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

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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>

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DOI: 10.1126/science.aar3689

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Title: The nearshore cradle of early vertebrate diversification.

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

One sentence summary: Early vertebrates diversified in restricted, shallow marine waters, with nearshore divergence in body form shaping their dispersal and fossil record.

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

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

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

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

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.

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

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

Ancestral states show that gnathostomes originated preferentially nearshore, even as diversity of species and body forms increased (Fig. 1A, fig. S2). Early occurrences are significantly different from later records within groups (Chi-squared $p < 0.00001$) (Fig. 1C, fig. S18); gnathostomes as a whole, as well as jawed and jawless fishes specifically, exhibit greater clustering in shallow marine settings (BA1-2) independent of exact time of first appearance in the mid-Paleozoic (Fig. 1C, fig. S18). Shallow ancestral habitats are always supported by our analyses despite variation in first appearances of jawed fishes (e.g. inclusion of potential Ordovician “chondrichthyan” material; 15), placoderm monophyly or paraphyly (8), and even increasing the minimum prior probability of occurrences in all zones to a minimum of 5% or 10% to account for potential of false absence, missing records or other sampling issues (Fig. 1A, figs. S2-S5; Table S1). Gnathostomes continued to show a strong tendency to diverge in shallow marine waters long after the invasion of deeper and freshwaters by older lineages, including after the 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 ever-higher thresholds for continued movement offshore, starting at BA2 (Fig. 1A, figs. S2-S5; Table S1).

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

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

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

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

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

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

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

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

Table 1. Best-Fit Model Parameters for Ancestral Habitats in Figures 1-3.

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

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Figure Legends:

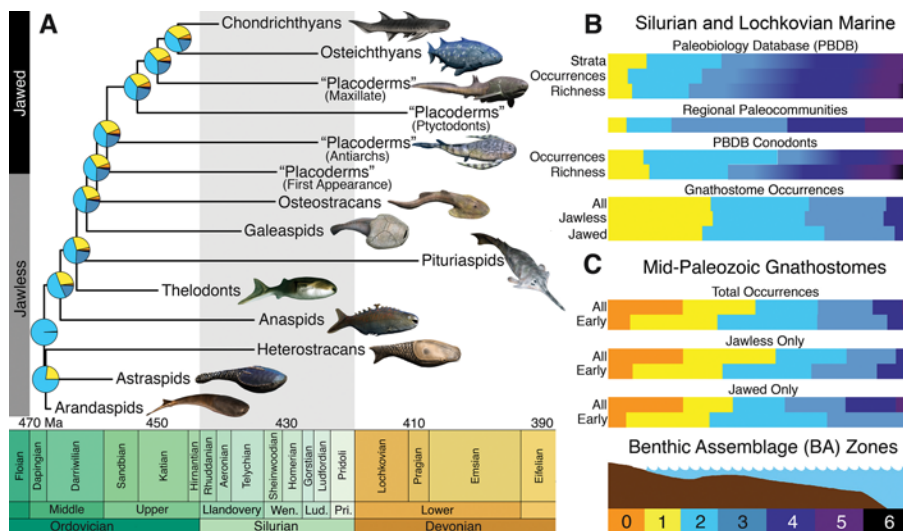


Figure 1. Mid-Paleozoic vertebrates preferentially originated in shallow marine

habitats. A) Intertidal (BA1) to subtidal (BA2-3) ancestral habitats for total-group gnathostome clades (n=188) assuming placoderm paraphyly and Silurian first occurrence for chondrichthyans. Full results shown in Figs. S2-S5. B) Silurian and Lochkovian marine distributions for Paleobiology Database fossiliferous strata (n=858), richness (n=6980) and occurrences (n=30004), conodont richness (n=505) and occurrences (n=7447), paleocommunities, (n=2401) and gnathostome occurrences (n=1035) show mid-Paleozoic records peaking on the mid-shelf (BA3-4) with few records in marginal marine settings, in contrast to the shallow water preferences of early gnathostomes. C) Early and overall occurrences for total-group gnathostomes (n=2827), jawed fishes (n=1343) and jawless fishes (n=1484) show that early occurrences were significantly more concentrated in shallow marine settings than overall or later occurrences. See Additional Data File S2 and Figs. S1, S5-S9

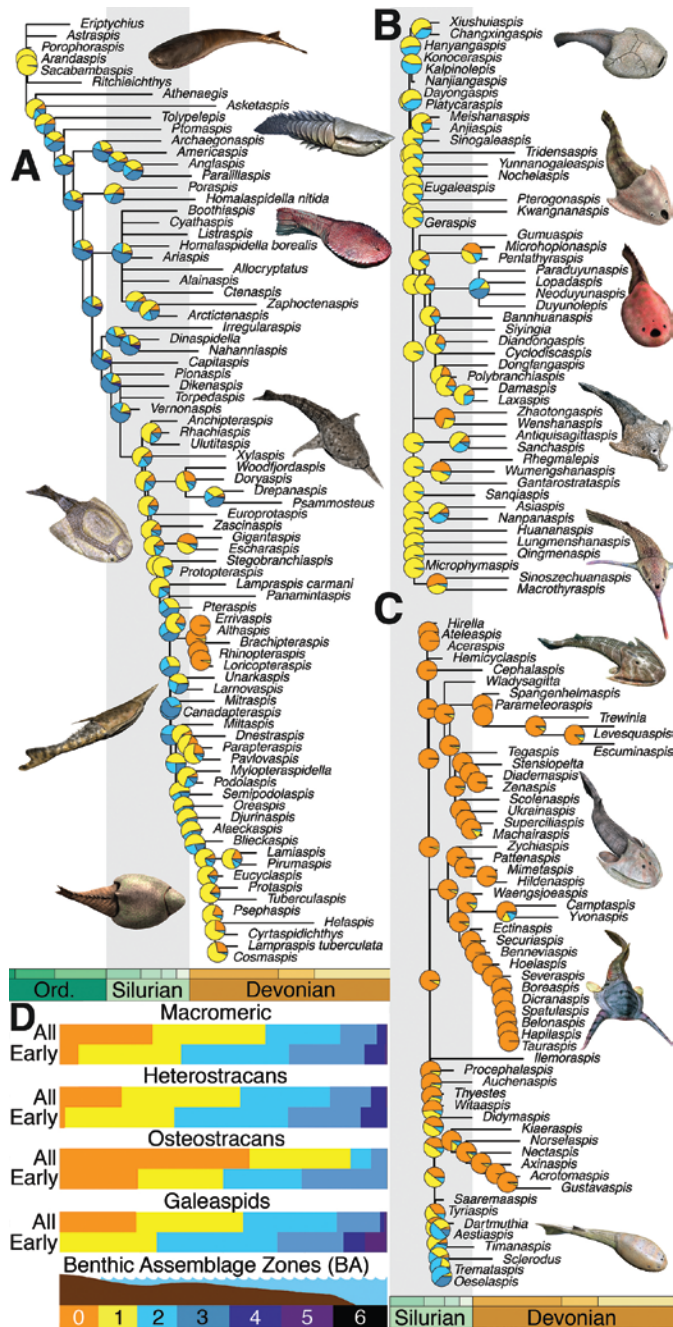


Figure 2. Macromeric, robust jawless fishes exhibit shallower-water diversification and greater habitat restriction. Ancestral states for A) heterostracans and Ordovician stem-gnathostomes (n=316), B) galeaspids (n=112), and C) osteostracans (n=158) show that macromeric genera preferentially originated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

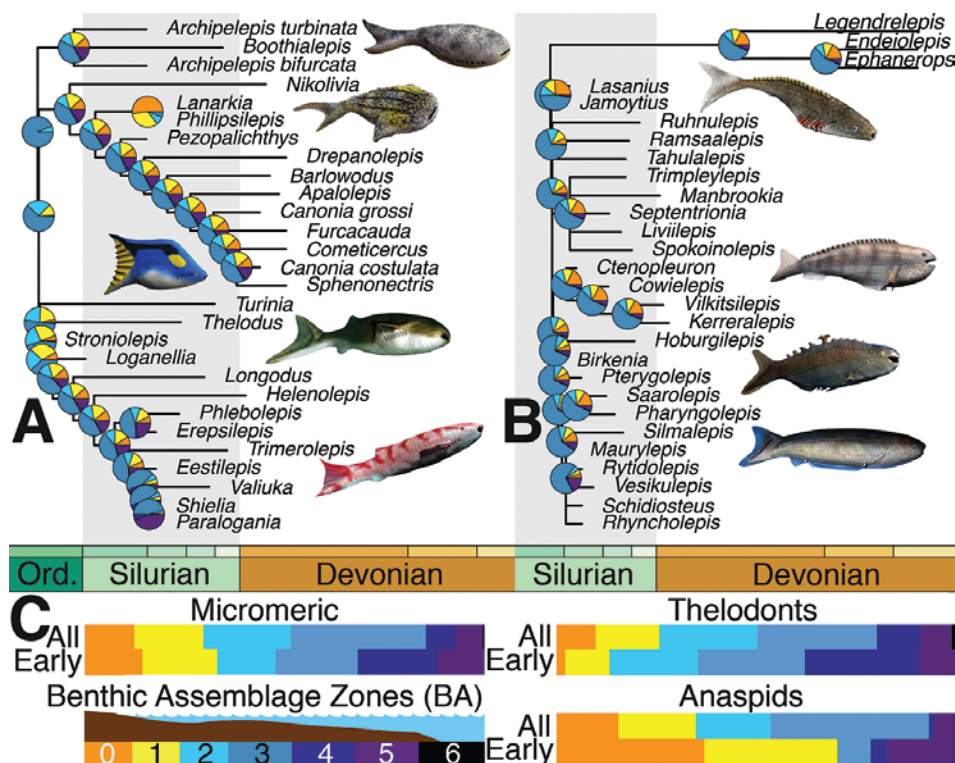


Figure 3. Micromeric, gracile jawless fishes exhibit deeper-subtidal later diversification and easier dispersal. Ancestral states for A) thelodonts (n=99), B) anaspids (n=100) showing diversification of genera in deeper subtidal waters during their evolutionary history. Full results shown in Figs. S9 and S10. C) Early and later occurrences for micromeric jawless fishes (n=353) show a rapid shift to deeper waters following nearshore origination. Full distributions shown in Figs. S21 and S22 and Additional Data File S1.

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	