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Ecological novelty at the start of the Cambrian and Ordovician radiations of echinoderms

by PHILIP M. NOVACK-GOTTSHALL[1]*, JACK PURCELL[1], ALI SULTAN[1,4], ISA RANJHA[1,5], BRADLEY DELINE[2] *and* COLIN D. SUMRALL[3]

[1]Department of Biological Sciences, Benedictine University, Lisle, IL, USA; pnovack-gottshall@ben.edu, jack132016@gmail.com, amisultan97@gmail.com, isaranjha@gmail.com
[2]Department of Natural Sciences, University of West Georgia, Carrollton, GA, USA; bdeline@westga.edu
[3]Department of Earth and Planetary Sciences, University of Tennessee, Knoxville, TN, USA; csumrall@utk.edu
[4]*Current address:* School of Law, University of Illinois Chicago, Chicago, IL, USA
[5]*Current address:* School of Information, University of Michigan, Ann Arbor, MI, USA
*Corresponding author

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Abstract: The Cambrian and Ordovician radiations marked the origins of all major echinoderm clades and established their Phanerozoic ecological blueprint. Recent claims of modest innovation of early echinoderms and other animals suggest constraints on novelty during the origins of phyla. Here, we document the life-habit richness, body size, tiering, habitat usage, mobility, diet and foraging habits of 366 Cambrian–Ordovician echinoderm genera across a time-scaled phylogeny to identify the timing and impact of novelty. Most early echinoderms were sedentary, filter-feeding microbivores, and their body sizes, diets and modes of locomotion were largely unchanged through time, despite major volatility in taxonomic composition. Cambrian echinoderms lived close to the seafloor, with stylophorans first evolving semi-infaunality. Many Ordovician echinoderms lived farther from the seafloor, with more complex filter-feeding organs and tiering structure, often using other organisms as substrates. Mobile carnivores and mass-feeders emerge then, too, across diverse asterozoans and echinozoans. Most of these novelties coincide with the origins of individual clades during the early and late Cambrian (Terreneuvian/Series 2 and Furongian), and 10–20 million years pass before most become ecologically important. Life-habit evolution within most taxa involved new variations in these traits, with crinoids and asterozoans better able to shift strategies. The Ordovician radiation records more new variability in pre-existing Cambrian life habits rather than radical re-invention, with important novelties (like mobile carnivory and mass-feeding, increased height off the seafloor, and biotic substrates) becoming ecologically more impactful. Taxa with these strategies were those best able to capitalize on the newly heterogeneous Ordovician world.

Key words: Cambrian radiation, Great Ordovician Biodiversification Event, functional trait database, evolutionary palaeoecology, functional diversity.

ECHINODERMS diversified more dramatically (phylogenetically, morphologically and ecologically) than any other phylum during the Cambrian and Ordovician radiations (Guensburg & Sprinkle 2001; Rozhnov 2002; Smith *et al.* 2013; Lefebvre *et al.* 2013; Zamora *et al.* 2013; Deline *et al.* 2020; Novack-Gottshall *et al.* 2022). Their unrivaled early-Palaeozoic inventiveness spawned approximately 20 taxonomic classes and 50 orders, encompassing all extant classes and every major body plan, including large numbers of extinct morphologies (Pisani *et al.* 2012; Lefebvre *et al.* 2013; Zamora *et al.* 2013). Such numbers confirm the early Palaeozoic as a time of unprecedented rapid echinoderm evolution, involving interactions of major anatomical change, novel ecological functionality, and divergence of major lineages. It is natural to assume that these changes occurred in a coordinated fashion.

However, a recent study demonstrated that the rate of early echinoderm morphological innovation was significantly faster and involved more volatile anatomical changes compared to their ecological (functional) evolution (Novack-Gottshall *et al.* 2022). The difference resulted in rapid gains in anatomical disparity throughout most of the Cambrian while slow-but-persistent Cambrian life-habit evolution allowed functional (ecological) disparity to catch up, and in some metrics outpace, anatomical disparity during the Ordovician. These disparity differences were manifested in distinct patterns of morphospace and ecospace evolution. Cambrian morphospace quickly established discrete clusters of echinoderm body plans, generally corresponding to subphyla (Deline *et al.* 2020). This pace of anatomical innovation ameliorated slightly during the Ordovician, when morphospace

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evolution transitioned to unceasing variation within body plans, with secondary expansion in clusters associated with diversifying crinoids (and especially camerates), asterozoans, and to a lesser extent echinozoans. Slower ecological evolution, in contrast, involved persistent partitioning of early ecospace combined with slow expansion, which continued throughout the Cambrian and Ordovician and involved substantially greater amounts of life-habit convergence. Ecologically, most early echinoderm evolution appears to have involved slow and steady tinkering of successful life habits evolved during the early Cambrian rather than addition of novel habits.

Similar patterns of dampened ecospace change during these fundamental evolutionary revolutions have been observed in other early taxa. For example, Topper *et al.* (2018) concluded that, except for the addition of infaunal and co-supportive habits in the Ordovician, early-Palaeozoic brachiopod life habits were essentially unchanged from the mid Cambrian. The proportional increase in number of brachiopod life habits they observed (from 7 in the Cambrian to 10 in the Ordovician, a 43% increase) is of a similar magnitude as observed in a global analysis of all fossiliferous marine animals (Bambach *et al.* 2007), which increased from 19 to 30 life habits (58%). Knope *et al.* (2015) drew similar conclusions in a larger study of all Phanerozoic marine animals, although the extent of their Cambrian–Ordovician increase was closer to 80%. (By focusing on the most common Phanerozoic classes, they may also have underrepresented the habits of potentially distinctive Cambrian taxa.) Using null models, they demonstrated that early-Palaeozoic biotas were functionally less diverse than expected under either an early-burst scenario where ecological differentiation occurs faster than taxonomic diversification, or under a scenario where there is a constant per-taxon production of ecological novelty.

It is increasingly well documented that the Cambrian and Ordovician radiations were separate events with distinct causes, and therefore the different ecological patterns during each event suggests differential limits to innovation. These radiations are now considered temporally more protracted than previously realized (Servais *et al.* 2016; Servais & Harper 2018; Zhuravlev & Wood 2018, 2020; Darroch *et al.* 2018; Rasmussen *et al.* 2019; Stigall *et al.* 2019). Although the details of timing differ across studies, the Cambrian radiation is thought to span the Ediacaran to mid Cambrian (Miaolingian). The Great Ordovician Biodiversification Event (GOBE) is thought to have begun in the Late Cambrian (Furongian) and continue until the Late Ordovician mass extinction, with peak diversification occurring in the Middle Ordovician (especially Darriwillian).

Two phases of biodiversity increase form the primary line of evidence in these studies, and the same pattern of genus richness is observed among echinoderms (Novack-Gottshall *et al.* 2022, and see below). Dual elevated rates of morphological and ecological echinoderm evolution during Series 2 and the Miaolingian coincide with the inferred peak manifestation of the Cambrian radiation (Novack-Gottshall *et al.* 2022), and both records exhibit a smaller, second pulse near the Cambrian/Ordovician boundary (Stage 10 – Tremadocian). However, the rate of morphological evolution continues to increase during the Ordovician, while the rate of ecological evolution is dampened and largely unchanged throughout the Ordovician. Combined with the discordant disparity patterns, these two taxonomic early echinoderm radiations express two parallel intervals of anatomical evolution, but ecological diversification was contiguous, revealing little evidence for any ecological impact of the GOBE once it started.

This modesty is especially curious given the distinct environmental regimes of the Cambrian and Ordovician worlds. Early and mid-Cambrian sea floors in which these echinoderms lived were largely a carry-over from the Ediacaran, consisting of stable microbial mats, transient firmgrounds, and fine-grained clastics with low levels of bioturbation (Dornbos 2006; Kloss *et al.* 2015). The Late Cambrian and Ordovician ushered in a new heterogeneity, including dispersing palaeocontinents, rising sea levels leading to development of broad epeiric seas and shallow shelves, ocean chemistry fostering calcite cementation and production of carbonate hardgrounds, and tectonic orogenies triggering increased clastic environments with enhanced terrestrial runoff (Seslavinski & Maidanskaya 2001).

Echinoderms must have reacted to these developments. The notion that most sessile Cambrian echinoderms attached to microbially stabilized softgrounds as '-sediment-stickers' (e.g. Dornbos & Bottjer 2000; Dornbos 2006, 2008) has been supplanted with the recognition that most of these forms instead attached to scattered skeletal debris occurring in such environments (Zamora *et al.* 2010, 2017). This 'sediment-sticking' lifestyle is still convincing for several early echinoderms (e.g. the edrioasteroid *Camptostroma*), and there is little doubt that increases in bioturbation associated with the Cambrian Substrate Revolution had a major impact on Cambrian echinoderms (Bottjer 2010). However, their early affinity for hard substrates allowed many echinoderm groups to take advantage of the carbonate hardgrounds that emerged during the late Cambrian and were especially widespread by the Early Ordovician (Guensburg & Sprinkle 1992, 2001; Sprinkle & Guensburg 1995; Sumrall *et al.* 1997; Zamora *et al.* 2010). Other Ordovician echinoderm groups continued to thrive in soft-substrate conditions (Lefebvre & Fatka 2003), evolved novel strategies for attaching within unconsolidated substrates (Sprinkle

& Guensburg 1995; Guensburg & Sprinkle 2001), or adapted to terrigenous-influenced facies (Lefebvre 2007).

Secular changes could also have affected how echinoderms fed. There is increasing evidence that diversification of plankton during the Late Cambrian and early Ordovician played a major role in the Ordovician radiation (Signor & Vermeij 1994; Servais *et al.* 2016; Servais & Harper 2018; Whalen & Briggs 2018; Pohl *et al.* 2018). This onset also corresponds with evidence for the first planktotrophic larval stages (Nützel *et al.* 2006; Laibl *et al.* 2023) and the initial record of pelagic predators (Kröger *et al.* 2009; Whalen & Briggs 2018). It seems certain such water-column changes would have impacted Ordovician echinoderms, given their affinity for filter feeding (Guensburg & Sprinkle 2001). This period also coincides with more extensive tiering structure among echinoderms (Ausich & Bottjer 1985; Bottjer & Ausich 1986; Rozhnov 2002; Dornbos 2008) and more complex feeding organs (Guensburg & Sprinkle 2001).

If the life habits of early echinoderms, at a global scale, were broadly similar during both the Cambrian and Ordovician radiations, despite such distinct environmental milieus and presumably different causes, it begs the question of how ecological function responds to changing worlds. Fundamentally, it might suggest that constraints to life-habit novelty are set during their earliest phase of innovation, which offers critical context for understanding the causes and consequences of these radiations and on the origins of phyla.

The basis of this study, a follow-up to our prior one (Novack-Gottshall *et al.* 2022), is to test whether the ecological evolution of early echinoderms was truly dampened in the face of such environmental changes, and despite major increases in genus richness and turnover in the composition of higher taxonomic groups. Alternatively, one might expect these secular changes would be captured through the evolution of novel echinoderm life habits. For example, the advent of planktonic food sources might lead to greater numbers of filter feeders, or a global proliferation of hardground facies might boost sessile echinoderms. To evaluate these trends, we interrogate a new database (Novack-Gottshall *et al.* 2022) that quantitatively describes the life-habits of Cambrian and Ordovician echinoderms. Using a time-scaled phylogeny, we evaluate how patterns of life-habit richness, body size, tiering structure, habitat usage, mobility, diet, and foraging habits were all impacted (or not) by the taxonomic and environmental revolutions of these early radiations. Because the coverage of the database includes all major lineages in a shared life-habit framework, it provides a more comprehensive and standardized 'whole life-habit' assessment compared to prior studies that focused individually on fewer classes, smaller intervals of time, or used different frameworks for comparing life habits.

DATA AND METHOD

Time-scaled phylogeny and lineage diversity

All trends reported here are extrapolated from a time-scaled phylogeny of 366 Cambrian and Ordovician genera. Because there is no consensus for the relationships of early echinoderm clades (Nanglu *et al.* 2022), we used two alternative topologies to build informal supertrees. The first uses an ambulacrarian model (Zamora & Rahman 2014) consistent with universal elemental homology (UEH) (e.g. Sumrall & Waters 2012; Kammer *et al.* 2013), and is the same as has been used in prior analyses of Cambrian and Ordovician echinoderms (Deline *et al.* 2020; Novack-Gottshall *et al.* 2022). This topology places ctenocystoids and cinctans as basal-most echinoderms, with early solutes, stylophorans, and helicoplacoids occurring shortly afterwards. The second topology uses the extraxial-axial theory (EAT) model (e.g. Mooi & David 1997; David *et al.* 2000), which differs by reconstructing crinoids as more closely related to asterozoans and stylophorans; rooting solutes, cinctans, and ctenocystoids within the eocrinoids; and placing helicoplacoids, eocrinoids, and early edrioasteroids as the earliest echinoderms. Subclades within each supertree were resolved cladistically from published phylogenies (e.g. Lefebvre 2005; Smith & Zamora 2009; Wright 2017; Sheffield & Sumrall 2019; see complete list in Deline *et al.* 2020). Although the relationships among many of these subclades have been formally studied, it is worth emphasizing that neither UEH nor EAT models have been evaluated within a single, phylum-wide phylogenetic analysis (Nanglu *et al.* 2022). Therefore, the use of two distinct informal supertrees allows results to encompass the range of topological variability that may be produced by more formal phylogenetic analyses in the future. Both phylogenies include 366 echinoderm tip genera, representing nearly all Cambrian and most Ordovician genera, plus five Silurian–Devonian genera (holothuroids *Palaeocucumaria* and *Porosothyone*, stem-holothuroid ophiocistioids *Rotasaccus* and *Gillocystis*, and asteroid *Palaeaster*) to better represent echinoderm crown groups. In total, the phylogenies encompass 21 classes, 42 orders and 141 families. Deline *et al.* (2020) and Novack-Gottshall *et al.* (2022) provide further details on how the informal supertree was compiled (e.g. Lefebvre 2005; Smith & Zamora 2009; Wright 2017; Sheffield & Sumrall 2019; see complete list in Deline *et al.* 2020; and Novack-Gottshall *et al.* 2022).

Where phylogenetic relationships are uncertain, polytomies are used. These occur in both models, and sporadically for genera not included in prior phylogenetic analyses (e.g. cinctan, edrioasteroid, eocrinoid, rhombiferan and cyclocistoid genera). For the ambulacrarian/UEH topology, polytomies occur at the rooting of

helicoplacoids, blastozoans and eleutherozoans. For EAT, they occur at the rooting of helicoplacoids and edrioasteroids and at the rooting of asterozoans, stylophorans and crinoids. These polytomies can push inferred ancestral origins backwards in time, and are discussed below when they have an impact on results.

We created 100 time-scaled phylogenies, implementing the 'cal3' algorithm in the paleotree R package (Bapst 2013, 2014; Bapst & Hopkins 2016), using the bin_cal3TimePaleoPhy R function with arguments dateTreatment = 'firstLast', FAD.only = FALSE, and randres = FALSE. Tip-genus stratigraphic ranges were downloaded from the Paleobiology Database (PBDB; https://paleobiodb.org/). The 'cal3' method stochastically builds time-scaled phylogenies while simultaneously accounting for per-lineage origination, extinction, and sampling (preservation) rates. 'cal3' moves the FADs of tip taxa (and their ancestral nodes) rootward based on stochastic sampling of the per-lineage rate model given observed stratigraphic ranges for each tip. Polytomies are resolved independently for each tree (using randres = FALSE) based on the bifurcation that is mostly likely given these rate calibrations. We generated 50 phylogenies for each UEH/EAT topology and equal numbers of versions allowing taxa to represent tip ancestors or not (using anc.wt = 0, and anc.wt = 1). When illustrating phyloecospaces, we only illustrate those for trees 49 (for UEH) and 57 (for EAT), which were found to represent for each model the statistically closest trees to the overall consensus.

Each of the resulting time-scaled phylogenies contains the 366 tip taxa noted above plus 365 ancestral nodes. It is worth emphasizing that these phylogenies do not incorporate the life-habit characters described below to infer phylogenetic relationships. Instead, as was done in our prior studies (Deline *et al.* 2020; Novack-Gottshall *et al.* 2022), the characters are simply mapped atop the tips of the independently reconstructed time-scaled phylogenies. The phylogenies are then used (see below) to infer the most probable life habits for ancestral nodes and their pattern of occurrences through time. The resulting 100 time-scaled phylogenies provide a direct measure of the sensitivity of trends to variations in time-scaling scenarios, ancestor-descendent relationships, ancestral-state inferences (inferred independently for each time-scaled tree), polytomy bifurcations, and topological differences for the alternative UEH and EAT phylogenetic models. Specific details of the 'cal3' implementation are reported in Novack-Gottshall *et al.* (2022), although the 50 amblacrarian/UEH trees used herein are stochastically different to those used in that study, and use updated stratigraphic ranges. We also report major trends in Supporting Information using the raw (non-time-scaled) stratigraphic ranges from the PBDB, which do not include ancestral state reconstructions nor phylogenetic inferences (Erwin *et al.* 2011; Simakov *et al.* 2015; Nanglu *et al.* 2022).

To convert time-scaled phylogenies to lineage diversity curves through time, we used a modification of paleotree::phyloDiv to obtain time-scaled stratigraphic ranges for all 731 tip and node lineages. To assign taxonomic class-level affinity to ancestral nodes, we algorithmically assigned a taxonomic class when both descendent tips are classified in the same class, and otherwise assigned them as 'uncertain'. Analysis of the time-scaled phylogenies supports that the majority of echinoderm taxonomic classes are monophyletic (Novack-Gottshall *et al.* 2022), and thus we simplify discussion below by treating class ranks as natural clades. Known exceptions include the eocrinoids, rhombiferans and diploporitans, and to a lesser extent edrioasteroids, stenuroids and somasteroids. However, many of these groups have monophyletic subclades, and the major patterns reported below will still stand if many of these groups turn out to represent ecological grades instead of clades.

To evaluate sensitivity of resulting trends to different binning and operational taxonomic units (OTUs), we used four treatments to count the richness of genera (or lineages), taxonomic classes, and unique life habits through time. The first uses raw PBDB genus ranges and discrete geological stage binning of the 2013 International Commission on Stratigraphy (ICS) timescale (Cohen *et al.* 2013), the timescale used in the PBDB. These stage bins have durations that are unequally distributed (mean = 5.7 myr ± standard deviation [SD] = 2.7 myr). The second treatment counts richness using the same discrete stage bins, but using the time-scaled ranges for tip genera. The third treatment is identical except for using 100 semi-continuous ('continuous') bins of equal duration (mean = 1.0 myr), spanning 541.0–443.4 Ma. The fourth treatment uses the 'continuous' binning scheme but adds in time-scaled ancestral lineages ('nodes') to the counts of tip genera. Pairwise correlation among the four treatments are evaluated using detrended Pearson product–moment correlation coefficient (Gould & Calloway 1980; Foote 1994). When visualizing trends, we use the age boundaries of the 2020/01 ICS timescale, and use Miaolingian instead of Series 3. Analyses, however, use the 2013 timescale boundary dates to match PBDB stratigraphic ranges.

Coding functional traits, body size and tiering height

Life habits (ecological functions) were coded using the ecospace framework in Novack-Gottshall *et al.* (2022), modified from Novack-Gottshall (2007). This framework was invented to describe the life habits for any marine organism, and is therefore general enough to represent all

potential ecological strategies, but narrow enough to distinguish their diversity in biologically nuanced ways. It represents a middle-ground between frameworks that are more general (e.g. Bush *et al.* 2007) and those focused on individual taxonomic groups (e.g. Cole *et al.* 2019; Cole & Hopkins 2021). The framework (Table 1) uses 40 discrete character traits (5 numeric, 1 ordered factor, 1 unordered factor and 33 binary [present/absent] characters) to describe the body size, reproduction, mobility, resting and feeding habitat, substrate preferences, diet, and foraging characteristics of echinoderms. Most of the characters are self-explanatory (see formal definitions in Novack-Gottshall 2007, and especially its appendix A), with specific details for its application to individual genera in Appendix S1, and general details provided in Appendix S2.

Although analyses herein (and in Novack-Gottshall *et al.* 2022) are conducted at the genus level, the database is coded at the species level, typically using the type species or the species whose palaeoecology has been best studied, and with information on other species incorporated when they provide contextual information. We used 169 references when coding echinoderm life habits for this study (cited individually in Appendix S1, with notes on codings for each genus; see also Novack-Gottshall *et al.* 2022, suppl. appendix 1, which aggregates the references in a list), supplementing these with others as necessary to obtain body-size measures (Novack-Gottshall *et al.* 2022, suppl. appendix 2) and tiering height (which includes not only the echinoderm body (including holdfast, stem/pelma and feeding appendages) but estimates of substrate height if raised epibiotically or attached to some no-living substrate). See Appendix S2 for additional details on how body size and tiering height were obtained. Although the majority of references systematically describe the anatomy of echinoderm species to infer evolutionary relationships, echinoderm workers routinely describe information on functional morphology (e.g. Guensburg 1988; Guensburg & Sprinkle 1994; Blake & Koniecki 2020), substrate relationships (e.g. Brett 1978; Guensburg 1991; Zamora & Smith 2010), ichnology (e.g. Daley 1995; Sutcliffe *et al.* 2000) and *in situ* preservation (e.g. Lefebvre *et al.* 2010; Cole *et al.* 2018), which collectively provide powerful data needed to code the life habits of these taxa. Many of these references focus explicitly on functional morphology, biomechanics and palaeoecology (e.g. Ausich 1986; Lefebvre 2003; Brower 2011; Rahman *et al.* 2015a; Parsley 2015; Noailles 2016). The average reference was used for 4.9 genus entries (median = 2.0, range = 1–106), and most genus entries used multiple references (median = 2.0, mean = 2.0, range = 1–9). The most heavily cited references were used to estimate filtration fan density (Syverson & Baumiller 2014) and substrate preferences (Zamora *et al.* 2017). Inferences in the literature sometimes disagree with one another, and so emphasis was made on being internally consistent across codings, and documenting in detail (Appendix S1) the logic used when settling such discrepancies so that decisions are resolved in a transparent manner that allows for replication.

When a life-habit character could not be confidently coded, it was inferred algorithmically, based on the most frequent (i.e. modal) character state observed among taxonomically closely related taxa of the smallest (least-inclusive) taxonomic rank that contains at least five other genus entries coded for the missing state. When no states are coded for a particular genus, the codings for the closest taxonomic relative are used as a proxy. (These inferences were done independently of the informal supertree, and before mapping them atop its tips.) After propagating this algorithm, 98.6% of tip genus states were coded. This data set is publicly available (Novack-Gottshall *et al.* 2023) and includes not only the codings for each of the 366 tip genera (held constant across the 100 time-scaled phylogenies) but also the inferred codings for all 365 ancestral nodes for each time-scaled phylogeny, which vary among trees (see below). Novack-Gottshall *et al.* (2022) compared two other algorithms for inferring missing states for tip genera, but only this 'mode' data set is used herein because it provides the most complete data set, and statistical analyses (Novack-Gottshall *et al.* 2022) show that the choice of algorithm has a negligible impact. These inferred codings were then checked manually to be biologically reasonable and internally consistent with how other taxa were coded. 63% of the genera in the data set used herein have life habits coded at the genus level (meaning that at least one species in the genus has life-habit content available in the published literature we have studied), 87% are at family-or-better level (meaning character-state codings are algorithmically filled-in from some confamilial set of species), and 95% are at order or better.

Inferring ancestral states

Unlike the tip genus states that were inferred prior to time-scaling (and are held constant across trees), discrete ancestral states were inferred independently for each time-scaled phylogeny, using a modification of the estimate_ancestral_states function in the Claddis R package (Lloyd 2016; Lloyd *et al.* 2020), as detailed in Novack-Gottshall *et al.* (2022). We used the recommended 'pre-OASE 1' implementation (Lloyd 2018) that only infers ancestral states when its tips are coded, and does not secondarily infer missing tip states. Because the algorithm is restricted to discrete states, we did not infer ancestral body sizes or tiering heights; therefore, statistics for these two measures are limited to the 366 tip genera with such measurements. The complete 731 lineage

TABLE 1. Life habit characters.

1. Body volume
   0 = ≤ 0.01 cm^3
   1 = 0.01–0.1 cm^3
   2 = 0.1–1 cm^3
   3 = 1–10 cm^3
   4 = 10–100 cm^3
   5 = 100–1000 cm^3
2. Microhabitat: Distance from habitat substrate
   0 = ≤1 mm
   1 = 1–10 mm
   2 = 10–100 mm
   3 = 100–1000 mm
3. Microhabitat: Distance from organism's immediate substrate
   0 = ≤ 1 mm
   1 = 1–10 mm
   2 = 10–100 mm
   3 = 100–1000 mm
4. Food location: Distance from habitat substrate
   0 = ≤1 mm
   1 = 1–10 mm
   2 = 10–100 mm
   3 = 100–1000 mm
5. Food location: Distance from organism
   0 = ≤1 mm
   1 = 1–10 mm
   2 = 10–100 mm
   3 = 100–1000 mm
6. Mobility
   0 = Sedentary
   1 = Facultatively mobile
   2 = Intermittently mobile
   3 = Habitually mobile
7. Sexual reproduction
   0 = Sexual (present)
8. Asexual reproduction
9. Substrate composition: Biotic
10. Substrate composition: Lithic
11. Substrate composition: Fluidic
12. Substrate consistency: Hard
13. Substrate consistency: Soft
14. Substrate consistency: Insubstantial
15. Attachment: Attached
16. Attachment: Free-living
17. Microhabitat: Above primary habitat substratum
18. Microhabitat: Within primary habitat substratum
19. Microhabitat (from organism's perspective): Above substratum
20. Microhabitat (from organism's perspective): Within substratum
21. Supported: Self-supported
22. Supported: Supported by others
23. Food location: Above primary habitat substratum
24. Food location: Within primary habitat substratum
25. Food location (from organism's perspective): Above substratum
26. Food location (from organism's perspective): Within substratum
27. Foraging method: Absorptive feeder
28. Foraging method: Filter feeder
29. Foraging method: Attachment feeder
30. Foraging method: Mass feeder
31. Foraging method: Raptorial feeder
32. Filter density (if filter feeding)
   0 = Low density
   1 = Moderate density
   2 = High density
33. Diet: Autotroph
34. Diet: Microbivore
35. Diet: Herbivore
36. Diet: Carnivore
37. Food condition: Incorporeal
38. Food condition: Solution feeding
39. Food condition: Particle feeding
40. Food condition: Bulk feeding

Table of characters and states used to code the life habits of early echinoderms. Characters 2, 4, 17, 18, 23 and 24 refer to the location of the organism with regard to the sea floor (the primary benthic habitat); characters 3, 5, 9–16, 19–22, 25 and 26 are coded with regard to the organism's immediate substrate. Refer to Novack-Gottshall (2007) for definitions of characters and states, with exception of character 32 (filter density) defined in Appendix S2. Filter density is dependent on character 28 (filter feeding). Unless noted, all characters are coded with state 0 = absent and 1 = present. Refer to text and Appendix S2 for additional explanation of characters, and the notes in Appendix S1 for information on how individual taxa were coded.

by 40 trait matrix is 98.7% complete, on average, across time-scaled phylogenies, with 0.03% of collective ancestral states coded as polymorphic (e.g. 0/1) when multiple states were equally supported by the evolutionary model. How such polymorphic states are handled when producing trends in life habits is described below. Because ancestral-state inferences depend in part on the branch lengths of descendent lineages, which varies among each of the time-scaled phylogenies, this means that error bars for the trends described below not only incorporate variation in time-scaling but also variation in ancestral-state inferences.

Counting unique life habits

Taxa with different combinations of character states have different life habits. When counting the number of unique life habits, we convert the lineage-by-trait matrix to a distance matrix, which is better able to distinguish taxa that only differ in missing or polymorphic states. As

further detailed in Novack-Gottshall *et al.* (2022), we use Wills generalized Euclidean distance (Wills 1998), using alpha = 0.5 (Hopkins & St John 2018) to correct for filter-density (char. 32; Table 1) being relevant only for filter feeders. Among our 366 tip genera, there are 164 unique life habits. Including inferred ancestral nodes, the complete data set of 731 tips and nodes describes an average of 193 unique life habits (± SD = 3.0, range = 186–201) across the 100 time-scaled phylogenies.

Documenting trends in life habits, body size and tiering

Most trends documented here report some measure of variability around the mean or median. For raw (non-sample-standardized) trends, variation is estimated as the standard deviation across 100 time-scaled phylogenies (Kowalewski & Novack-Gottshall 2010), which provides a measure of variability in phylogenetic uncertainty regarding temporal ranges as well as ancestral trait inference. For sample-standardized trends, variation is estimated as the standard deviation across 2000 subsampling replicates, evenly sampling 20 replicates for each of 100 time-scaled phylogenies per interval (Kowalewski & Novack-Gottshall 2010); this provides a measure of variability across time-scaled trees as well as sampling error across subsamples. We also report trends in Supporting Information using the raw (i.e. non-time-scaled) stratigraphic ranges for tip genera from the PBDB, and without inferred ancestral states.

Trends in body size (body volume) and tiering height are analysed statistically to demonstrate whether the changes are consistent with a driven (biased), random walk (unbiased), or stasis model of evolution (Hunt 2006), using the paleoTS package (Hunt 2022). These tests are conducted only using the 366 tip genera that document these continuous measurements, and only for the epifaunal filter-feeding subset for the tiering trend. The distributions of tiering heights are also tested to determine whether they consist of discrete multimodal tiers, using the mclust R package (Fraley & Raftery 2002, 2007; Fraley *et al.* 2022). Body sizes and tiering heights are $\log_{10}$-transformed prior to conducting these tests. Details on test implementations are provided in Appendix S2.

RESULTS

Taxonomic and life-habit diversity trends through time

Alternative ways of resolving the time-scaled phylogeny into temporal bins and of tallying OTUs (using only tip genera vs tips plus ancestral nodes) produce little difference in the resulting taxonomic (genus and class-levels) and life-habit richness trends during the Cambrian and Ordovician (Fig. 1). The four treatments are significantly positively correlated with each other. Pearson product–moment correlation coefficients using first-differences (Gould & Calloway 1980; Foote 1994) to detrend the genus-richness time series (Fig. 1A) yields pairwise correlation coefficients ranging from +0.789 (for discrete PBDB vs continuous binning of the tips only) to +0.967 (for continuous binning of tip vs tips plus nodes), and a maximum *p*-value of 0.0048. Time-scaling the phylogeny inflates standing lineage richness by a small amount as the estimated first appearance datum (FAD) of tip genera and ancestral nodes are pulled rootwise, earlier in time. Because of the high preservation potential of Palaeozoic echinoderms (Foote & Raup 1996), the magnitude of such range extensions is relatively minor (see Novack-Gottshall *et al.* 2022, suppl. info.). This additional diversity is enhanced when including ancestral lineages in these tallies, but again with negligible effect on resulting trends. The fourth treatment (using continuous binning of tip genera combined with their inferred ancestral lineages) is used for most analyses below because of its significant correlations with the other treatments, and because it is recommended as offering the best record of evolutionary history (Brusatte *et al.* 2011; Guillerme & Cooper 2018; Guillerme *et al.* 2020).

The earliest echinoderms undergo two major genus-level diversifications (Fig. 1A), the first peaking during Cambrian Series 2 – Miaolingian, and the second starting during the late Cambrian (Furongian) and continuing until the Middle Ordovician, when standing global diversity peaks at approximately three-times that observed during the Cambrian. Because of the impact of rootward FAD extensions, these diversifications commence one-to-two epochs earlier when using the time-scaled phylogeny compared to raw stratigraphic ranges recorded in the literature (as recorded in the PBDB), but with peak intervals remaining unchanged. The drop in diversity during the terminal Ordovician (Hirnantian epoch) is primarily an artefact of our lack of Silurian and later taxa, which would have contributed additional hidden diversity during this interval because of range extensions from post-Ordovician taxa.

The relative completeness of this early echinoderm fossil record (and our representation of it in our data set) and its intensive focus in modern field and systematic studies (e.g. Lefebvre *et al.* 2013; Smith *et al.* 2013; Smith & Zamora 2013; Zamora *et al.* 2013, 2017) mitigates against casting aside this trend as a simple artefact of differential preservation, sampling and fossil discovery, although these all operate to some extent. The frequency-ratio method (Foote & Raup 1996) applied to the raw PBDB stratigraphic ranges estimates a 0.835 per-interval sampling probability (see Novack-Gottshall *et al.* 2022,

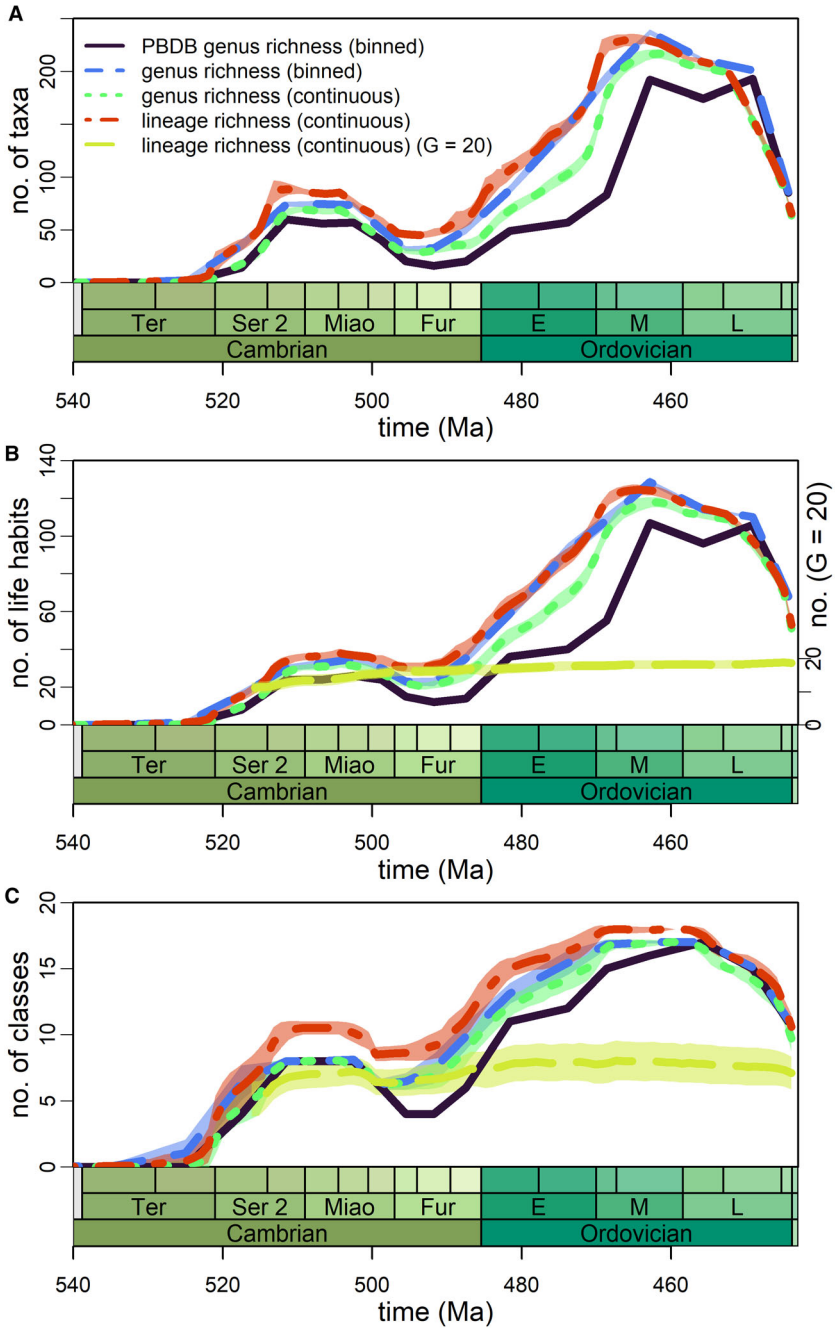


FIG. 1. Diversity trends through time for Cambrian–Ordovician echinoderms. A–C compare trends for the same data treatments, as identified in the legend. PBDB (binned) reports genus richness using raw (non-time-scaled) stratigraphic ranges from the Paleobiology Database (PBDB) for the 366 tip genera. Genus richness (binned) reports the tree-based geological ranges for the same 366 tip genera, as inferred across the 100 'cal3' time-scaled phylogenies. Genus richness (continuous) is the same, but using 100 equal-duration bins for geological intervals. Lineage richness (continuous) includes 366 tips and 365 nodes from the time-scaled phylogenies using 100 equal-duration bins. The last treatment uses subsampling (2000 replicates) to standardize this trend to 20 lineages (tip genera and nodes) per interval. For treatments using time-scaling, the trends report the average value across 100 time-scaled phylogenies. Error bars report the standard deviation across these phylogenies, except for the subsampling trends, which reports the standard deviation in the resampling distribution (drawing each time-scaled phylogeny 20 times). A, number of genera through time. B, number of unique life habits through time; note that the sample-standardized trend is scaled to the right vertical axis. C, number of taxonomic classes through time. Epoch names for this and subsequent figures are abbreviated from Terreneuvian, Series 2, Miaolingian, Furongian, and Early, Middle and Late Ordovician; ages are illustrated but not labelled.

suppl. info. for details of calculation), ranking among the highest calculated among major fossil groups. This pattern of two diversification pulses, each corresponding to the Cambrian and Ordovician radiations, is likely to reflect a true first-order signal of their global evolutionary history.

The trend in life-habit richness strongly parallels that for genus richness, with two pulses of ecological diversification during the mid Cambrian and middle–late Ordovician (Fig. 1B). Depending on the binning and OTU treatment, standing life-habit richness in the Ordovician is 2.7 to 4.1 times greater than during the Cambrian. The magnitude of this increase is dampened when the trend is standardized to maintain a common genus richness through time, to approximately 12% greater, averaging across periods. The standardized number of life habits per resampled genus pool rises persistently in the mid Cambrian through to the Ordovician, reaching an asymptote of approximately 19 life habits per sample of 20 genera by the end of the Ordovician, 70% greater than the earliest subsampled Cambrian interval. Whether the trend in Figure 1B is taken at face value as reflecting ecological history or treated as an artefact of varying sampling intensity, the absolute and relative numbers of life habits continues to increase throughout the Cambrian and Ordovician.

Echinoderms diversified dramatically during their earliest evolution into numerous taxonomic classes, reflecting not only their rapid evolution of morphological novelty but also their ecological innovation (Deline *et al.* 2020; Novack-Gottshall *et al.* 2022). The increase in echinoderm life habits and genera during this interval (Fig. 1A, B) reflects not only the origination, diversification, and turnover among these classes, but also genus-level diversification within classes (Figs 1C, 2). Class-level diversification occurs in discrete mid Cambrian and basal Ordovician pulses, in both the raw data and when standardized. It is interesting that the impacts of these radiations are not evident when both life habit and class richness trends are sample-standardized. In both, standardized diversity remains greater in all Ordovician intervals than during any Cambrian interval. It is also notable that, despite the reduced sampling of lineages in our data set during the latest Ordovician, sampling-standardized class richness and life-habit richness remain essentially unchanged from earlier intervals.

Although there are no unambiguous echinoderm fossils yet known from the Terreneuvian (Zamora *et al.* 2013), our time-scaled phylogenies infer that they existed during this epoch (Fig. 2). The median root age across 100 time-scaled trees is 527.1 million years ago (Ma) (interquartile range 523.9–532.9 Ma; range 520.7–555.9 Ma), estimating the most likely origin of phylum Echinodermata in the Terreneuvian (Stage 2), consistent with molecular dating

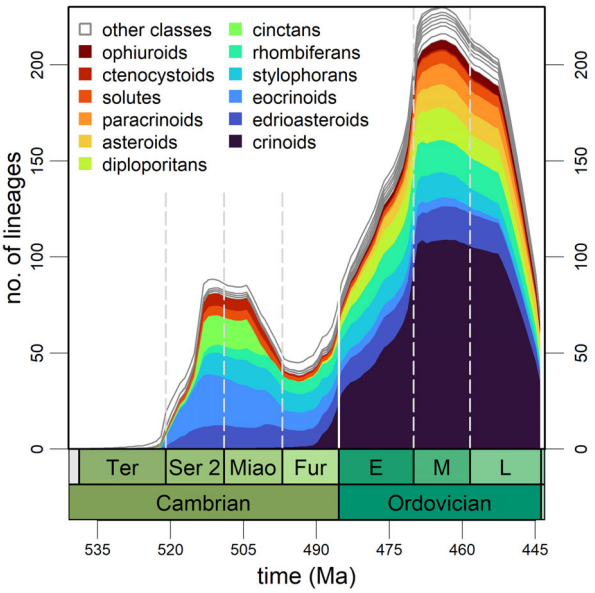


FIG. 2. Stacked trend in class richness. Values are the average numbers of each class across the 100 time-scaled phylogenies. The top trend is the same as illustrated in Figure 1B for the lineage richness (continuous) treatment, in which tallies include tree-based ranges for 731 tip genera and ancestral nodes. Ancestral lineages were assigned to taxonomic classes when both descendent tips were classified in the same class, and left as 'uncertain' otherwise. The legend is in the same order as in the stacked curves, with most-diverse (crinoids, primarily Ordovician) at bottom right. Other classes, not identified by individual colours, include (in this order) cyclocystoids, echinoids, holothuroids, helicoplacoids, blastoids, parablastoids, somasteroids, stenuroids, and (at top) other lineages of uncertain affiliation. (See Novack-Gottshall *et al.* (2022, ext. data fig. 1c) for a version of this data using PBDB stratigraphic ranges without time-scaling.)

and other estimates (Erwin *et al.* 2011; Smith *et al.* 2013; Zamora & Rahman 2014; Simakov *et al.* 2015; Nanglu *et al.* 2022). This is also consistent with claims for a Terreneuvian stem echinoderm (Topper *et al.* 2019), which is not included in these analyses, and whose echinoderm affinity is not without doubt (Topper *et al.* 2020; Zamora *et al.* 2020). All but two time-scaled phylogenies infer the existence of echinoderms during Stage 2, with 61% of 100 trees inferring at least one tip genus known from later strata: all three helicoplacoid genera (in 29–30%, depending on genus), stem echinoderm *Helicocystis* (24%), early edrioasteroid *Camptostroma* (19%), eocrinoid *Felbabkacystis* (13%), solute *Coleicarpus* (9%), and 16 other genera of cinctans, edrioasteroids, eocrinoids, and stylophoran *Ceratocystis*, but each in five or fewer time-scaled phylogenies. Only the stem echinoderm *Ctenoimbricata* (Zamora *et al.* 2012), helicoplacoid *Helicoplacus*, and edrioasteroids *Kailidiscus* and *Walcottidiscus* are

inferred during the Fortunian, but each in only one time-scaled phylogeny. 39 phylogenies infer the existence during the Fortunian of ancestral representatives (i.e. not tip genera) of ctenocystoids (1%), solutes (1%), cinctans (4%), edrioasteroids (6%), helicoplacoids (10%), or ancestral nodes of uncertain class affinity (an average of 2.9 nodes for the 39 trees that infer their existence, range 2–5 per tree). Only eight time-scaled phylogenies (two UEH model and six EAT) infer echinoderm origins during the Ediacaran, all as ancestral nodes, with one EAT tree inferring root helicoplacoids during this time. However, the majority of time-scaled phylogenies, under both the UEH and EAT models, are consistent with echinoderm origins during Stage 2, with few time-scaled phylogenies inferring earlier origins, especially of tip genera.

The Series 2 diversification pulse coincides with the inferred origins of many taxonomic classes, plus extensive divergence of genera within them. Eocrinoids, edrioasteroids, cinctans, stylophorans and solutes diversify significantly, while rhombiferans, ctenocystoids and cyclocystoids remain at low diversities (Fig. 2). Helicoplacoids go extinct during Series 2. The inferred time-scaled Series 2 origination of cyclocystoids (median = 518.2 Ma) suggests either a long interval of undiscovered fossils because the oldest known cyclocystoid fossils are in Lower Ordovician strata (Lefebvre *et al.* 2013; Reich *et al.* 2017), or its inferred origination is an artefact of rooting the clade in the informal supertrees as an unresolved polytomy with stromatocystitids and other Cambrian edrioasteroids. Similarly, the time-scaled phylogenies also infer that blastoids originate during Series 2 (median = 512.9 Ma), long before the first appearance of *Macurdablastus* and coronate *Mespilocystites* during the Middle Ordovician (Brett *et al.* 1983a; Broadhead 1984; Bauer *et al.* 2019). This extension is caused by rooting the blastoids basal to Cambrian rhombiferans in both the UEH and EAT topologies. The Miaolingian and Furongian maintains the relative proportion of these Series 2 classes, with the extinction of cinctans during the Miaolingian. Collectively, Cambrian echinoderm biotas are dominated by eocrinoids, edrioasteroids, stylophorans, cinctans, rhombiferans, ctenocystoids, solutes and helicoplacoids.

Of the echinoderm classes that occur in the Ordovician, the time-scaled phylogenies infer that all but the echinoids may have had possible ancestral roots during the Cambrian. However, only a small number provide majority support for such early roots, and so such claims should be treated with hesitation. Most likely, with median FADs in Stage 10, are the stenuroids (in 54% of 100 time-scaled trees, all with tip genera), diploporitans (80%, 73% with tip genera), and somasteroids (in all 100, and all inferring the important early somasteroid *Ophioxenikos*). All time-scaled phylogenies place the origins of crinoids in the Cambrian, but with substantial dependence on the topological model used. The UEH topology infers an origin in the late Furongian (median = 488.3 Ma; IQR = 486.9–489.4 Ma; maximum = 494.5 Ma). This date is consistent with other analyses of early crinoid phylogenetics (Ausich *et al.* 2015). In contrast, EAT infers a much older Miaolingian origin (median = 514.5 Ma; IQR = 513.7–515.9 Ma; maximum = 520.6 Ma), in large part because of this model's inferred close relationship between crinoids and Cambrian stylophorans. Late Cambrian origins (in 100% of trees) are suggested for several crinoid genera known only in Ordovician rocks, with median time-scaled first appearances (487.9–485.6 Ma) at or just prior to the base of the Ordovician. The most likely candidates include *Aethocrinus*, *Apektocrinus* and *Tripatocrinus*, each inferred as having Cambrian origins across all 100 trees, and *Titanocrinus*, *Glenocrinus*, *Alphacrinus* and *Eknomocrinus*, inferred with Cambrian origins in 54–77% of trees.

Major class-level evolutionary changes occur at the base of the Ordovician (Fig. 2). The time-scaled phylogenies infer several classes originated during the early Tremadocian, or perhaps just before. Asteroids (e.g. *Eukrinaster* and *Cnemidactis*), ophiuroids (e.g. *Stenaster*), and paablastoids (e.g. *Meristoschisma*) all have median FADs during this epoch, consistent with prior claims for their times of origin (Lefebvre *et al.* 2013), and all three classes having confirmed Early Ordovician fossil records. The majority of time-scaled phylogenies suggest the origins of other classes, but with less support. Early Ordovician origins are likely for paracrinoids (in 87% of trees, 65% inferring the existence of Middle Ordovician *Schuchertocystis*), holothuroids (86%, all as ancestral nodes), and echinoids (65%, but only 33% inferring the existence of Middle Ordovician tip genus *Bothriocidaris*). The median time-scaled FADs for echinoids (470.5 Ma) and holothuroids (473.9 Ma) are consistent with root ages inferred using more formal time-calibrated phylogenetic methods (Miller *et al.* 2017; Thompson *et al.* 2021), records of echinoid plates and putative isolated holothuroid sclerites in the lower Middle Ordovician (Reich 2009a, 2009b; Lefebvre *et al.* 2013), and the Middle Ordovician appearance of stem-holothuroid ophiocistioids (Smith & Reich 2013; Rahman *et al.* 2019; Ausich & Thompson 2021). Several classes add important early genera, including stenuroid *Palaeura* and somasteroid *Villebrunaster*. Crinoids and diploporitans diversify throughout the Early Ordovician, and edrioasteroids, eocrinoids, rhombiferans and stylophorans continue as major classes.

In general, the Middle and Late Ordovician experiences dramatic increases in the numbers of genera in these classes, but maintain the same relative proportions (Fig. 2). Crinoids remain the dominant Ordovician class, representing nearly half of all echinoderm genera. Asterozoans remain a relatively small proportion of the global

echinoderm record, but continue to diversify throughout the Middle and Late Ordovician, adding ophiuroids such as *Taeniaster* during the Middle Ordovician. Paracrinoids also diversify. Although echinoderm diversity declines with the Late Ordovician mass extinction (and the decline in Fig. 2 is magnified because of the lack of many Silurian taxa that would have Ordovician time-scaled FADs), only the already-rare ctenocystoids are a victim of the extinction. The paracrinoids appear to have gone extinct just before the mass extinction, somasteroids in the middle Late Ordovician, and parablastoids in the early Late Ordovician.

Trends in body size

The typical Cambrian–Ordovician echinoderm had a moderately small body size of 1.49 cm^3, although there are orders of magnitude of size variation around this mean (Fig. 3A). (As a reminder, we here technically report size as body volume, and only include sizes here for tip genera; see Data and Method above and Appendix S2.) Whether using time-scaled ranges, sample standardization (Fig. S1A), or raw (non-time-scaled) ranges from the PBDB (Fig. S1C), average body size is low during the mid Cambrian (Series 2 – Miaolingian), rises continuously throughout the Furongian, and remains largely constant throughout the Ordovician. Small sample size and variability among time-scaled tip genus ranges makes it difficult to interpret body size during the Terreneuvian and earliest Series 2; however, a similar mid Cambrian downturn is observed if using non-time-scaled stratigraphic ranges (Fig. S1C), which suggests this is a genuine signal that the first echinoderms were on average the same size as Ordovician echinoderms. The mid Cambrian decline can be attributed to diverse numbers of small, thin-bodied cinctans and ctenocystoids rather than a loss of larger echinoderms.

The smallest echinoderm observed here is the Cambrian cinctan *Sokkaejaecystis* (with median time-scaled range Series 2 – Furongian), followed by several ctenocystoids (e.g. *Courtessolea* and *Etoctenocystis*). The largest bodied echinoderm is the Middle–Late Ordovician diploporitan *Calix*, with a pineapple-sized calyx that alone is *c.* 37 cm tall by 14 cm wide (Beaver *et al.* 1967). Although many post-Ordovician echinoderms (especially asteroids, echinoids, holothuroids, and late Palaeozoic crinoids) will regularly evolve larger sizes than their typical Ordovician relatives (Mongiardino Koch 2021), the only echinoderms we know with body volumes exceeding *Calix* are the Miocene echinoid *Trachypatagus* (Durham *et al.* 1966; Heim *et al.* 2015), extant crown-of-thorns sea star *Acanthaster* (Mueller *et al.* 2011), and brittlestar *Gorgonocephalus*, reportedly the largest extant echinoderm (McClain & Boyer 2009). It is noteworthy that all three of these genera are only slightly larger than the calyx alone of *Calix*, demonstrating that physiological solutions to achieving the largest echinoderm body sizes were achieved rapidly during echinoderm evolution.

In contrast, echinoderms with the smallest sizes comparable to those observed in the Cambrian become less common during the Ordovician. A few smaller echinoderms, including microcrinoids whose affinity as juveniles or as minituarized adults is uncertain, will evolve during the Silurian to Carboniferous (Sevastopulo 2008). The smallest post-Palaeozoic fossil echinoderm appear to be the pelagic crinoid *Roveacrinus* (Hess *et al.* 2011), with a calyx body volume *c.* 10mm^3 (or −2.0 $\log_{10}$ cm^3), the same order of magnitude as the smallest Cambrian echinoderms. Emerging discoveries of tiny but exceptionally diverse and abundant Palaeozoic ophiuroids (Thuy *et al.* 2023) warn that there may be preservational or investigator biases against recognizing the tiniest of echinoderms, as these are much larger than the smallest known extant echinoderm, the minute holothuroid *Parvotrochus* (McClain & Boyer 2009).

These raw body-size measures are not included directly in the ecospace framework used to describe ancient life habits; rather, they are converted to $\log_{10}$ size bins that serve as discrete functional traits (Table 1). Aside from the smallest (= *Sokkaejaecystis*) and largest (= *Calix*) size bins, there are proportionally subequal numbers of size classes throughout the Cambrian–Ordovician. It is worth noting that, taken at face value, the earliest Cambrian echinoderms were of intermediate body size (1–10 cm^3), rather than starting among the smallest body sizes, as is often assumed for the evolution of body size (Stanley 1973; Gould 1988; Heim *et al.* 2015).

Maximum-likelihood analyses (Hunt 2006, 2022) support Cambrian–Ordovician echinoderm body-size evolution as being best fit by a model of an unbiased random walk (Fig. S2A), although we cannot rule out a weakly driven model. These model conclusions jibe with prior studies of echinoderm body-size evolution at larger scales, including those focused on Palaeozoic crinoids (Salamon *et al.* 2021) and Phanerozoic echinoderms as a whole (Heim *et al.* 2015; Smith *et al.* 2016). Novack-Gottshall (2008) found greater support for the stasis model during the Cambrian–Devonian, but that study used a much smaller sample of body sizes, from a single habitat, and the unbiased random-walk model received sufficient support that it could not be ruled out.

Trends in tiering

Tiering conceptualizes how filter feeders partition space above (and below) the seafloor, traditionally implying

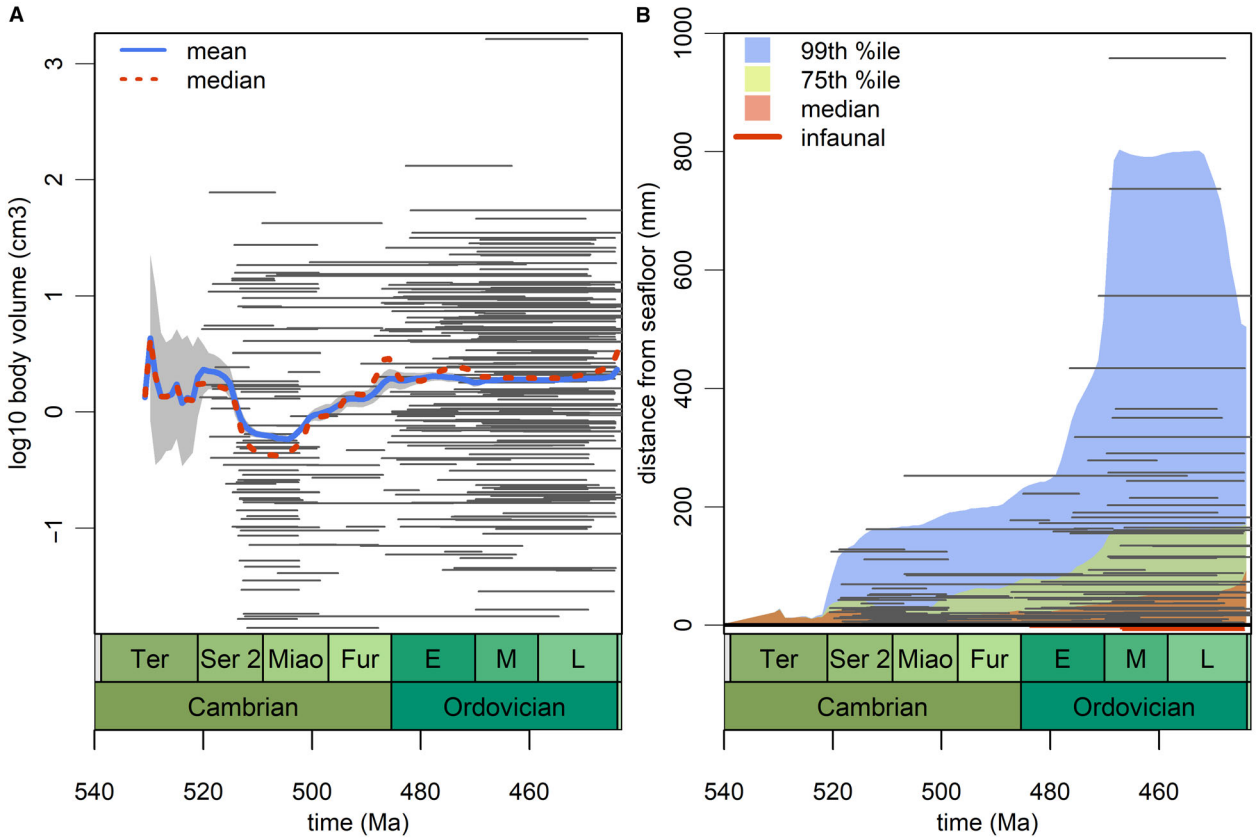


FIG. 3. Trends in echinoderm body sizes and tiering throughout the Cambrian and Ordovician. Horizontal lines represent the $\log_{10}$-transformed body volume and (for filter-feeding echinoderms) absolute stratigraphic distance (AbsStratDist, not log-transformed) above or below the seafloor, for individual tip genera, using their median time-scaled geological ranges across the 100 time-scaled phylogenies. Because these continuous variables were not inferred for ancestral nodes, these figures only report measures for tip genera. A, the mean and median body size trend is calculated across the 100 time-scaled phylogenies, using the individual (non-averaged) time-scaled geological ranges for each genus; the grey error bar represents the standard deviation around this mean trend through time; Terreneuvian variation is caused by variability in which lineages are inferred to have FADs during this series across time-scaled phylogenies. B, the trend in tiering only reports values for filter-feeding tip genera; the black horizontal line at zero denotes the sea floor; very shallowly semi-infaunal stylophorans in the Middle–Late Ordovician are represented by red horizonal lines just below this line; the red envelope illustrates the median height (50th percentile), yellow the 75th percentile, and blue the 99th percentile for epifaunal echinoderms through time (calculated using the $\log_{10}$-transformed distances, and displaying the mean across 100 time-scaled phylogenies).

some role for competitive displacement in partitioning the water currents (or infaunal habitat) in which these animals collect their food (Lane 1963; Ausich & Bottjer 1982, 1985; Bottjer & Ausich 1986; Dornbos 2008; Novack-Gottshall 2016a). The trends presented here accordingly only include 167 filter-feeding tip genera for which we could obtain reliable estimates of tiering height (absolute stratification distance (AbsStratDist), compiled separately to characters in Table 1). Because the majority of early echinoderms are filter-feeders (see Trends in habitat usage below), the trends are likely to be representative of early echinoderms as a whole. Individual trends for discrete, multistate characters 2 and 3 (Table 1) are not reported, as they are concordant with those reported here for tiering distance, on account of the rarity of reef-dwelling and epibiotically elevated habits in early echinoderm habitats, and because these early echinoderms are exclusively benthic (i.e. they do not swim or live within the water column).

Whereas the body sizes of early echinoderms were relatively constant throughout the Cambrian and Ordovician, these same echinoderms substantially changed how they used space above the seafloor, and to a small extent below it during the Ordovician (Fig. 3B). Tiering structure was relatively stable throughout the mid Cambrian, increased slightly throughout the Furongian and earliest Ordovician, before expanding during the Middle and Late Ordovician. The earliest Cambrian echinoderms (such as

helicoplacoid *Helicoplacus*, solute *Coleicarpus*, and sediment-sticking edrioasteroid *Camptostroma*) all lived less than 25 mm above the sea floor. Throughout the Cambrian, the median distance inhabited above the sea floor was just 14 mm (±1.6 mm SD), with the 75th percentile only 34 mm (±1.7 mm) above the sea floor. (Given the challenges of obtaining precise estimates of distance lived above the seafloor, as noted in Appendix S2, we report our actual data estimates herein, but base overall conclusions on the general orders-of-magnitude patterns suggested by these data.) By the mid Cambrian, the origin of eocrinoids (such as *Felbabkacystis*, *Lepidocystis*, *Nolichuckia* and *Lyracystis*) substantially increased echinoderm heights, over 100 mm above the sea floor. (The largest plotted Cambrian height of *c.* 250 mm can be ignored as an artefact of a polytomy rooting the Late Ordovician *Cardiocystites* with Cambrian eocrinoids.) No Cambrian echinoderms are known to have lived more than *c.* 150 mm above the sea floor.

The Ordovician diversification of stemmed crinoids and other classes greatly expanded the range of distances that echinoderms could live above the seafloor, with many genera evolving to live in the 200–400 mm tier, but few at greater heights (Fig. 3B). Across the period, Ordovician tiering heights were three-times greater than during the Cambrian (median = 42 ± 1.4 mm; 75th percentile = 131 ± 1.4 mm). However, this increased tiering range was more incremental than immediate, with modest increases continuing throughout the Furongian and Early Ordovician before reaching the tallest heights during the Middle and Late Ordovician. The rapid diversification of crinoids during the Early Ordovician (Fig. 2; Ausich *et al.* 2015; Wright 2017) contributed substantially to these increases, but these earliest crinoids were only modestly taller than co-existing eocrinoids. For example, the early crinoids *Cnemecrinus* and *Aethocrinus* (with tiering heights *c.* 200 mm: Ubaghs *et al.* 1978; Guensburg & Sprinkle 2003) were only slightly taller than the eocrinoids (e.g. *Rhipidocystis* and *Rhopalocystis*) they co-existed with, and the Early Ordovician crinoid *Trichinocrinus* was probably much shorter than the shortest (*c.* 85 mm) co-existing eocrinoids *Haimacystis* and *Bockia* (Beaver *et al.* 1967; Sumrall *et al.* 2001). Shorter tiers, less than the Early Ordovician median height of 42 mm, were dominated by edrioasteroids, stylophorans, rhombiferans, and the early diploporitan *Aristocystites*.

The Early Ordovician witnessed the earliest echinoderms to possess specializations for partially infaunal habits. Earlier, several Cambrian stylophorans (Lefebvre 2003; Lefebvre *et al.* 2010; Noailles 2016) and the edrioasteroid *Camptostroma* (Zamora *et al.* 2017) lived semi-infaunally, but most of their body remained above the seafloor and so they are reported as having positive tiering (AbsStratDist) values. Although only living surficially within the top 4 mm of sediment, starting in the Early Ordovician several species of stylophorans (*Anatiferocystis*, *Guichenocarpos* and *Mitrocystella*) lived fully buried, with just their feeding arm above the seafloor (Lefebvre 2003). This a strategy that would be exploited to greater depths during the remainder of their Palaeozoic existence, with all post-Ordovician stylophorans infaunal to some extent (Lefebvre 2003).

Echinoderms achieved significantly greater tiering heights during the Middle Ordovician (median = 47 mm; 75th percentile = 161 mm; 99th percentile = 783 mm), with modest increases continuing into the Late Ordovician (median = 59 mm; 75th percentile = 165 mm; 99th percentile = 703 mm). It is notable that these median heights are approximately the same as the Furongian 75th percentile, and that approximately 25% of Ordovician echinoderms were elevated more than the Cambrian 99% percentile. The tallest tier (>200 mm) was dominated by crinoids such as *Pycnocrinus*, *Glyptocrinus*, *Merocrinus*, and the nearly metre-tall *Cotylacrinna*, but also included the large diploporitan *Calix*, paracrinoid *Comarocystites*, and eocrinoids *Petalocystites* and *Cardiocystites*. Moderately tall heights (100–200 mm) were similarly dominated by crinoids, some eocrinoids (e.g. *Rhipidocystis*), plus the edrioasteroids *Belochthus* and *Euryeschatia* known to have lived epibiotically atop large conulariids (Sumrall & Zamora 2011). The early blastoid *Macurdablastus* probably also lived within this tier (Broadhead 1984), although its stem and brachioles are not known. Intermediate heights (50–100 mm) include several shorter crinoids (e.g. *Cornucrinus*), eocrinoids (e.g. *Mandalacystis*), rhombiferans (*Cheirocystis*), diploporitan *Holocystites*, and paracrinoid *Oklahomacystis*. The shortest tier was inhabited by a diverse number of small, reclining, epibiotic or recumbently living crinoids (e.g. *Calceocrinus* and *Ottawacrinus*), edrioasteroids (e.g. *Edrioaster* and *Isorophus*), rhombiferans (e.g. *Amecystis*), stylophorans (e.g. *Cothurnocystis*), solutes (e.g. *Dendrocystites*), diploporitans (e.g. *Aristocystites*), cyclocystoids (e.g. *Moroccodiscus*), and a few eocrinoids (*Hexedriocystis*).

The most elevated Ordovician crinoids in our dataset (>600 mm tall: *Merocrinus* and *Cotylacrinna*) went extinct during the Late Ordovician mass extinction. Equally very long-stemmed crinoids quickly re-evolved during the Llandovery, with at least three genera (*Dimerocrinites*, *Periechocrinus*, and *Scyphocrinites*) living well above 1 m above the sea floor (with some claims, see Brett 1984, for scyphocrinitids having stems up to 3 m long, albeit likely living in a much curved posture rather than vertically erect). Such giant Silurian tiers will remain unchallenged through the remainder of the Palaeozoic, and their record will be exceeded only by Jurassic *Lilliocrinus*, thought to have been raised more than two metres above the sea floor (Ausich *et al.* 1999).

Several Middle–Late Ordovician stylophorans continued to live semi-infaunally with only their feeding arm raised above the sea floor, with *Barrandeocarpus* and *Enopleura* living as deep as 9 mm below the seafloor. For context, mid-Palaeozoic stylophorans will later nestle only slightly deeper, with Devonian *Anomalocystites disparilis* estimated to bury to 14 mm depth (Beaver *et al.* 1967). We know of no truly infaunal (nor deeper-buried semi-infaunal), filter-feeding echinoderms until the evolution of Cenozoic clypeasteroids (such as *Encope*; Durham *et al.* 1966; Lawrence *et al.* 2004; Mancosu & Nebelsick 2013). However, based on records of shallowly buried Late Palaeozoic *Aganaster* (<1 mm; Kokorin 2015) and extant *Amphiura* (*c.* 6 mm; Durham *et al.* 1966), it is possible that some undocumented Palaeozoic ophiuroids may have been buried at greater depths than these early stylophorans, even if only during feeding activities (Dean 1999). Of course, infaunal habits become *de rigueur* among many non-filter-feeding asteroids, ophiuroids, holothuroids, and especially echinoids, which will eventually colonize deep infaunal microhabitats even exceeding 100 mm, but not anywhere near such depths until the Jurassic (Buatois *et al.* 2016).

Taxonomically, there is great variation among filter-feeders in terms of the tier they were able to inhabit. Crinoids (and to lesser extent eocrinoids, paracrinoids, and diploritans) inhabited the tallest tiers (those greater than 30 mm). Intermediate tiers (approximately 5–30 mm) were most common for edrioasteroids, rhombiferans and solutes. Ctenocystoids, cyclocystoids, cinctans, the early echinoderm genus *Ctenoimbricata*, and, to a lesser extent, stylophorans inhabited the lowest tiers, with many of this last group living semi-infaunally. These patterns are consistent with those previously reported for helicoplacoids, eocrinoids and edrioasteroids (Rozhnov 2002; Dornbos 2008) and for those of Phanerozoic filter feeders as a whole (Ausich & Bottjer 1982; Bottjer & Ausich 1986; Bush & Bambach 2011), although the current study represents the first (we know of) where direct measurements are analysed statistically for an entire phylum.

Using the same methods as conducted for body size, average tiering height during the Cambrian–Ordovician is best fit by a model of an unbiased random walk, although we again cannot rule out a weakly driven model, which retains slightly greater support than for body size (Fig. S2B). Likelihood-based statistical analysis of the distribution of epifaunal tiering heights provide little evidence that discrete tiers existed during these periods, supporting the hypothesis that the earliest epifaunal echinoderms were not ecologically partitioning themselves into discrete tiers, at least when considered at global and epoch-wide scales. Instead, tiering height is best considered as a continuous variable, with a modest but increasing central tendency throughout the Cambrian and Ordovician (Fig. 3B), and with intervals of tall tiering heights caused more by increasing variance through time as a result of greater genus richness than by increasing vertical body size (Gould 1988).

The tiering trends remain essentially unchanged when using sample standardization to subsample time intervals at a constant genus richness (Fig. S1B) or using raw (non-time-scaled) ranges for tip genera (Fig. S1D). The resampled 99th percentiles diminish by approximately 25% on average, but that is to be expected because extrema are biased by sample sizes (Kowalewski & Novack-Gottshall 2010), and time-scaled genus richness is computationally greatest during the Middle Ordovician when the tallest echinoderm tier is also inhabited.

Trends in habitat usage

The distance an animal lives from the seafloor is just one aspect of how they interact with their immediate environment. Their preferred substrate (whether sediment, skeletal debris, living organism, or fluidic medium; whether firm or soft; whether attached or free-living; and whether to use their substrate to raise themselves into habitats otherwise not achievable on their own) adds other vital considerations. When including such discrete life-habit characters, the same temporal patterns in how echinoderms utilized tiering microhabitat during the Cambrian and Ordovician generally remain evident, but with important nuances (Fig. 4A). By including these additional categories, moreover, these trends allow inclusion of echinoderms that were not filter feeders (or lack reliable records of tiering heights), as well as inclusion of time-scaled ancestors whose life-habit states can be inferred phylogenetically.

Whether represented in absolute (Fig. 4A) or relative (Fig. S3A) terms or using time-scaling or not (Fig. S3C), the majority of Cambrian echinoderms were epifauna that lived close to the sea floor and attached or rested on lithic (sedimentary or skeletal debris) substrates (*c.* 35% within 10 mm of sea floor and 48% 10–100 mm above it). These proportions are relatively constant across the period, with a small increase in short epifauna during the mid Cambrian attributable to the diversification of surface-dwelling cinctans. Although constituting a small number of Cambrian echinoderms, the stylophorans (and edrioasteroid *Camptostroma*) are responsible for approximately 10% of echinoderms living semi-infaunally (although most maintained the majority of their bodies above the sea floor). The slight proportional increase in epibiotic lifestyles during the latest Cambrian (defined here in the simplest way, *sensu* Novack-Gottshall 2007, of having a living substrate, and not necessarily as being parasitic, bioclaustric, or substantially elevated above the

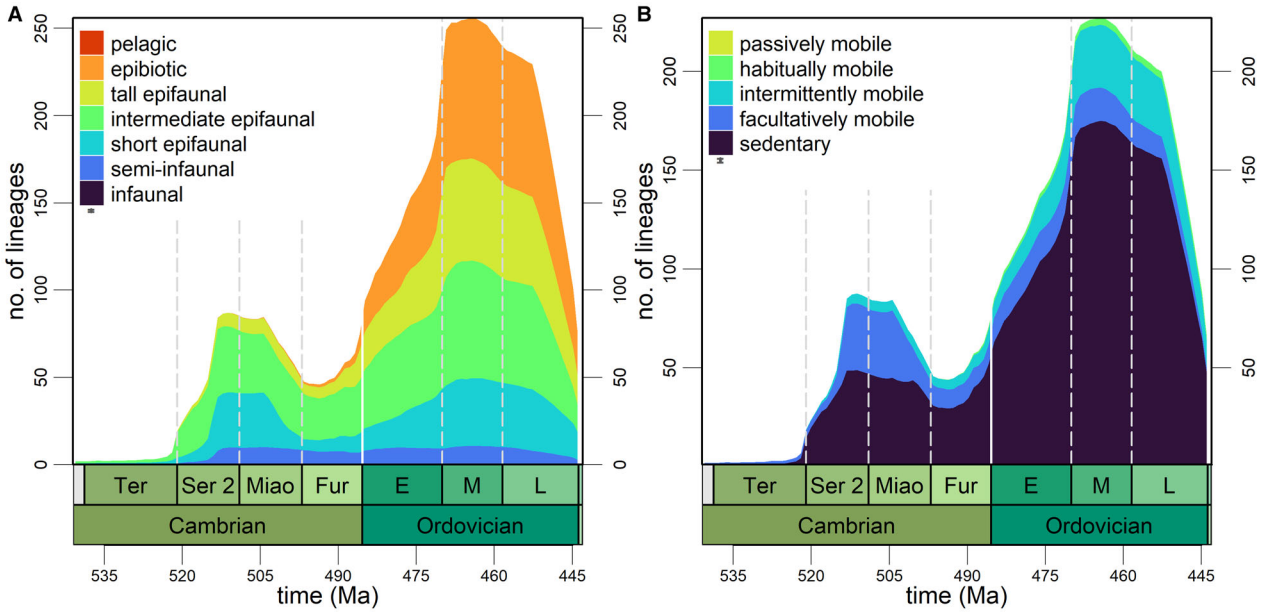


FIG. 4. Stacked frequency trends in Cambrian–Ordovician echinoderm habitats and modes of locomotion. Figured frequencies include the mean number of time-scaled lineages (including tip genera and ancestors) of a given state across 100 time-scaled phylogenies, with mean standard deviation across all states, time intervals, and trees illustrated as the small error bar below each legend. Vertical lines denote geological stages. Because some lineages may be coded for more than one state (e.g. an ancestor coded polymorphically as 0/1), the total number of lineages in a given time interval may be greater than the lineage richness trend figured in Figure 1A. A, habitats, using combinations of characters 2, 9–11 and 17–18 (Table 1; see Data and Method for state combinations); no pelagic echinoderms are known to exist during the Cambrian–Ordovician, but this habitat is included in the legend for completeness. B, modes of locomotion, using character 6 (Table 1); no passively mobile echinoderms are known to exist during the Cambrian–Ordovician, but this mode of locomotion is included in the legend for completeness. See Figure S3 for this data figured using proportional frequencies and without time-scaling.

seafloor) is the result of a few ancestral edrioasteroids inferred to have had this lifestyle in some time-scaled phylogenies (Fig. S4A). The lack of any unambiguously 'epibiotic' echinoderm known during the Cambrian, combined with a small global Furongian echinoderm genus richness that artificially inflates their proportional occurrence, suggests that organism-dwelling echinoderms probably only originated this way of living during the Ordovician (Fig. S3A, C). Similarly, there is no evidence of wholly infaunal echinoderms during the Cambrian.

Across the Ordovician, approximately one-third of echinoderms live at least partially attached to some living organism, and the number increases through time (Figs 4A, S4). These 'epibiotic' habits are most common among crinoids, but many edrioasteroids and some rhombiferans and coronate blastoids also use other organisms as their exclusive or occasional substrate. The living substrates for these echinoderms were shells, bryozoans or other animals that did not significantly elevate the animal into the water column (Fig. S4B), and that only served as a firm attachment site. Indeed, one-third (35%) of them are generalists in their substrate preference, being non-specific whether their substrate is biotic or lithic, so long it is a firm one (char. 12; Table 1; Fig. S4C).

There is less of a temporal change in hard versus soft substrate preferences (Fig. S4C), with 63% of echinoderms at any one time utilizing hard substrates, on average. However, while hard substrates are generally more common throughout the Cambrian and Ordovician, there is greater preference for soft substrates among Stage 4–Miaolingian echinoderms dominated by cinctans.

A similar preference for non-attached, free-living habits is also evident for these same mid-Cambrian lineages (Fig. S4D), although the late Cambrian shift toward free-living habits ends by the Furongian, a series earlier than does the transition for soft-substrate dwelling forms. Examples of such attached but soft-substrate forms include the mid-Cambrian edrioasteroids *Stromatocystites* and *Totiglobus* that attached to microbially stabilized softgrounds (Bell & Sprinkle 1978; Parsley & Prokop 2004; Dornbos 2006; Zhao *et al.* 2010; Zamora *et al.* 2017), the early crinoid *Aethocrinus* with its unique *Hohlwurzel* holdfast (Ubaghs *et al.* 1978), and the rhombiferan *Macrocystella* with its distinctive stem that was probably used more for stability in soft substrates than for permanent attachment (Paul 1968; Mergl & Prokop 2006; Dornbos 2006).

Semi-infaunal echinoderms remain relatively uncommon during the Ordovician and maintain a similar

absolute number of lineages as in the Cambrian (Figs 4A, S3C), but they become proportionally less common when compared to all Ordovician microhabitat strategies (Figs S3A, S4E). These semi-infaunal echinoderms include diverse stylophorans, but also the ctenocystoid *Conollia* (Rahman *et al.* 2015b) and the edrioasteroid *Rhenopyrgus* (Holloway & Jell 1983; Dornbos 2006; Lefebvre *et al.* 2013; Sumrall *et al.* 2013; Ewin *et al.* 2020). Although the time-scaled phylogenies infer holothuroid ancestors in the Ordovician, their infaunality remains uncertain. Some evidence suggests that stem-apodids (e.g. *Porosthyone*; Reich 2010; Jell 2011; Smith & Reich 2013) may have been infaunal. No pelagic echinoderms are known during the Cambrian or Ordovician; in fact, this habit is quite unusual among the echinoderm body plan, having only been explored by tiny Mesozoic roveacrinids (including *Roveacrinus* (Schneider 1989, 1995; Hess *et al.* 2011) and *Saccocoma* (Hess *et al.* 1999; Hess & Etter 2011)) and a few extant, deep-sea, swimming holothuroids that lack a fossil record (Billett *et al.* 2020).

Trends in mobility

Approximately 75% of early echinoderms were incapable of active locomotion (Figs 4B, S3B, D), typically attached to some hard (whether living or not) substrate (Fig. S4C, D). These sedentary habits were practiced by a diverse group of crinoids, edrioasteroids, eocrinoids, rhombiferans, diploporitans, paracrinoids, helicoplacoids, parablastoids, and even the Cambrian early-solute *Coleicarpus* (Daley 1996; Zamora *et al.* 2017). It is important to note that while many of these taxa were not able to actively relocate, all were still able to move portions of their body, such as when feeding, maintaining posture, or defending themselves. A lack of mobility does not imply a lack of functionally important musculature (Baumiller 2008). Moreover, 25% of early echinoderms were able to move about to some extent.

Approximately 14% of early echinoderms were facultatively mobile (Fig. 4B, S3B, D), able to move but generally remaining immobile, typically only relocating if disturbed. Most of these echinoderms were stylophorans (Lefebvre 2003; Noailles 2016) and cinctans (Friedrich 1993; Rahman *et al.* 2020), but several solutes and stenuroids also shared this ability. This habit became much less frequent after the Cambrian, when it occurred among 30% of lineages on average, compared to less than 8% of Ordovician lineages. Nearly 13% of early echinoderms were intermittently mobile (typically at rest but regularly moving when foraging for food or for other reasons) and this habit was most common among asteroids, ophiuroids, echinoids, holothuroids and ctenocystoids, plus most solutes (e.g. *Belemnocystites*; Kolata *et al.* 1977), rhombiferans (e.g. *Amecystis*; Broadhead & Strimple 1975; Sumrall 2000; Gorzelak & Zamora 2016) and possibly the early stem-echinoderm *Ctenoimbricata* (Zamora *et al.* 2012). Habitual mobility (typically moving except when at rest) was almost nonexistent among Cambrian echinoderms, first appearing in the Furongian with the scavenging Cambrian somasteroid *Ophioxenikos* (Blake & Guensburg 1993) and persisting in the Ordovician by several predatory asteroids (e.g. *Promopalaeaster* and *Urasterella*; Blake & Guensburg 1994; Blake & Rozhnov 2007). It is possible that the record of mobile forms is obscured by taphonomic biases (Brett *et al.* 1997). However, the magnitude of such a bias is offset because such high-energy activities collectively only account for 2% of Ordovician echinoderm modes of locomotion. Despite a proportional conversion in facultative to intermittent mobility (Fig. S3B), the overall frequencies of these modes of locomotion remained quite unchanging throughout the Cambrian and Ordovician, despite substantial increases in genus richness and dramatic turnovers in taxonomic classes.

An additional locomotory strategy also exists, but no early echinoderms are known to have taken advantage of it. Passive mobility describes movement by planktonic drifting, being dragged by a current along or near the sea floor, or by being attached to some floating raft or moving animal host. The earliest current-dragged echinoderms first evolve in Middle Palaeozoic crinoids (e.g. Silurian *Scyphocrinites*; Brett 1984; Gorzelak *et al.* 2020; and Devonian *Ancyrocrinus*; Plotnick & Bauer 2014), and the Silurian–Devonian rhombiferan *Lepocrinites* (Brett 1984) also shared this habit. Several Mesozoic crinoids specialized in attaching to floating driftwood (e.g. *Pentacrinites* and *Traumatocrinus*; Ausich *et al.* 1999; Wang *et al.* 2006; Hagdorn *et al.* 2007; Hess 2010; Baumiller & Janevski 2011; Hagdorn & Wang 2015). The earliest freely planktonic echinoderms also first occur during the Mesozoic with the roveacrinids mentioned above. It may be evolutionarily significant that most fossil echinoderm examples of passive mobility occurred among crinoids.

Trends in diet and foraging

Throughout the early Palaeozoic, nearly all echinoderms had microbivorous diets (Figs 5A, S5A, C), here defined as living or non-living organic matter derived from archaea, bacteria, algae or other protists, or other organic foodstuffs not animal or plant-based (*sensu* Novack-Gottshall 2007). The earliest at-least-partially carnivorous echinoderm is the scavenging late Cambrian to early Ordovician somasteroid *Ophioxenikos*, inferred to be a mass-feeding carcass scavenger based on a stout mouth and relatively inflexible arms that would have made

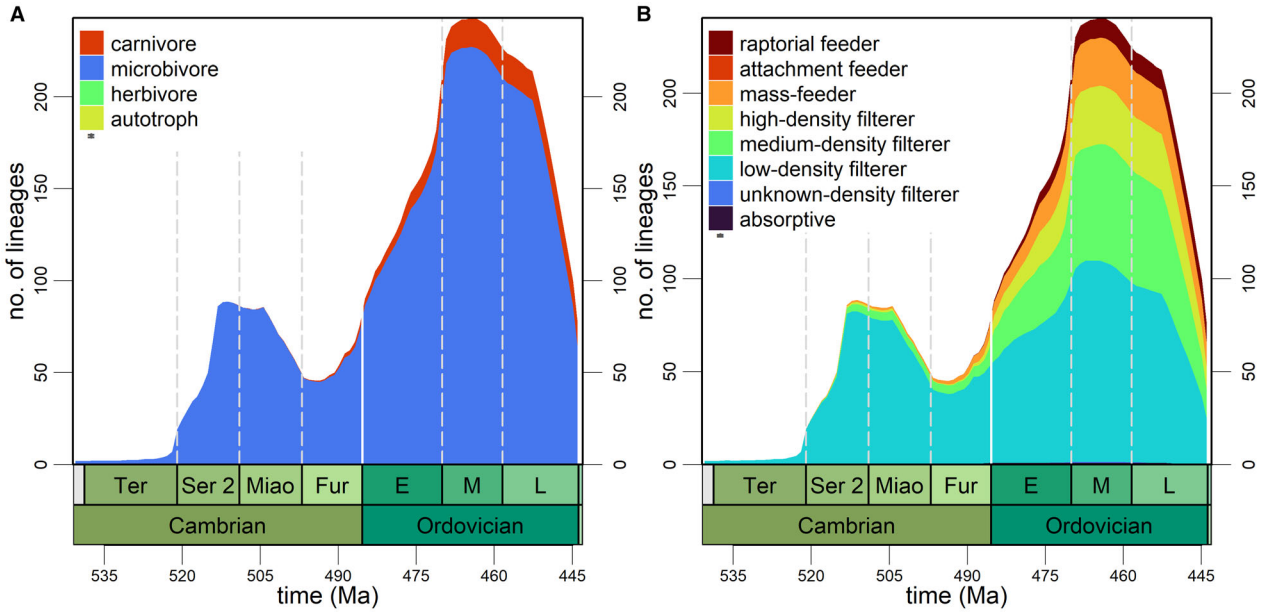


FIG. 5. Stacked frequency trends in Cambrian–Ordovician echinoderm diets and foraging habits. Figured frequencies include the mean number of time-scaled lineages (including tip genera and ancestors) of a given state across 100 time-scaled phylogenies, with mean standard deviation across all states, time intervals, and trees illustrated as the small error bar below each legend. Vertical lines denote geological stages. Because some lineages may be coded for more than one state (e.g. a scavenger that feeds on both animals and decomposing microbivorous matter), the total number of lineages in a given time interval may be greater than the lineage richness trend figured in Figure 1A. A, diets, using characters 33–36 (Table 1); no echinoderms are autotrophic and no herbivorous (*sensu strictu*, plant-eating) echinoderms are known to exist during these intervals, but these characters are included in the legend for completeness. B, foraging habits, using characters 27–31 (Table 1). See Figure S4 for this data figured using proportional frequencies and without time-scaling.

manipulating prey difficult (Blake & Guensburg 1993). Stronger inferences can be drawn for several Ordovician habitually mobile asteroids (cited above), which have been preserved in the act of predation, typically on shallowly infaunal or semi-infaunal bivalves. Aside from the novelty of partial plant-based herbivory by several crown-group echinoids in the Mesozoic, the nature of echinoderm diets appears to have remained essentially unchanged since the latest Cambrian.

Despite this stasis, substantial innovation occurs in how these animals collect their food (Figs 5B, S5B, D). Filter feeders dominate throughout the Cambrian and Ordovician, with a combined average of 91% of echinoderms feeding this way, most of them also with microbivorous and particle-feeding diets (chars 34 and 39; Table 1). However, the complexity of filter-feeding organs increases through time (char. 32; Table 1), with intermediate-density organs occurring in just 6% of Cambrian echinoderms and increasing substantially to 28% during the Ordovician, on average. Similarly, the highest density filterers account for less than 3% of Cambrian forms, and 14% of Ordovician ones. The absolute number of low-density filterers is of a similar order of magnitude between the periods (Fig. 5B), suggesting that the increase in complex filtering organs is more one of addition rather than replacement. The majority of this increase is caused by the origin and radiation of crinoids, with their diverse and generally more sophisticated feeding arms with myriad branching arrangements, plating structures, and pinnules (Guensburg & Sprinkle 2001; Brower 2006; Guensburg *et al.* 2020). The only high-density-filtering non-crinoid is the mid-Cambrian eocrinoid *Lyracystis* (Sprinkle & Collins 2006). Even medium-density filterers are rare among non-crinoids, limited primarily to eocrinoids (*Acanthocystites*, *Cardiocystites*, *Haimacystis*, *Rhopalocystis* and *Tatonkacystis*), a few paracrinoids and rhombiferans (e.g. *Amygdalocystites* and *Caryocrinites*) and the parablastoid *Meristoschisma*.

Mass feeding is used herein (*sensu* Novack-Gottshall 2007) to describe animals that ingest large quantities of food *en mass*, which could include both nonselective deposit feeders and scavengers late to the party. It can be used here more-or-less interchangeably with the more widely used term ‘deposit-feeder’, although that term is avoided because of its primary emphasis on *where* food is located rather than as a general strategy for ingesting it. Mass feeding has remained a viable strategy for echinoderms since their origins, becoming more frequent in the

Ordovician (with a mean of 11% throughout the period). The scavenging somasteroid *Ophioxenikos* is the only time-scaled late Cambrian tip genus with a presumed mass-feeding habit (Blake & Guensburg 1993), but many time-scaled phylogenies infer that a few Cambrian asterozoan and echinozoan ancestors shared this habit. Ordovician mass feeders include many more taxa, including asteroids, ophiuroids, stenuroids, somasteroids, echinoids and holothuroids. Aside from the classes that go extinct, these are the same echinoderms that maintain this feeding habit in today's oceans, placing the early Ordovician (or perhaps latest Cambrian) as the primary origin of this important way of foraging.

The advent of asteroids (but not the other asterozoans) at the start of the Ordovician also ushered in the earliest raptorial feeding habits (*sensu* Novack-Gottshall 2007), in which large chunks of food (i.e. prey, but potentially also macroalgal seaweed, not observed among these early echinoderms) are ingested intact (chars 31 and 40; Table 1). Some of these asteroids are also coded as particle-feeding mass feeders if interpreted as generalist scavengers rather than predators *sensu strictu*. Most unusual among these 'raptors' are the crinoids *Euspirocrinus* (Ubaghs *et al.* 1978; Brett 1984) and *Protaxocrinus* (Meyer & Lane 1976; Ausich 1978), whose stout, ramous and nonpinnulate arms cause them to be considered microcarnivores, a specialized but generally rare crinoid feeding strategy maintained throughout the Palaeozoic for numerous cyathocrin, sagenocrinid and taxocrinid crinoids (Meyer & Lane 1976; Brett 1984). However, raptorial habits account for only 5% of Ordovician feeding strategies.

Two additional foraging strategies, absent among early echinoderms (and never more than a trivial footnote in their Phanerozoic history) are worth brief mention. Attachment feeding is most common among parasites, such as for the corallivorous crown-of-thorns starfish *Acanthaster* (Deaker *et al.* 2020). Many echinoderms (and other marine animals) can absorb dissolved organic matter across their epidermis (Ferguson 1982), and this strategy can prove advantageous after surviving predation or other major bodily injury (Donovan & Schmidt 2001). However, echinoderms herein are coded in this manner only when it accounts for their primary feeding strategy (cf. Rozhnov 2002 who claimed this may have been a much more common strategy among the earliest echinoderms). A few Ordovician microcrinoids related to Silurian *Paracolocrinus* are interpreted as such epidermal feeders (Brett 1980, 1984), leading them to be coded as absorptive feeders (a replaced term for the original 'ambient feeder' of Novack-Gottshall 2007). Never common, several mid-Palaeozoic cyathocrinine, eustenocrinid, allagecrinid and pygmaeocrinid microcrinoids, several lacking arms, will continue to feed at least partially this way (Brett 1980, 1984).

Regardless of diet and how they foraged for it, most early echinoderms fed on food located above the sea floor, which here includes organic material resting *on* the sea floor for surficial deposit feeders (Fig. S4F). There is a slight increase in the number of echinoderms with infaunal foods starting in the late Cambrian (Furongian) and continuing throughout the Ordovician (Fig. S4F). These are driven exclusively by the diversification of asterozoans (ophiuroids, somasteroids, stenuroids, and especially asteroids), which include scavenging, predatory and deposit-feeding forms, although some, like *Promopalaeaster* (Blake & Guensburg 1994; Blake & Rozhnov 2007), are coded as feeding on organic matter both above and below the sea floor.

DISCUSSION

Cambrian–Ordovician ecological changes involved rapid early novelty followed by modest-but-continuous partitioning and expansion of new strategies

Most of the successful echinoderm life-habit strategies that define the phylum (even today) evolved in the Cambrian. Early echinoderms typically exhibited one of four canonical strategies, which can be summarized by state-combinations of the life-habit dimensions described above, and which are visible in principal coordinates analysis (PCoA) ecospace (Figs 6, S6; Novack-Gottshall *et al.* 2022, fig. 2, extended data fig. 4):

1. Tall-tiered, epifaunal filter feeders with large bodies and complex feeding organs attached to hard substrates or epibiotically living atop organisms.
2. Smaller, sedentary, epifaunal filter-feeders living close to the sea floor and typically attached to shelly debris.
3. Free-living (not attached) or mobile epifaunal filter feeders living on soft substrates.
4. Mobile deposit-feeders/mass-feeders, carnivores, and scavengers living partially infaunally or feeding on partially buried organic matter.

Three of these four strategies were already inhabited during the early Cambrian (Series 2) echinoderms (Figs 3–6, S3–S6). Although the first 'tall-filterers' strategy would become much more common in the Ordovician, it was invented by several Cambrian long-stemmed eocrinoids. The second 'short-filterers' strategy was inhabited by helicoplacoids, *Helicocystis*, and the earliest edrioasteroids, short-stemmed eocrinoids, and solutes. The third 'mobile-filterers' strategy was represented by the earliest stylophorans, cinctans, ctenocystoids and *Ctenoimbricata*. (Note that we interpret *Ctenoimbricata* as feeding more like a filter-feeding tunicate with pharyngeal basket than as an enteropneust-like deposit feeder, in slight contrast to the

claims by Zamora *et al.* (2012) and similar to the 'detritus filter feeder' style Fatka & Kordule (1985) infer for ctenocystoids.) Many of these animals had semi-bilaterally symmetrical bodies, and the stem-echinoderm *Ctenoimbricata* lacked a water vascular system (Zamora *et al.* 2012). Our time-scaled phylogenies infer that each of these three strategies included multiple lineages (representing multiple taxonomic classes) during the Terreneuvian, even though no undisputed echinoderms are known from this stage (Zamora *et al.* 2013). All three strategies became well established across numerous fossilized genera during Series 2, coinciding with rising taxonomic diversity during the Cambrian radiation (Fig. 6).

The UEH and EAT topologies that we include in our time-scaled phylogenies make different inferences for the life habit of the earliest echinoderm (compare Figs 6 and S6), but have no impact on the structure of later Cambrian–Ordovician ecospace. All time-scaled UEH trees infer the ancestral echinoderm habit was the 'mobile-filterers' strategy shared by *Ctenoimbricata* and cinctans: relatively small (less than 1 cm^3 in body volume), short epifaunal (1–10 mm tier), free-living (unattached), facultatively mobile, microbivorous filter feeders with low-density feeding elements, resting atop a soft substrate. This habit plots as the darkest point in the bottom-left Terreneuvian panel of Figure 6 (but not Fig. S6). In contrast, all time-scaled EAT trees infer the 'short-filterer' life habit shared by *Helicoplacus* and *Helicocystis* as the ancestral echinoderm habit: intermediate body size (1–10 cm^3), raised epifaunal (10–100 mm tier), attached, sedentary, microbivorous filter feeders with low-density feeding elements living atop a hard substrate. This habit plots near the origin in Figure S6 (and in the same place in Fig. 6). All reconstructions concur that the ancestral foraging habit involved filter feeding using simple organs. By the end of the Terreneuvian, the time-scaled UEH tree infers that all three of these iconic early echinoderm life habits had evolved across diverse classes, while the *Helicoplacus*-like habit does not evolve until the start of Series 2 in the time-scaled EAT topology. Despite their differences, both reconstructions suggest the earliest echinoderms, whether the truly first echinoderms or rapidly evolving descendants, were attached to isolated skeletal debris and localized firmgrounds in soft-substrate settings, rather than to carbonate hardgrounds *sensu strictu* (Rozhnov 2002; Zamora *et al.* 2010, 2017).

The remainder of the Cambrian involved experimentation with novel combinations of these three early canonical strategies, varying in body size, tiering height, degrees of mobility, attachment, and other facets of their ecology. Most of this ecological evolution (involving eocrinoids, edrioasteroids, stylophorans, solutes and cinctans) involved iterative admixing of the (second) sedentary and (third) mobile filter-feeding strategies, visible along the left gradient of PCoA axis 1 (Figs 6, S6). This partitioning is also evident in the relatively unchanging proportions of life-habit characters, tiering structure, and body-size distribution reported above, despite substantially increasing numbers of taxa and life habits (Fig. 1). Nearly all mid–late Cambrian echinoderms occupied ecospace established rapidly during the Terreneuvian, or earliest Series 2 (Figs 6, S6). These later Cambrian echinoderms did invent several novel life-habit combinations. For example, the glyptocystitid rhombiferans *Cambrocrinus* and *Barroubiocystis* were free-living and sedentary on soft substrates, anchoring their stems deeply within the seafloor (Dzik & Orłowski 1993; Ubaghs 1998; Zamora *et al.* 2017). The stylophorans and edrioasteroid *Camptostroma* were the first to live partially buried in the seafloor (Lefebvre 2003; Noailles 2016; Zamora *et al.* 2017). These unique habits, however, were otherwise quite typical for soft-substrate-dwelling, filter-feeding echinoderms, and represent novel combinations of pre-existing habits rather than fundamentally novel ways of living. Other new life habits (such as that of the miniscule stylophoran *Sokkaejaecystis* plotting in the extreme bottom-left of the first two ecospace axes (Figs 6, S6), and the expansion in the third and fourth ecospace axes) are caused primarily by the evolution of substantially smaller and larger body sizes (Fig. 3A), which resulted in greater variability in their tiering structure (Fig. 3B). There was less Cambrian exploration among higher-tiering filter feeders, which remained dominated only by long-stemmed eocrinoids (e.g. *Lepidocystis*, *Felbabkacystis* and *Nolichukia*), most of which had simple filter-feeding brachioles. However, several early eocrinoids (e.g. *Acanthocystites*, *Lyracystis* and *Tatonkacystis*) evolved more complex, multi-armed, or denser feeding organs. Collectively, as Cambrian echinoderms doubled or tripled their number of taxonomic classes and diversified into even larger numbers of genera, their overall ecological divergence was rather modest after their earliest appearance in the fossil record. These patterns are also evident in their low (but slowly increasing) Cambrian ecological disparity (Novack-Gottshall *et al.* 2022).

The time-scaled phylogenies suggest that several echinoderm classes originated during the late Cambrian (Furongian) and earliest Ordovician. These include the earliest crinoids (although the time-scaled EAT trees place their origins quite earlier, Fig. S6), diploporitans, somasteroids, stenuroids, and perhaps the asteroids, these last three also marking the origin of the asterozoans. Mitrate stylophorans also originated at this time (Zamora *et al.* 2013). Despite most of these classes lacking unambiguous Cambrian fossils, such early origins are consistent with their immediate cladistic diversity and widespread palaeogeographic distributions early in the Ordovician (Lefebvre *et al.* 2013; Blake 2013, 2018; Ausich *et al.* 2015; Blake

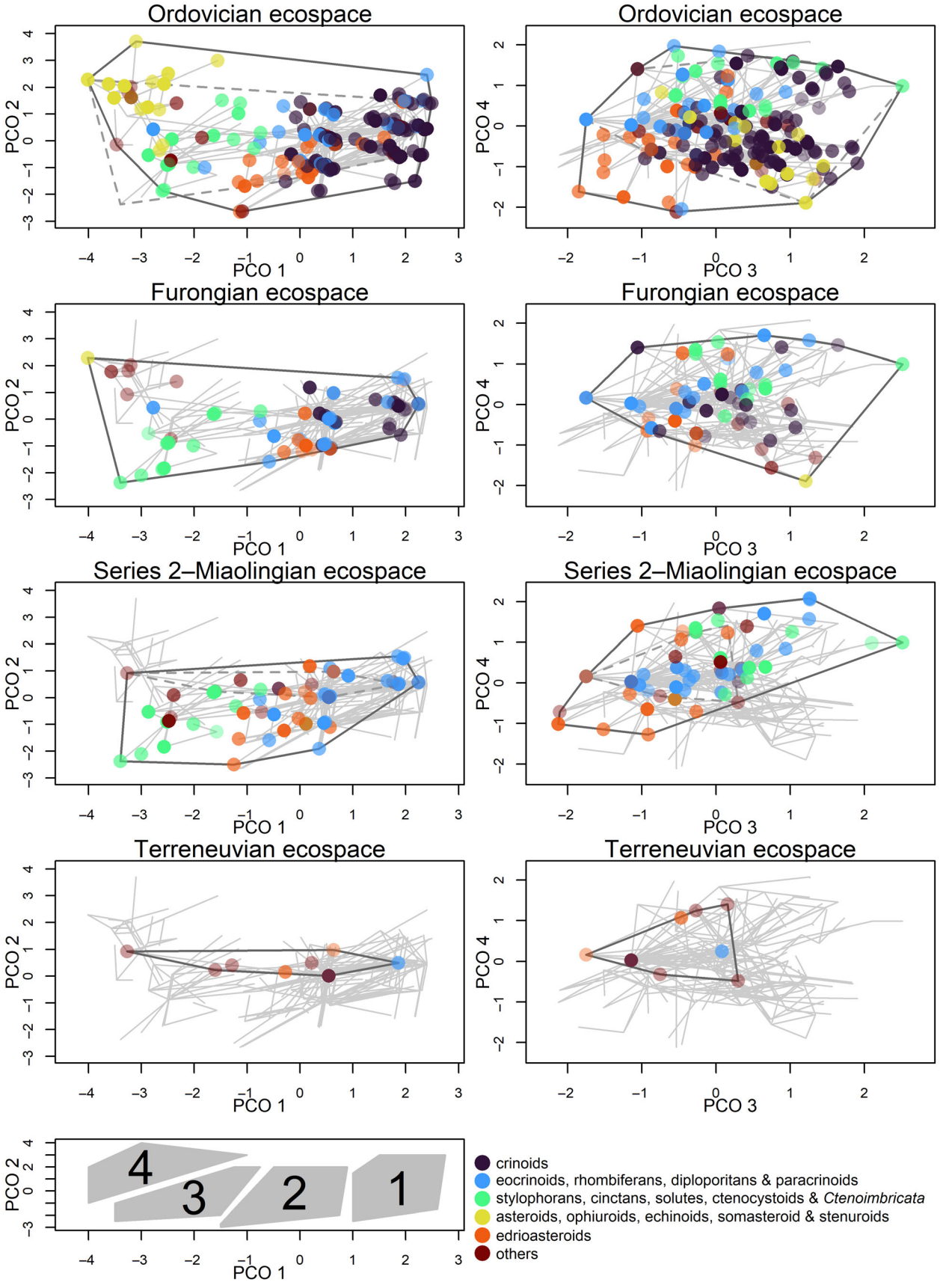

Ordovician ecospace
PCO 2
PCO 1
Ordovician ecospace
PCO 4
PCO 3
Furongian ecospace
PCO 2
PCO 1
Furongian ecospace
PCO 4
PCO 3
Series 2–Miaolingian ecospace
PCO 2
PCO 1
Series 2–Miaolingian ecospace
PCO 4
PCO 3
Terreneuvian ecospace
PCO 2
PCO 1
Terreneuvian ecospace
PCO 4
PCO 3
4
3
2
1
PCO 2
PCO 1
crinoids
eocrinoids, rhombiferans, diploporitans & paracrinoids
stylophorans, cinctans, solutes, ctenocystoids & Ctenoimbricata
asteroids, ophiuroids, echinoids, somasteroid & stenuroids
edrioasteroids
others

FIG. 6. Echinoderm phyloecospace through the Cambrian and Ordovician periods. Only the ecospace for the time-scaled UEH phylogeny number 49 is illustrated as one example; the remaining 49 time-scaled UEH phylogenies produce similar ordination structures. See Figure S6 for an alternative representation of ecospace using the EAT topology. Terreneuvian and Furongian epochs are plotted separately to the remaining Cambrian and Ordovician epochs to highlight changes occurring prior to diversification during the Cambrian and Ordovician radiations. First four principal coordinate (PCO) axes are illustrated, with each point representing some unique life habit, and colour-coded according to taxonomic class. The underlying time-scaled phylogeny represents the phylogenetic distribution of tip genera and ancestral nodes in the ecospace. The convex hull in each ordination is provided as a simple measure of overall ecospace occupied during each interval; the Terreneuvian and Furongian convex hulls are plotted as dashed lines in the subsequent temporal interval for comparison. Points are transparent to illustrate regions where multiple tips and ancestors overlap, with ancestral classes assigned when all descendants are assigned the same class, and with nodes illustrated as more transparent than tips. Taxonomic group 'other' includes the early blastoid *Macurdablastus*, coronate blastoid *Mespilocystites*, cyclocystoids, helicoplacoids, parablastoids, and taxa of uncertain class affiliation. The legend at bottom left illustrates the approximate positions of the four iconic ecological strategies mentioned in text. The first four axes account for 1.40, 0.40, 0.32, and 0.27% of explained relative eigenvalues in the 731-dimensional distance matrix. This figure is updated from Novack-Gottshall *et al.* (2022, fig. 2), which provides additional context.

et al. 2016; Sheffield & Sumrall 2019), and the poor Furongian echinoderm fossil record (Sumrall *et al.* 1997; Zamora *et al.* 2013). The life habits for these new Furongian classes continued the Cambrian trend of ongoing partitioning of preexisting strategies (Figs 6, S6), but the asterozoans, and later the crinoids, ushered in major expansions to the echinoderm life habit. Although limited to few genera (and their phylogenetically inferred ancestors) at their start, these Furongian originations are evident in the small-but-lasting inflection in the ecological trends reported above, which also have the effect of substantially increasing ecological (and anatomical) disparity of the entire phylum (Deline *et al.* 2020; Novack-Gottshall *et al.* 2022). These inferred earliest (Furongian) crinoids plot in ecospace (Figs 6, S6) in the same location as the eocrinoids, and so their impacts on expanding ecospace are not evident. Starting with the somasteroid *Ophioxenikos* (plotted in yellow in the top-left corner of Figs 6 and S6), however, the earliest asterozoans invented several novel and enduring additions to the echinoderm life-habit toolkit. This first asterozoan was a moderately small, habitually mobile (albeit likely slow-moving), mass-feeding carcass scavenger (Blake & Guensburg 1993), and this genus marks three novel echinoderm life habits: mass feeding, a partially carnivorous diet, and habitual mobility. Most of these traits are shared by later asterozoans, which will maintain some degree of mobility, with many lineages adding more carnivorous diets, raptorial foraging, and the ability to hunt animals, including infaunal prey.

The Ordovician witnessed the diversification of numerous filter-feeding classes that added to the diversity of edrioasteroids, eocrinoids, rhombiferans and stylophorans carrying on from the Cambrian, on top of the newly originating Furongian classes. New fossiliferous classes include the crinoids, diploporitans, paracrinoids and parablastoids, plus blastoids in the Middle Ordovician (although it is likely that their origins were earlier). Despite their taxonomic diversity, most of these echinoderms continued to feed in a similar manner as their Cambrian ancestors, and thus their diversification did not substantially expand echinoderm ecospace (Figs 6, S6). In fact, there are numerous examples of marked ecological convergence among these filter-feeding taxa, typically crossing classes and even subphyla (Novack-Gottshall *et al.* 2022). The greatest impacts of these diversifying filter-feeding classes included the evolution of more complex feeding organs (Guensburg & Sprinkle 2001), a greater range of body sizes and stem lengths, and thus a greater differentiation in tiering structure and characters often related to body size (e.g. chars 1–4; Table 1). Most of these changes were pioneered by crinoids, although small numbers of eocrinoids, diploporitans, edrioasteroids and others converged on these innovations. These additional life-habit combinations helped fill in the ecospace between 'short-filterers' (group 2) and 'tall-filterers' (group 1), which was largely left vacant during the Cambrian (Figs 6, S6). Crinoids, but also edrioasteroids, rhombiferans, and coronate blastoids, also began to attach to other living organisms as a hard substrate, typically brachiopods or bryozoans. These new substrate affinities slightly expanded the ecospace of the phylum, but had a larger impact on individual classes. For example, the edrioasteroid *Euryeschatia*, which lived in tall tiers (*c.* 150 mm) atop conulariids (Sumrall & Zamora 2011), plots in 'tall-crinoid' ecospace rather than where typical edrioasteroids are clustered (Fig. 6). Several Ordovician stylophorans buried to slightly deeper depths than in the Cambrian (though no more than approximately 4 mm), but these continue to plot in the ecospace of their Cambrian relatives.

Asterozoans diversified during the Early–Middle Ordovician, and their greater degrees of mobility and hunting predation pushed echinoderm ecospace farther in this dimension than ever before (Figs 6, S6). Echinozoans (echinoids and holothuroids, including ophiocistioids) are inferred to have originated during the Ordovician

(Lefebvre *et al.* 2013), but their earliest members had life habits similar to other asterozoans (typically mass-feeders of surficial or shallowly buried organic matter, and with some degree of mobility) and thus their early life habits largely juxtapose atop the asterozoans. Echinozoan evolutionary originations do not add substantial novelty or increase the ecological disparity of the phylum as a whole, which awaits the diversification of genuinely infaunal holothuroids during the Middle Palaeozoic. These mass-feeding and predatory habits are important additions to the echinoderm playbook, and they largely define these two major subphyla today, making the early Ordovician (or perhaps latest Cambrian) their inception.

The totality of these new Ordovician life habits resulted in a substantial increase in new life habits, and led to increasing overall ecological disparity (Novack-Gottshall *et al.* 2022), to the highest levels observed during their evolution thus far. However, the increases for most disparity metrics during the Ordovician were modest, with most occurring at or just before the onset of the Ordovician (see Novack-Gottshall *et al.* 2022, ext. data fig. 3), and with the dominant Ordovician pattern more one of filling in of ecospace rather than in expanding it (Figs 6, S6). In contrast, the impact of these additions had a more muted impact on anatomical disparity because most crinoids plot morphologically in the same region as eocrinoids, rhombiferans, diploporitans and paracrinoids, with most of the new impact associated only with the origins of camerate crinoids (Deline *et al.* 2020; Novack-Gottshall *et al.* 2022).

Ecological novelty during the evolution of early echinoderms

In the context of echinoderm evolution, all of the Cambrian taxa were pioneers, and they set the path for future echinoderm ecological evolution. There are no confirmed raptorial echinoderms during the Cambrian, nor echinoderms that were attached to living animals; these are truly novel Ordovician habits. There are similarly no Cambrian carnivores aside from the latest Cambrian somasteroid *Ophioxenikos*. Despite the preponderance of reefs during the early Palaeozoic (Kröger *et al.* 2017; Cordie *et al.* 2019) and the frequency of reef-adapted echinoderms from the Silurian to the present day (Brett 1984; Hess *et al.* 1999; Goldberg 2013), it is notable that very few early Palaeozoic echinoderms are known from these environments (Clausen 2004; Álvaro *et al.* 2013). However, several early Ordovician echinoderms, and occasionally Late Cambrian ones, are associated with stromatolite bioherms that offered a firm substrate for attachment (Brett *et al.* 1983b; Zamora *et al.* 2017; Rozhnov 2019). The onset of fully infaunal habits are unclear but may coincide with the advent of mid-Palaeozoic holothuroids; herbivorous (plant-eating), pelagic and passively mobile habits do not evolve until the Mesozoic, long after the Ordovician.

We are not staking claims that the novel echinoderm life habits discussed above represent the earliest invention of these life habits in the marine biosphere. The phylum, with their well-preserved skeletal architecture, are thought to have originated slightly later than most other bilaterian phyla (Zamora *et al.* 2013; Nanglu *et al.* 2022). Archaeocyathids and other sponges, possibly even Ediacaran *Namacalathus* (Zhuravlev *et al.* 2015; Cordie *et al.* 2019), were among the earliest to filter feed, many with complex tiering structures (Yuan *et al.* 2002). Brachiopods (Topper *et al.* 2015) and chancelloriids (Bengtson & Collins 2015) attached to living substrates by the mid Cambrian, and possibly *Namapoikia* did so atop Ediacaran thrombolitic and stromatolitic mats (Wood & Penny 2018). Hyolithids (Liu *et al.* 2021), gastropods (Thomas *et al.* 2020), helcionelloids (Gubanov & Peel 2000), diverse stem annelids (Parry *et al.* 2014), and other Cambrian animals are likely to have fed earlier as surficial deposit feeders. Many of the earliest trilobites are interpreted as deposit feeders or feeding on infaunal prey (Chatterton *et al.* 1994; Fortey & Owens 1999; Bush & Bambach 2011; Kraft *et al.* 2023), although powerfully bioturbating deposit feeders were of minor importance until the Silurian (Tarhan & Droser 2014; Tarhan *et al.* 2015). A large number of small, vermiform bilaterians were fully infaunal (Tarhan *et al.* 2015; Buatois *et al.* 2020). Thus, the new life habits mentioned above are solely novel in the context of echinoderm evolution.

Most novel echinoderm habits were invented during two pulses. The first occurred at the origins of the phylum (in the Terreneuvian, or at their first appearance in the fossil record at the base of Series 2), when most iconic echinoderm life habits existed. The second pulse occurred in the latest Cambrian (terminal Furongian), just before or perhaps coincident with the base of the Ordovician, and is associated primarily with the origins of asterozoans, crinoids and several other classes. Subsequent evolution in each period primarily involved new combinations of these novel habits. These two intervals of enhanced evolution are captured in the per-lineage rate of life-habit character change (Novack-Gottshall *et al.* 2022), with three pulses occurring in the early Terreneuvian, mid Cambrian (Series 2 – Miaolingian), and late Furongian (Stage 10), and reflected by increasing ecological disparity at these times (Novack-Gottshall *et al.* 2022). The pace of ecological evolution was reduced throughout the Ordovician, but the consistent diversification of many new lineages continued to increase ecological disparity. These pulses also coincide with when most of the inflection points in the life-habit trends presented herein occur (Figs 4, 5, S3, S4).

Additional context for the nature of echinoderm ecological novelty is provided by variability in the rates at which individual characters evolved. The slowest-evolving characters (Novack-Gottshall *et al.* 2022, suppl. table 4) involved foraging habit, diet, food condition, and location of food (chars 23–40, excluding char. 32; Table 1), as well as mode of reproduction (chars 7, 8) and microhabitat affinity (chars 10, 11, 14, 17–22). All of these characters tend to be shared across most members of a taxonomic class, and are generally proportionally unchanging through time (Figs 4, 5, S3–S5). These patterns amplify claims that feeding and habitat strategies are largely set during the origins of major taxa (Slater *et al.* 2010; Price *et al.* 2012; Hopkins & Smith 2015; Slater & Friscia 2019).

In contrast, the significantly fastest-evolving characters involved body size, complexity of the filter-feeding organ, mobility, characters related to distance from the seafloor or from where food is located, and, to a lesser extent, substrate preferences and whether attached or free-living (chars 1–6, 12, 13, 15, 16, 32). Part of the rate difference is associated with these characters having greater numbers of states (Lloyd *et al.* 2012; Novack-Gottshall *et al.* 2022) or by being covariates of body size or mode of locomotion. However, these characters do genuinely vary across taxa within any given class, and appear to be less constrained by phylogenetic legacy. Body size is also known to evolve faster than other types of organismal trait (Hunt 2007; Harmon *et al.* 2010).

This pattern (of rapid early inception followed by continuing admixture) helps reconcile the notion that early ecological evolution from the Cambrian to the Ordovician was subdued in the face of such major increases in lineage diversity (Bambach *et al.* 2007; Knope *et al.* 2015; Topper *et al.* 2018), at least for early echinoderms. If ecological strategies for a clade are fundamentally set at their origins, and if later evolving clades are pursuing ecological strategies that are either convergent with or involve new combinations of pre-existing habits, then later intervals of evolution will be ecologically redundant to prior intervals, even if there is substantial turnover in constituent clades.

From the Cambrian to the Ordovician, there was an approximate 300–400% increase in the number of unique life habits inhabited by early echinoderms, depending on the time-scaling method used (Fig. 1B). This is much greater than the 43–80% increase previously reported for other taxa (Bambach *et al.* 2007; Knope *et al.* 2015; Topper *et al.* 2018). Much of the discrepancy is explained by the different number of character dimensions considered by each study. The earlier studies were styled upon the same three-dimensional ecospace framework (Bambach *et al.* 2007; Bush *et al.* 2007; based on Bambach 1983). By comparison, the framework used herein has 40 characters (facilitating more subtle life-habit distinctions, as well as additional habitat characters not included in the prior ones) that allow for more life habits to be recognized. Given these differences, it is not surprising to find fewer changes through time in the smaller frameworks. The strength of the simpler, more intuitive frameworks is that they are well suited to categorizing major adaptive strategies, but less suited to recognizing subtle but ecologically important variations on these strategies.

This can be demonstrated with our data. When the 87 Cambrian echinoderms (including tips only and PBDB ranges) with 33 unique life habits are coded into the 'ecocube' framework (Bambach *et al.* 2007; Bush *et al.* 2007), they represent just 8 modes of life (Fig. S7). Ordovician echinoderms represent 13 modes of life, a 63% increase consistent with other studies, with most of the increase due to the addition of echinozoans and asterozoans (Appendix S2). Thus, the simpler frameworks are better suited to capturing major changes in fundamental adaptive strategies (by design: Bambach 1983), particularly when considering a wide range of taxa, some of which are not characterized ecologically in great detail, but less powerful for distinguishing the many minor variations that biologically distinguish the specific life habits occupied by animals (Novack-Gottshall 2016a, 2016b).

All of these studies concur that the major adaptive strategies evolved by a range of animal phyla were set fundamentally during their earliest (Cambrian) origins, with much less novelty during the Ordovician than might be predicted given its dramatic diversification of genera, volatile replacement of classes, and origins of many new orders and subclades. What we contribute to this discussion is the claim that most of the new combinations in life-habit evolution that occur subsequent to their fixation at the origin of each class (i.e. those that are involved in progressive partitioning and minor expansion of life habits; Figs 6, S6) occur primarily among the rapidly evolving characters that are not typically included in alternative ecospace frameworks. During echinoderm evolution, these intervals of combinatorical admixture primarily occurred during the enhanced mid-Cambrian pulse of ecological evolution and throughout the Ordovician, millions of years after the origins of these novel adaptive strategies. Intervening intervals of rampant experimentation among subvariants coincided with dramatic increases in the number of echinoderm genera (and phylogenetic lineages) as well as parallel increases in the number of unique life habits (Fig. 1A, B), and also yielded corresponding increases in ecological disparity (Novack-Gottshall *et al.* 2022). This overall pattern of character recombination is also evident in how these same genera evolved anatomically throughout the Ordovician (Deline *et al.* 2020; Novack-Gottshall *et al.* 2022).

The GOBE records the proliferation of Cambrian clades and life habits more than ecological novelty

Recent studies suggest the Cambrian and Ordovician radiations began earlier than traditionally thought (Servais *et al.* 2016; Servais & Harper 2018; Zhuravlev & Wood 2018, 2020; Darroch *et al.* 2018; Rasmussen *et al.* 2019; Stigall *et al.* 2019), with the Cambrian radiation beginning in the late Ediacaran to Terreneuvian, and the GOBE beginning in the late Cambrian (Furongian). The patterns for echinoderms above (combined with the rates of ecological (and morphological) evolution and records of disparity; Deline *et al.* 2020; Novack-Gottshall *et al.* 2022) are consistent with such claims. Most echinoderm ecological strategies were established rapidly during the origins of the phylum during the Terreneuvian (or base of Series 2), with a secondary pulse of novelty in the terminal Cambrian (or basal Ordovician), coinciding with the origins of major classes. New discoveries of Terreneuvian and Furongian echinoderm fossils are key for documenting these changes, which may be hampered by the poor fossil record (Zamora *et al.* 2013; Smith *et al.* 2013; Harper *et al.* 2019; Du *et al.* 2023).

Other phyla appear to share similar 'novelty' pulses during these epochs. Trilobites, and most arthropod classes, appear to have evolved rapidly during the Terreneuvian, despite similarly lacking unambiguous fossils during this epoch (Lee *et al.* 2013; Paterson *et al.* 2019; Aria 2020). Early brachiopods, molluscs and lophophorates are inferred to have originated during the latest Ediacaran, with crown-group members of these phyla occurring during the early Terreneuvian (Zhuravlev & Wood 2018). Even bryozoans may have originated near this time (Erwin *et al.* 2011; Zhang *et al.* 2021; but see Yang *et al.* 2023). There is little question this is a genuine evolutionary signal of primary Cambrian radiation diversification. Less study has focused on the 'Furongian gap' (Harper *et al.* 2019; Du *et al.* 2023), but emerging evidence suggests a similarly widespread pulse of originations, including the earliest cephalopods (Fang *et al.* 2019), planktonic graptoloids (Servais *et al.* 2016), and possibly rostroconchs and crown-group gastropods, and annelids (Parry *et al.* 2014; Wood & Erwin 2018), in addition to the origins of crinoids, diploporitans, somasteroids, stenuroids, and possibly blastoids inferred here and elsewhere (Lefebvre *et al.* 2013; Ausich *et al.* 2015). Given the many classes and orders whose fossil records first appear in the Tremadocian (Webby *et al.* 2004), it is likely that many other taxa shared Furongian origins.

One hypothesis that has been offered to explain these intervals of heightened taxonomic divergence is that they were driven, in part, by periodic transitions of anoxic–oxic conditions (Wood & Erwin 2018) that also accompany the Permian–Triassic transition. The Furongian records the onset of the major SPICE carbon-isotope excursion that involves global transgression and cycles of dysaerobic/anoxic facies (Zamora *et al.* 2013; Saltzman *et al.* 2015). Similar episodes accompanied the latest Ediacaran to earliest Cambrian transition (Canfield *et al.* 2007; Lyons *et al.* 2014). These intervals of dynamic anoxia followed by enhanced oxygenation have been suggested as possible 'innovation intervals' for driving evolutionary novelty during the Cambrian and Ordovician radiations (Wood & Erwin 2018).

The Furongian, indeed, was a pivotal time in the ecological evolution of echinoderms. Although most early echinoderms were sedentary and attached to hard substrates, progressive partitioning of novel trait combinations during the Miaolingian produced new substrate combinations, such as edrioasteroids attached to microbial softgrounds, as well as the greatest proportion of unattached, soft-substrate echinoderms (primarily small, mobile cinctans) observed during the early Palaeozoic. Holdfast-based attachment styles that typify Ordovician pelmatozoans appear to have first evolved at this time, presumably among eocrinoids (Zamora *et al.* 2010) but perhaps also the earliest crinoids (Brett *et al.* 1983b). These were first restricted to patchy Miaolingian firmgrounds (Zamora *et al.* 2010) but expanded to newly emerging carbonate hardgrounds and flat-pebble conglomerates during the Furongian (Brett *et al.* 1983b; Sprinkle & Guensburg 1995; Sumrall *et al.* 1997). The Furongian also witnessed the earliest proliferation of phytoplankton in the water column (Signor & Vermeij 1994; Servais *et al.* 2016; Servais & Harper 2018; Whalen & Briggs 2018; Pohl *et al.* 2018). Echinoderms, essentially all filter feeders at the time, were beneficiaries of these changes. The Furongian also marks when the earliest actively mobile and partially carnivorous asterozoan echinoderms first evolved.

The transition to the Ordovician ushered in a fundamentally new and more heterogeneous world, and this transition also began in the Furongian. As continents dispersed (Torsvik & Cocks 2013), rising sea levels flooded continents and oceanographic chemistry facilitated the advent of widespread carbonate hardgrounds (Seslavinski & Maidanskaya 2001). Global temperatures become exceptionally hot in the late Cambrian to Early Ordovician, before cooling slightly through the remainder of the Ordovician (Goldberg *et al.* 2021; Grossman & Joachimski 2022). Phytoplankton and zooplankton responded by diversifying within the water column (Signor & Vermeij 1994; Servais *et al.* 2016; Servais & Harper 2018; Whalen & Briggs 2018; Pohl *et al.* 2018).

Echinoderms (most of whose constituent classes had evolved during one of the two Cambrian pulses of ecological novelty) were able to take advantage of these propitious opportunities (Guensburg & Sprinkle 1992, 2001;

Sprinkle & Guensburg 1995; Zamora *et al.* 2010). Fundamentally, the GOBE marks more the diversification of many new genera (within classes of Cambrian origin, and mostly ecological variants of one another rather than pursuing truly novel strategies) instead of a major transition in ecology. As they did during the mid Cambrian, these new genera occupied new combinations of pre-existing life-habit characters, having more diverse body sizes, tiering structures, modes of locomotion, and substrate preferences. Convergent increases in filter-feeding organ complexity (largely within crinoids but also apparent among eocrinoids, paracrinoids, parablastoids and rhombiferans, and associated with increasing size of the food groove; Rozhnov 2002) are probably associated with the increase in phytoplankton availability. Increases in maximum echinoderm body sizes, longer column lengths, and greater tiering variability may also support this conclusion. The advent of mobile and carnivorous asteroids may indicate more stable trophic networks and availability of increased ecosystem energetics (Bush & Pruss 2013; Bush & Payne 2021). More frequent usage of living organisms (largely brachiopods and bryozoans) as substrates (but not yet biohermal reefs) also indicates greater persistence of stable, engineered ecosystems (Erwin & Tweedt 2011; Butterfield 2011; Bush & Payne 2021). Throughout the remainder of the Ordovician, echinoderms increased their number of new life habits three-to-four-fold, adapting to the new conditions occurring throughout the Ordovician world. However, except for the invention of predatory asterozoan habits, and to a lesser extent the mass-feeding habits of asterozoans and echinozoans, all of these life habits involved new combinations of the ways of living that the phylum had invented during the Cambrian. Many of these new life-habit solutions were evolved convergently, typically by members of unrelated classes and subphyla (Novack-Gottshall *et al.* 2022). In this light, the Ordovician radiation of echinoderms primarily records the proliferation of Cambrian clades and life habits more than ecological novelty.

Douglas Erwin (2015, 2021) recently drew a distinction between the concepts of 'novelty' (the origin of new traits) and 'innovation' (their ecological and evolutionary impacts), emphasizing that a temporal lag can occur between the origin of a novel trait and its eventual consequences. Alternatively, exponential diversification also appears to be nearly invisible during its earliest phases before producing great diversity (Sepkoski 1978). There is also no requirement that the evolution of a novelty must result in new functions or the origins of a new taxon (Jablonski 2017; Erwin 2021). However, the ecological patterns apparent among early echinoderms provide evidence for two apparent lags between when new ecological strategies originate and when taxa sharing those traits achieve peak diversity. These lags occur on the order of 10–20 million years, between the Terreneuvian and mid Cambrian and again from the Furongian to the Middle Ordovician. These records confirm a distinction between the evolution of novelty and its later impact, even if that impact is limited to generation of genera instead of higher taxa.

CONCLUSION

Most early echinoderm ecological novelties evolved during the Terreneuvian/Series 2 and, to a lesser extent, late Furongian. These events coincided with the origins of most echinoderm classes, and parallel the origins of higher taxa across many other phyla. Although moderately small and living close to the seafloor, the earliest echinoderms already pursued most of the strategies that define the phylum throughout their Phanerozoic history, including filter-feeders reclining on soft sea floors (or living semi-infaunally) and sedentary ones attached to shelly substrates. The origins of asterozoans close to, or just before, the base of the Ordovician ushered in the novelties of greater mobility, carnivory, and mass-feeding, enhanced slightly later in the Ordovician with the origins of echinozoans and more advanced predatory habits in the asteroids. Ordovician filter feeders diversified in terms of tiering structure, more complex feeding organs, and usage of living substrates, but most of these Ordovician strategies were variations of those that previously existed in the Cambrian. In nearly all these cases, the new strategies were invented by a range of classes, but these pioneers remained at low global genus richness. They would not reach peak diversity in the mid Cambrian, and again in the Middle Ordovician, until 10–20 million years after their inception, when their global genus and life-habit richness increased many times over. In this context, the Cambrian and Ordovician radiations may simply record the consequences of the earlier intervals of ecological novelty that were evolved rapidly by each class (Bambach 1985; Bush & Bambach 2011), but evident and ecologically impactful only later when they were able to capitalize on the permissive environmental milieus in which they now existed. The perceived radiation intervals in the early Palaeozoic may largely represent innovative tinkering with previously invented life-habit combinations rather than the evolution of genuine ecological novelty.

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Author contributions. **Conceptualization** PM Novack-Gottshall (PMN-G), B Deline (BD); **Data Curation** PMN-G, J Purcell (JP), A Sultan (AS), I Ranjha (IR), BD, CD Sumrall (CDS); **Formal Analysis** PMN-G; **Funding Acquisition** PMN-G, BD, CDS; **Investigation** PMN-G, JP, AS, IR, BD, CDS; **Methodology** PMN-G; **Software** PMN-G; **Visualization** PMN-G, BD, CDS; **Writing–Original Draft Preparation** PMN-G; **Writing–Review & Editing** PMN-G, BD, CDS.

DATA ARCHIVING STATEMENT

This is Paleobiology Database official publication 474; the dataset was downloaded on 18 July 2023 and is available here: https://dataverse.harvard.edu/file.xhtml?fileId=7617376&version=2.2. All data and R code scripts for this study are available at https://dataverse.harvard.edu/dataverse/CamOrdEchinoEcology.

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1111/pala.12688):

Appendix S1. References and notes used when coding life-habit characters for the 366 Cambrian and Ordovician echinoderm tip genera.
Appendix S2. Supplementary text providing additional discussion of statistical tests and ancillary results and discussion.
Figure S1. Sample-standardized and raw (non-time-scaled) trends in body size and tiering.
Figure S2. Model support (Akaike weight) for general (biased or driven) and unbiased random walk models for each of the 100 time-scaled phylogenies, sorted by their model support.
Figure S3. Stacked frequency plot of Cambrian–Ordovician echinoderm habitats and modes of locomotion.
Figure S4. Mean and median state values for six life-habit characters.
Figure S5. Stacked frequency plot of Cambrian–Ordovician echinoderm diets and foraging habits.
Figure S6. Echinoderm phyloecospace through the Cambrian and Ordovician periods using the EAT topology.
Figure S7. Echinoderm ecospace during the Cambrian and Ordovician periods, plotted in the 'ecocube' format.

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