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

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1	Title: The nearshore cradle of early vertebrate diversification.
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3	Authors: Lauren Sallan ^{1a*} , Matt Friedman ² , Robert S. Sansom ³ , Charlotte M. Bird ⁴ , Ivan
4	J. Sansom ^{4a*}
5	
6	Affiliations:
7	
8	¹ Department of Earth and Environmental Science, University of Pennsylvania,
9	Philadelphia, Pennsylvania 19104.
10	
11	² Museum of Paleontology, University of Michigan, Ann Arbor, MI 48109.
12	2
13	³ School of Earth and Environmental Sciences, University of Manchester, Manchester,
14	M13 9PT UK.
15	
16	⁴ School of Geography, Earth and Environmental Sciences, University of Birmingham,
17	Birmingham, B15 2TT UK.
18	
19	^a These authors contributed equally.
20	*
21	*Correspondence to: lsansom@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.
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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.
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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

(BA3), mid- to outer-shelf zone (BA4 and BA5) and shelf margin towards the bathyal
region (BA6) and have been widely used in studies of mid-Paleozoic paleocommunities
(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 midshelf, but are highly correlated with sampled strata (linear regression: $r^2=0.96$, p=0.0004 90

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

Jawed and jawless fish distributions are highly clustered in BA0-2 early in clade history (n=478), in the Silurian and Lochkovian (n=1035), and over the mid-Paleozoic (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.

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

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

101	(Fig. 14 fig. (12)) This notton is reflected in the proston representation of heathic
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 endemicity, 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	Endemicity 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.
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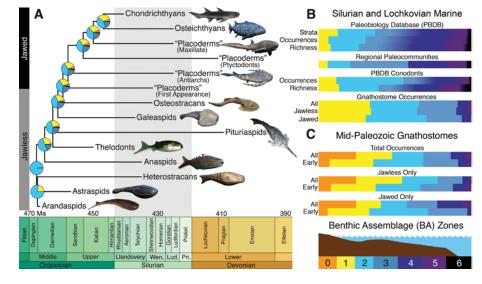
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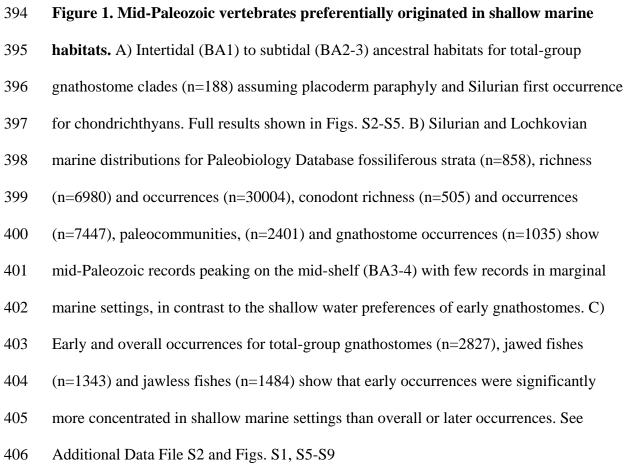
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380	L.S., R.S.S., C.M.B., and I.J.S. contributed data. L.S. performed analyses. L.S., M.F.,
381	R.S.S., C.M.B., and I.J.S. participated in designing analyses, discussion of results, and
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383	Availability: 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.

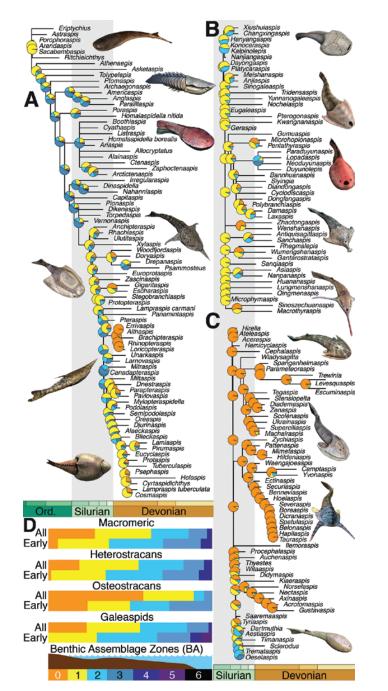
- 387 Values for parameters are means after excluding "burn-in." See Figs. S2-S10 and
- 388 Database S1 for ancestral states.

	Mean	Thres	hold L	iabilitie	S					
Clade	(20 mil. gen., 20% burn-in)							Log	Alpha	Half-life
	BA0	BA1	BA2	BA3	BA4	BA5	BA6	Likeliho	od	(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

Figure Legends:









409 Figure 2. Macromeric, robust jawless fishes exhibit shallower-water diversification

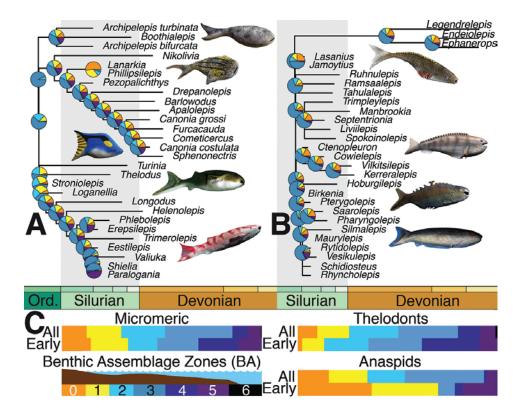
410 **and greater habitat restriction.** Ancestral states for A) heterostracans and Ordovician

411 stem-gnathostomes (n=316), B) galeaspids (n=112), and C) osteostracans (n=158) show

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
- shallower water subsequent to their origination. Full distributions shown in Figs. S19 andS20 and Additional Data File S1.
- 417





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

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428	Supplementary Materials
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440	Additional Data Tables S1-S3
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442	Database S1 (doi:10.5061/dryad.g08m87q)
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