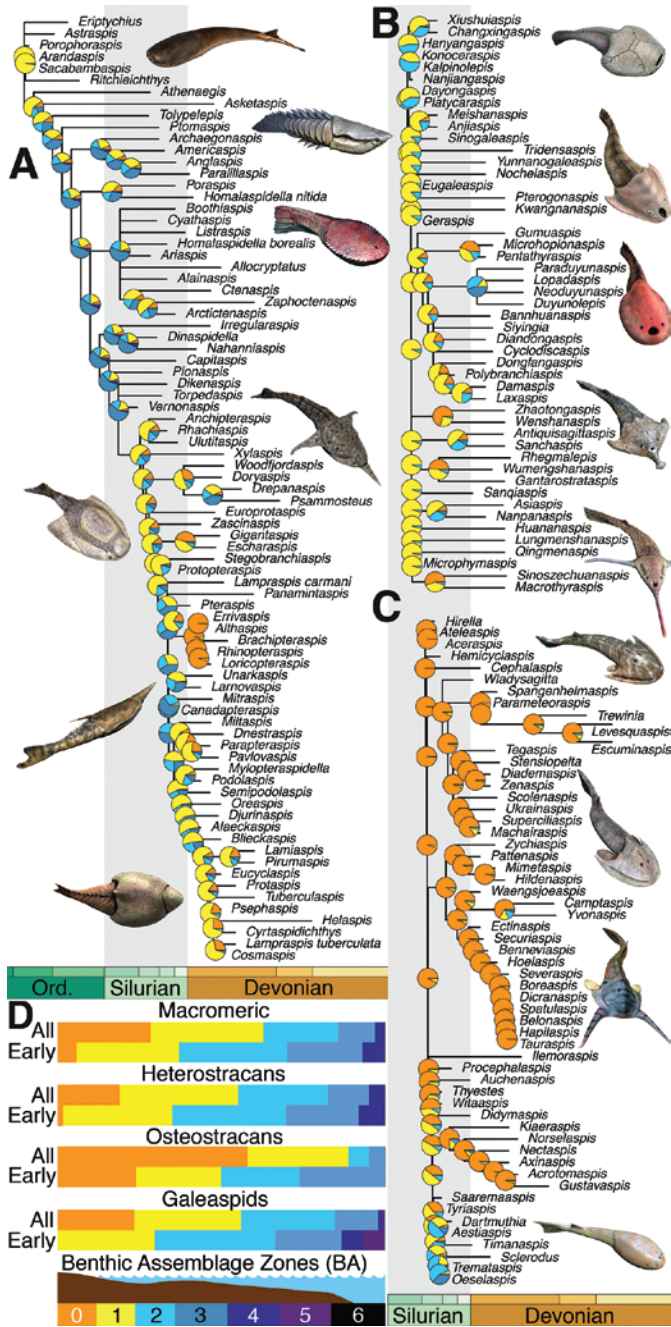
403 Early and overall occurrences for total-group gnathostomes (n=2827), jawed fishes

404 (n=1343) and jawless fishes (n=1484) show that early occurrences were significantly

405 more concentrated in shallow marine settings than overall or later occurrences. See

406 Additional Data File S2 and Figs. S1, S5-S9

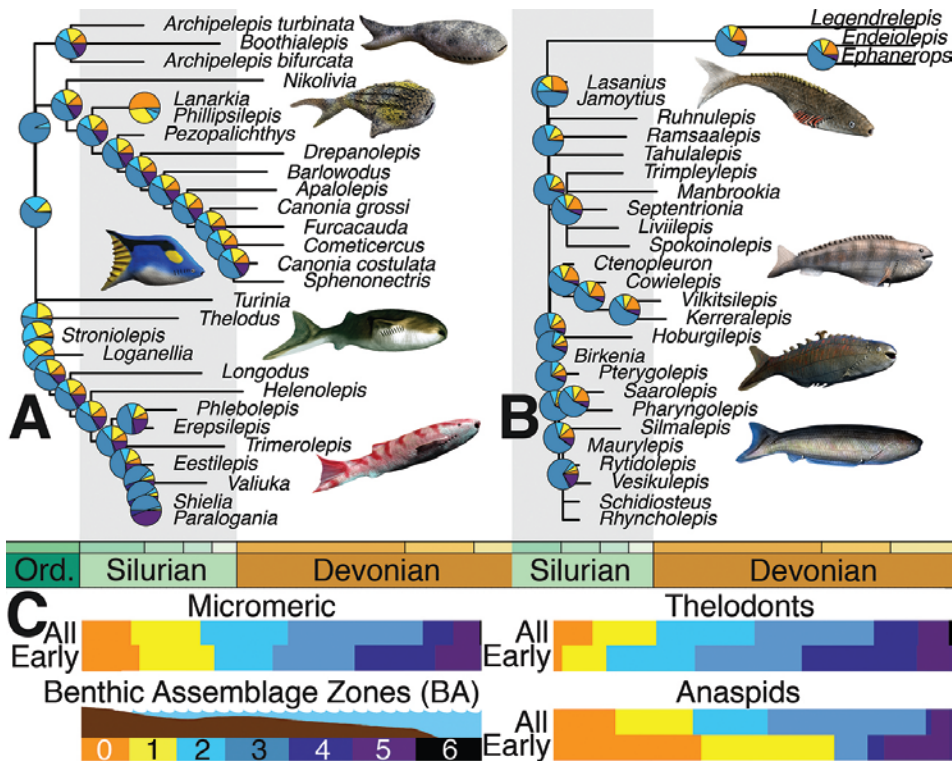
407



408

409 **Figure 2. Macromeric, robust jawless fishes exhibit shallower-water diversification**
 410 **and greater habitat restriction.** Ancestral states for A) heterostracans and Ordovician
 411 stem-gnathostomes (n=316), B) galeaspids (n=112), and C) osteostracans (n=158) show
 412 that macromeric genera preferentially originated in very shallow waters (BA0-2) with the
 413 exception of more streamlined forms. Full results shown in Figs S6-S8. D) Early and later
 414 habitat distributions for macromeric clades (n=1123) showing significant shifts towards
 415 shallower water subsequent to their origination. Full distributions shown in Figs. S19 and
 416 S20 and Additional Data File S1.

417



418

419 **Figure 3. Micromeric, gracile jawless fishes exhibit deeper-subtidal later**

420 **diversification and easier dispersal.** Ancestral states for A) thelodonts (n=99), B)

421 anaspids (n=100) showing diversification of genera in deeper subtidal waters during their

422 evolutionary history. Full results shown in Figs. S9 and S10. C) Early and later

423 occurrences for micromeric jawless fishes (n=353) show a rapid shift to deeper waters

424 following nearshore origination. Full distributions shown in Figs. S21 and S22 and

425 Additional Data File S1.

426

427	
428	Supplementary Materials
429	
430	Materials and Methods
431	
432	Supplementary Text
433	
434	References (29-60)
435	
436	Tables S1-S3
437	
438	Figures S1-S23
439	
440	Additional Data Tables S1-S3
441	
442	Database S1 (doi:10.5061/dryad.g08m87q)
443	
444	