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

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 Information, University of Michigan, Ann Arbor, MI, USA.

[5]Current address: School of Law, University of Illinois Chicago, Chicago, IL, USA.

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

Author Manuscript

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/pala.12688

This article is protected by copyright. All rights reserved.

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 paleoecology, functional diversity.

Running head: Early echinoderm ecological novelty

ECHINODERMS diversified more dramatically (phylogenetically, morphologically and ecologically) than any other phylum during the Cambrian and Ordovician radiations (Guensburg and 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

Author Manuscript

of unprecedentedly rapid echinoderm evolution, involving interactions of major anatomical change, novel ecological functionality, and divergence of major lineages. It is natural to assume 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 *etal.* 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 *etal.* 2020). This pace of anatomical innovation ameliorated slightly during the Ordovician, where morphospace 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 involve 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-

Author Manuscript

Palaeozoic brachiopod life habits were essentially unchanged since 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 and Harper 2018; Zhuravlev and 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 through 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).

Author Manuscript

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 *etal.* 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 paleocontinents, 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 and 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 and Bottjer 2000; Dornbos 2006, 2008) has been supplanted with the recognition that

Author Manuscript

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 and Sprinkle 1992; Sprinkle and Guensburg 1995; Sumrall *et al.* 1997; Guensburg and Sprinkle 2001; Zamora *et al.* 2010). Other Ordovician echinoderm groups continued to thrive in soft-substrate conditions (Lefebvre and Fatka 2003), evolved novel strategies for attaching within unconsolidated substrates (Sprinkle and Guensburg 1995; Guensburg and Sprinkle 2001), or adapted to terrigenous-influenced facies (Lefebvre 2007).

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

Author Manuscript

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

Author Manuscript

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 and Rahman 2014) consistent with universal elemental homology (UEH) (e.g. Sumrall and 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 and 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 and Zamora 2009; Wright 2017; Sheffield and 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

Author Manuscript

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 and Zamora 2009; Wright 2017; Sheffield and 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 and 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

Author Manuscript

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, like 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 that 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

Author Manuscript

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 and Calloway 1980; Foote 1994). When visualizing trends, we use the age boundaries of the 2020 ICS timescale, and use Miaolingian instead of Series 3. Analyses, however, use the 2013 timescale boundary dates to match PBDB stratigraphic ranges.

Author Manuscript

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 and 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 paleoecology 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 (Supplementary Appendix 2 of Novack-Gottshall *et al.* 2022) 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

Author Manuscript

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 and Sprinkle 1994; Blake and Koniecki 2020), substrate relationships (e.g. Brett 1978; Guensburg 1991; Zamora and 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 focused explicitly on functional morphology, biomechanics, and paleoecology (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 and 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

Author Manuscript

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 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-by-40 trait matrix is 98.7% complete, on average, across time-scaled

Author Manuscript

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 and St John 2018) to correct for filter-density (character 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 and Novack-Gottshall 2010), which provides a measure of variability in phylogenetic uncertainty regarding temporal ranges as well as ancestral trait

Author Manuscript

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 and 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 analyzed 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 and 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. (Fraley and Raftery 2002, 2007; Fraley *et al.* 2022)

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 versus 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 and Calloway

Author Manuscript

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 and Raup 1996), the magnitude of such range extensions is relatively minor (see Supplementary Information of Novack-Gottshall *et al.* 2022). 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 and 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 artifact 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.

Author Manuscript

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 and Zamora 2013; Zamora *et al.* 2013; Zamora *et al.* 2017) mitigates against casting aside this trend as an simple artefact of differential preservation, sampling, and fossil discovery, although these all operate to some extent. The frequency-ratio method (Foote and Raup 1996) applied to the raw PBDB stratigraphic ranges estimates a 0.835 per-interval sampling probability (see Novack-Gottshall *et al.* 2022, 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, likely reflects 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 mid-to-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 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 artifact of varying sampling intensity, the absolute and relative numbers of life habits continues to increase throughout the Cambrian and Ordovician.

Author Manuscript

Echinoderms diversify 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 (Fig. 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 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 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 and other estimates (Erwin *et al.* 2011; Smith *et al.* 2013; Zamora and 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 (Zamora *et al.* 2020; Topper *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),

Author Manuscript

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 model, 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 artifact of rooting the clade in the informal supertrees as an unresolved polytomy with stromatocystitids and other Cambrian edrioasteroids. Similarly, the time-scaled phylogenies also

Author Manuscript

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

Author Manuscript

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 parablastoids (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 (aca, 2009b; Lefebvre *et al.* 2013), and the Middle Ordovician appear of stem-holothuroid ophiocistioids (Smith and Reich 2013; Rahman *et al.* 2019; Ausich and 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.

Author Manuscript

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 like *Taeniaster* during the Middle Ordovician. Paracrinoids also diversify. Although echinoderm diversity declines with the Late Ordovician mass extinction (and the decline in figure 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 mid 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 cubic centimetres, 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

Author Manuscript

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.(Novack-Gottshall and Wang 2019)

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 ca. 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 and 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 through 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 ca. 10 cubic millimetres (or -2.0 $\log_{10}$ cm^3), the same order of magnitude as the

Author Manuscript

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 and 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; Hunt 2022) support that Cambrian–Ordovician echinoderm body-size evolution is 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

Author Manuscript

Tiering conceptualizes how filter feeders partition space above (and below) the seafloor, traditionally implying some role for competitive displacement in partitioning the water currents (or infaunal habitat) in which these animals collect their food (Lane 1963; Ausich and Bottjer 1982, 1985; Bottjer and 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 than characters in Table 1). Because the majority of early echinoderms are filter-feeders (see Trends in habitat usage below), the trends are likely 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 to 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 standard deviation), 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,

Author Manuscript

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 ca. 250 mm can be ignored as an artifact of a polytomy rooting the Late Ordovician *Cardiocystites* with Cambrian eocrinoids.) No Cambrian echinoderms are known to have lived more than ca. 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 Mid 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 ca. 200 mm: Ubaghs *et al.* 1978; Guensburg and Sprinkle 2003) were only slightly taller than the eocrinoids (e.g. *Rhipidocystis* and *Rhopalocystis*) they co-existed with, and the Early Ordovician crinoid *Trichinocrinus* is likely much shorter than the shortest (ca. 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*.

Author Manuscript

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 millimetres 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 and Zamora 2011). The early early blastoid *Macurdablastus* likely also lived within this tier (Broadhead 1984), although its stem and brachioles are not known. Intermediate heights (50–100 mm) include several shorter crinoids

Author Manuscript

(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 metre above the sea floor (with some claims, see Brett 1984, for scyphocrinitids having stems up to 3 metres 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 (like *Encope*; Durham *et al.* 1966; Lawrence *et al.* 2004; Mancosu and Nebelsick 2013). However, based on records of shallowly buried Late Palaeozoic *Aganaster* (<1 mm; Kokorin 2015) and extant *Amphiura*

Author Manuscript

(*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 for Phanerozoic filter feeders as a whole (Ausich and Bottjer 1982; Bottjer and Ausich 1986; Bush and Bambach 2011), although the current study represents the first (we know of) where direct measurements are analyzed 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 that the earliest epifaunal echinoderms were not ecologically partitioning themselves into discrete tiers, at least

Author Manuscript

when considered at global and epoch-wide scales. Instead, tiering height is best considered 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 and 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.

Author Manuscript

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 (ca. 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 seafloor) is the result of a few ancestral edrioasteroids inferred to have had this lifestyle in some time-scaled phylogenies (Fig. S5A). 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 organism-dwelling echinoderms likely only originated this way of living during the Ordovician (Fig. S3A, C). Similarly, no evidence of wholly infaunal echinoderms are known to have existed 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, S3A,C, S5A). 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 substrate for these echinoderms were shells, bryozoans, or other

Author Manuscript

animals that did not significantly elevate the animal into the water column (Fig. S5B), 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 as the substrate is a firm one (character 12, Table 1; fig. S5C).

There is less of a temporal change in hard versus soft substrate preferences (Fig. S5C), 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. S5D), 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 and Sprinkle 1978; Parsley and 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 likely used more for stability in soft substrates than for permanent attachment (Paul 1968; Mergl and 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 (Fig. 4A, S3C), but they become proportionally less common when compared to all Ordovician microhabitat strategies (Fig. S3A, S5E). These semi-infaunal echinoderms include diverse stylophorans, but also the ctenocystoid *Conollia* (Rahman *et al.* 2015b) and the edrioasteroid *Rhenopyrgus* (Holloway and

Author Manuscript

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, no truly infaunal echinoderms are known until the Silurian origin of stem-apodid *Porosothyone* (Smith and Reich 2013). 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 and 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 (Fig. 4B, S3B,D), typically attached to some hard (whether living or not) substrate (Fig. S5C, D). These sedentary habits were practiced by a diverse group of crinoids, edrioasteroids, eocrinoids, rhombiferans, diploporitans, paracrinoids, helicoplacoids, parablastoids, and even the Cambrian stem-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 (Rahman *et al.* 2020; Friedrich 1993), but several solutes and stenuroids also shared this ability. This habit

Author Manuscript

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 and Strimple 1975; Gorzelak and Zamora 2016; Sumrall 2000), 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 and Guensburg 1993) and persisting in the Ordovician by several predatory asteroids (e.g. *Promopalaeaster* and *Urasterella*; Blake and Guensburg 1994; Blake and 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

Author Manuscript

Ancyrocrinus; Plotnick and Bauer 2014), and the Silurian–Devonian rhombiferan *Lepocrinites* (Brett 1984) also shared this habit. Several Mesozoic crinoids specialized on attaching to floating driftwood (e.g. *Pentacrinites* and *Traumatocrinus*; Ausich *et al.* 1999; Wang *et al.* 2006; Hagdorn *et al.* 2007; Hess 2010; Baumiller and Janevski 2011; Hagdorn and 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 (Fig. 5A, S4A,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–early Ordovician somasteroid *Ophioxenikos*, inferred as a mass-feeding carcass scavenger based on a stout mouth and relatively inflexible arms that would have made manipulating prey difficult (Blake and 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 (Fig. 5B, S4B,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

Author Manuscript

microbivorous and particle-feeding diets (characters 34 and 39, Table 1). However, the complexity of filter-feeding organs increases through time (character 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 and Sprinkle 2001; Brower 2006; Guensburg *et al.* 2020). The only high-density-filtering non-crinoid is the mid-Cambrian eocrinoid *Lyracystis* (Sprinkle and 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

Author Manuscript

habit (Blake and Guensburg 1993), but many time-scaled phylogenies infer 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 (characters 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 and 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 and 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 and Schmidt

Author Manuscript

2001). However, echinoderms herein are coded in this manner only when it accounts for their primary feeding strategy (c.f., 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. S5F). 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. S5F). 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 and Guensburg 1994; Blake and 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,

Author Manuscript

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; and
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 and 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

Author Manuscript

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 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 cubic cm 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 cubic cm), 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 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

Author Manuscript

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 and 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—like 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.

Author Manuscript

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) through 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; Ausich *et al.* 2015; Blake *et al.* 2016; Blake 2018; Sheffield and Sumrall 2019), and the poor Furongian echinoderm fossil record (Zamora *et al.* 2013; Sumrall *et al.* 1997). The life habits for these new Furongian classes continued the Cambrian trend of ongoing partitioning of preexisting strategies (Fig. 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

Author Manuscript

above, which also have the effect of substantially increasing ecological (and anatomical) disparity of the entire phylum (Novack-Gottshall *et al.* 2022; Deline *et al.* 2020). 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 and 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 their origins were likely 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 and Sprinkle 2001), a greater range of body sizes and stem lengths,

Author Manuscript

and thus a greater differentiation in tiering structure and characters often related to body size (e.g. characters 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 (ca. 150 mm) atop conulariids (Sumrall and 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-to-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

Author Manuscript

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 Extended Data Fig. 3 of Novack-Gottshall *et al.* 2022), 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 through today (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,

Author Manuscript

are associated with stromatolite bioherms that offered a firm substrate for attachment (Brett *et al.* 1983b; Zamora *et al.* 2017; Rozhnov 2019). Fully infaunal habits do not evolve until the advent of Silurian holothuroids, and 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 and Collins 2015) attached to living substrates by the mid Cambrian, and possibly *Namapoikia* did so atop Ediacaran thrombolitic and stromatolitic mats (Wood and Penny 2018). Hyolithids (Liu *et al.* 2021), gastropods (Thomas *et al.* 2020), helcionelloids (Gubanov and Peel 2000), diverse stem annelids (Parry *et al.* 2014), and other Cambrian animals likely 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 and Owens 1999; Bush and Bambach 2011; Kraft *et al.* 2023), although powerfully bioturbating deposit feeders were of minor importance until the Silurian (Tarhan *et al.* 2015; Tarhan and Droser 2014). 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

Author Manuscript

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 4–7).

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 (Supplementary Table 4 of Novack-Gottshall *et al.* 2022) involved foraging habit, diet, food condition, and location of food (characters 23–40, excluding no. 32; Table 1), as well as mode of reproduction (characters 7–8) and microhabitat affinity (characters 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 and Smith 2015; Slater and 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

Author Manuscript

where food is located, and, to a lesser extent, substrate preferences and whether attached or free-living (characters 1–6, 12, 13, 15, 16, and 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 traits (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

Author Manuscript

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 284 Cambrian echinoderms (including tips and nodes) with 75 unique life habits (averaged across our time-scaled phylogenies) 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, b).

All 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—that is, that are involved in progressive partitioning and minor expansion of life habits (Fig. 6, S6)—occur primarily among the rapidly evolving characters that are not typically included in alternative

Author Manuscript

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 and Harper 2018; Zhuravlev and Wood 2018; 2020; Darroch *et al.* 2018; Rasmussen *et al.* 2019; Stigall *et al.* 2019), with the Cambrian radiation beginning in the late Ediacaran–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

Author Manuscript

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, mollusks, and lophophorates are inferred as originating during the latest Ediacaran, with crown-group members of these phyla occurring during the early Terreneuvian (Zhuravlev and 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 and 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 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 and Erwin 2018), and that also accompany the Permian-Triassic. 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

Author Manuscript

accompanied the latest Ediacaran–earliest Cambrian (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 and 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 and Guensburg 1995; Sumrall *et al.* 1997). The Furongian also witnessed the earliest proliferation of phytoplankton in the water column (Signor and Vermeij 1994; Servais *et al.* 2016; Servais and Harper 2018; Whalen and 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 Trond and Cocks 2013), rising sea levels flooded continents and oceanographic chemistry facilitated

Author Manuscript

the advent of widespread carbonate hardgrounds (Seslavinski and Maidanskaya 2001). Global temperatures become exceptionally hot in the late Cambrian through Early Ordovician, before cooling slightly through the remainder of the Ordovician (Goldberg *et al.* 2021; Grossman and Joachimski 2022). Phytoplankton and zooplankton responded by diversifying within the water column (Signor and Vermeij 1994; Servais *et al.* 2016; Servais and Harper 2018; Whalen and 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 and Sprinkle 1992; Sprinkle and Guensburg 1995; Guensburg and Sprinkle 2001; Zamora *et al.* 2010). Fundamentally, the GOBE marks more the diversification of many new genera—within classes of Cambrian origins, and mostly ecological variants of one another rather than pursuing truly novel strategies—instead of a major transition in ecology. Like 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 likely 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 and Pruss 2013; Bush and 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

Author Manuscript

ecosystems (Erwin and Tweedt 2011; Butterfield 2011; Bush and 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.

Author Manuscript

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 and 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.

Author Manuscript

Acknowledgements. We thank Nick Smith, Kathryn Hanson, Rachel Lively, Clayton Collins, and Runeshia Parker for discussion; Ron Parsley, Bill Ausich, and Lena Cole for discussion of echinoderm life habits; Gary Motz, David Polly, Claudia Johnson (Indiana University) for access to museum collections; Scott Lidgard, Ken Angielczyk, Paul Mayer, Olivier Rieppel, and Thorsten Lumbsch for access to the Field Museum Library; Silvia Larrondo for locating rare publications; Gene Hunt, Graeme Lloyd, Melanie Hopkins, David Bapst, and Liam Revell for programming and analytical advice; J. Sepkoski, P. Wagner, V. Villier, D. van Oyen, B. Kröger, S. Finnegan, A. Lin, B. Mamo, D. Mathieson, F. Fearnhead, U. Merkel, V. Syverson, S. Cole, G. Webster, and 17 others who contributed data to the PBDB. BD was supported by 'Assembling the Echinoderm Tree of Life' supplementary grants NSF #1036416 and #1036356 and Benjamin Meaker Visiting Professorship and University of West Georgia Faculty Research Grants. CDS was supported by NSF #1036260, 1213530, 1314236 and 1519658. PMN-G was supported by NSF grant #2322080, Indiana University Summer Repository Research Fellowship and sabbatical fellowships supported by Robin Rylaarsdam, Jayashree Sarathy, Cheryl Heinz, Bart Ng, William Law, Cheryl Mascarenhas, Maria de la Cámara, Kenneth Newbold, and Benedictine University Faculty Development Committee. Andy Bush provided permission to use the 'ecocube' figure. We sincerely thank him, an anonymous reviewer, and Editor Jeff Thompson for their thorough, thoughtful, and critical reviews that substantially improved this work.

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;

Author Manuscript

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.

Supporting information

Additional supporting information can be found online:

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 (A, C) habitats and (B, D) modes of locomotion.

Figure S4. Stacked frequency plot of Cambrian–Ordovician echinoderm (A, C) diets and (B, D) foraging habits.

Figure S5. Mean and median state values for six life-habit characters.

Figure S6. Echinoderm phyloecospace through the Cambrian and Ordovician periods using the EAT topology.

Figure S7. Echinoderm ecospace during the (A) Cambrian and (B) Ordovician periods, plotted in the 'ecocube' format.

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.

Author Manuscript

FIGURE CAPTIONS

FIG. 1. Diversity trends through time for Cambrian–Ordovician echinoderms. Figure parts 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. Series names for this and subsequent figures are abbreviated from Terreneuvian, Series 2, Miaolingian, Furongian, and Lower, Mid, and Upper Ordovician; stages are illustrated but not labelled.

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 Fig. 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

Author Manuscript

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 Extended Data Fig. 1c in Novack-Gottshall *et al.* 2022 for a version of this data using PBDB stratigraphic ranges without time-scaling.)

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 gray 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 Mid-Late Ordovician are represented with 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).

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

Author Manuscript

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 Fig. 1A. A. Habitats, using combinations of characters 2, 9–11, and 17–18 (Table 1; See Data and Methods 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.

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 Fig. 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.

Author Manuscript

Figure 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 than 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 Fig. 2 of Novack-Gottshall et al. (2022), which provides additional context.

Data archiving statement

Author Manuscript

This is Paleobiology Database official publication XXX; the dataset was downloaded on 18 July 2023 and is available here: https://paleobiodb.org/data1.2/occs/taxa.csv?base_name=Echinodermata&rank=genus&interval=Cambrian,Devonian&show=app,entname. All data and R code scripts for this study are available at https://dataverse.harvard.edu/dataverse/CamOrdEchinoEcology.

REFERENCES

ÁLVARO, J. J., ZAMORA, S., CLAUSEN, S., VIZCAÏNO, D. and SMITH, A. B. 2013. The role of abiotic factors in the Cambrian Substrate Revolution: A review from the benthic community replacements of West Gondwana. *Earth-Science Reviews*, **118**, 69-82.

ARIA, C. 2020. Macroevolutionary patterns of body plan canalization in euarthropods. *Paleobiology*, **46**, 569-593.

AUSICH, W. I. 1978. Community organization, paleontology, and sedimentology of the lower Mississippian Borden Delta platform (Edwardsville Formation, Southern Indiana). Unpublished PhD thesis, Indiana University.

AUSICH, W. I. 1986. Palaeoecology and history of the Calceocrinidae (Palaeozoic Crinoidea). *Palaeontology*, **29**, 85-99.

AUSICH, W. I. and BOTTJER, D. J. 1982. Tiering in suspension feeding communities on soft substrata throughout the Phanerozoic. *Science*, **216**, 173-174.

AUSICH, W. I. and BOTTJER, D. J. 1985. Phanerozoic tiering in suspension-feeding communities on soft substrate: Implications for diversity. *In* VALENTINE, J. W. (ed.) *Phanerozoic diversity patterns: Profiles in macroevolution*. Princeton University Press.

Author Manuscript

AUSICH, W. I. and THOMPSON, J. R. 2021. A possible Laurentian volchoviid ophiocistioid from the Katian of southwestern Ohio. *Journal of Paleontology*, **95**, 1097-1098.

AUSICH, W. I., BRETT, C. E., HESS, H. and SIMMS, M. J. 1999. Crinoid form and function. 3-30. *In* HESS, H., AUSICH, W. I., BRETT, C. E. and SIMMS, M. J. (eds). *Fossil crinoids*. Cambridge University Press, 300 pp.

AUSICH, W. I., KAMMER, T. W., RHENBERG, E. C. and WRIGHT, D. F. 2015. Early phylogeny of crinoids within the pelmatozoan clade. *Palaeontology*, 937-952.

BAMBACH, R. K. 1983. Ecospace utilization and guilds in marine communities through the Phanerozoic. 719–746. *In* TEVESZ, M. J. S. and McCALL, P. L. (eds). *Biotic interactions in Recent and fossil benthic communities*. Plenum.

BAMBACH, R. K. 1985. Classes and adaptive variety: the ecology of diversification in marine faunas through the Phanerozoic. 191–253. *In* VALENTINE, J. W. (ed.) *Phanerozoic diversity patterns: Profiles in macroevolution.* Princeton University Press.

BAMBACH, R. K., BUSH, A. M. and ERWIN, D. H. 2007. Autecology and the filling of ecospace: key metazoan radiations. *Palaeontology*, **50**, 1-22.

BAPST, D. W. 2013. A stochastic rate-calibrated method for time-scaling phylogenies of fossil taxa. *Methods in Ecology and Evolution*, **4**, 724-733.

BAPST, D. W. 2014. Assessing the effect of time-scaling methods on phylogeny-based analyses in the fossil record. *Paleobiology*, **40**, 331-351.

BAPST, D. W. and HOPKINS, M. J. 2016. Comparing cal3 and other a posteriori time-scaling approaches in a case study with the pterocephaliid trilobites. *Paleobiology*, **43**, 49-67.

Author Manuscript

BAUER, J. E., WATERS, J. A. and SUMRALL, C. D. 2019. Redescription of *Macurdablastus* and redefinition of Eublastoidea as a clade of Blastoidea (Echinodermata). *Palaeontology*, **62**, 1003-1013.

BAUMILLER, T. K. 2008. Crinoid ecological morphology. *Annual Review of Earth and Planetary Sciences*, **36**, 221-249.

BAUMILLER, T. K. and JANEVSKI, G. A. 2011. On the swimming function of crinoid cirri. *Swiss Journal of Palaeontology*, **130**, 19-24.

BEAVER, H. H., CASTER, K. E., DURHAM, J. W., FAY, R. O., FELL, H. B., KESLING, R. V., D.B. MACURDA Jr, MOORE, R. C., UBAGHS, G. and WANNER, J. 1967. *Treatise on Invertebrate Paleontology. Part S. Echinodermata 1. General characters, Homalozoa–Crinozoa (except Crinoidea), vols 1–2.* Geological Society of America & University of Kansas Press.

BELL, B. M. and SPRINKLE, J. 1978. *Totiglobus*, an unusual new edrioasteroid from the Middle Cambrian of Nevada. *Journal of Paleontology*, **52**, 243-266.

BENGTSON, S. and COLLINS, D. 2015. Chancelloriids of the Cambrian Burgess Shale. *Palaeontologia Electronica*, **18**, 1-67.

BILLETT, D., HANSEN, B. and HUGGETT, Q. 2020. Pelagic Holothurioidea (Echinodermata) of the northeast Atlantic. 399-411. *Echinodermata*. CRC Press, 662 pp.

BLAKE, D. B. 2013. Early asterozoan (Echinodermata) diversification: A paleontologic quandary. *Journal of Paleontology*, **87**, 353-372.

BLAKE, D. B. 2018. Toward a history of the Paleozoic Asteroidea (Echinodermata). *Bulletins of American Paleontology*, **394**, 1-93.

Author Manuscript

BLAKE, D. B. and GUENSBURG, T. E. 1993. New Lower and Middle Ordovician stelleroids (Echinodermata) and their bearing on the origins and early history of the stelleroid echinoderms. *Journal of Paleontology*, **67**, 103-113.

BLAKE, D. B. and GUENSBURG, T. E. 1994. Predation by the Ordovician asteroid *Promopalaeaster* on a pelecypod. *Lethaia*, **27**, 235-239.

BLAKE, D. B. and KONIECKI, J. 2020. Taxonomy and functional morphology of the Urasterellidae (Paleozoic Asteroidea, Echinodermata). *Journal of Paleontology*, 1-24.

BLAKE, D. B. and ROZHNOV, S. 2007. Aspects of life mode among Ordovician asteroids: implications of new specimens from Baltica. *Acta Palaeontologica Polonica*, **52**, 519-533.

BLAKE, D. B., GUENSBURG, T. E. and LEFEBVRE, B. 2016. New Early Paleozoic Asterozoa (Echinodermata) from the Armorican Massif, France, and the western United States. *Annales de Paléontologie*, **102**, 161-181.

BOTTJER, D. J. 2010. The Cambrian substrate revolution and early evolution of the phyla. *Journal of Earth Science*, **21**, 21-24.

BOTTJER, D. J. and AUSICH, W. I. 1986. Phanerozoic development of tiering in soft substrata suspension-feeding communities. *Paleobiology*, **12**, 400-420.

BRETT, C. E. 1978. Attachment structures in the rhombiferan cystoid *Caryocrinites* and their paleobiological implications. *Journal of Paleontology*, **52**, 717-726.

BRETT, C. E. 1980. *Paracolocrinus*, a new inadunate crinoid genus from the Rochester Shale (Silurian, Wenlockian) of New York. *Journal of Paleontology*, **54**, 913-922.

Author Manuscript

BRETT, C. E. 1984. Autecology of Silurian pelmatozoan echinoderms. 87-120. *In* BASSETT, M. G. and LAWSON, J. D. (eds). *Autecology of Silurian organisms*. Palaeontological Association, Special Papers in Palaeontology, **32**, 295 pp.

BRETT, C. E., FREST, T. J., SPRINKLE, J. and CLEMENT, C. R. 1983a. Coronoidea: a new class of blastozoan echinoderms based on taxonomic reevaluation of *Stephanocrinus*. *Journal of Paleontology*, **57**, 627-651.

BRETT, C. E., LIDDELL, W. D. and DERSTLER, K. L. 1983b. Late Cambrian hard substrate communities from Montana/Wyoming: the oldest known hardground encrusters. *Lethaia*, **16**, 281-289.

BRETT, C. E., MOFFAT, H. A. and TAYLOR, W. L. 1997. Echinoderm taphonomy, taphofacies, and Lagerstätten. 147-190. *In* WATERS, J. A. and MAPLES, C. G. (eds). *Geobiology of echinoderms*. Paleontological Society Papers, **3**.

BROADHEAD, T. W. 1984. *Macurdablastus*, a middle Ordovician blastoid from the southern Appalachians. *University of Kansas Paleontological Contributions*, **110**, 1-9.

BROADHEAD, T. W. and STRIMPLE, H. L. 1975. Respiration in a vagrant Ordovician cystoid, *Amecystis*. *Paleobiology*, **1**, 312-319.

BROWER, J. C. 2006. Ontogeny of the food-gathering system in Ordovician crinoids. *Journal of Paleontology*, **80**, 430-446.

BROWER, J. C. 2011. Paleoecology of suspension-feeding echinoderm assemblages from the Upper Ordovician (Katian, Shermanian) Walcott-Rust Quarry of New York. *Journal of Paleontology*, **85**, 369-391.

Author Manuscript

BRUSATTE, S. L., MONTANARI, S., YI, H.-Y. and NORELL, M. A. 2011. Phylogenetic corrections for morphological disparity analysis: new methodology and case studies. *Paleobiology*, **37**, 1-22.

BUATOIS, L. A., CARMONA, N. B., CURRAN, H. A., NETTO, R. G., MÁNGANO, M. G. and WETZEL, A. 2016. The Mesozoic Marine Revolution. 19-134. *In* MÁNGANO, M. G. and BUATOIS, L. A. (eds). *The trace-fossil record of major evolutionary events. Vol. 2: Mesozoic and Cenozoic*. Springer.

BUATOIS, L. A., MÁNGANO, M. G., MINTER, N. J., ZHOU, K., WISSHAK, M., WILSON, M. A. and OLEA, R. A. 2020. Quantifying ecospace utilization and ecosystem engineering during the early Phanerozoic—The role of bioturbation and bioerosion. *Science Advances*, **6**, eabb0618.

BUSH, A. M. and BAMBACH, R. K. 2011. Paleoecologic megatrends in marine Metazoa. *Annual Review of Earth and Planetary Sciences*, **39**, 241-269.

BUSH, A. M. and PAYNE, J. L. 2021. Biotic and abiotic controls on the Phanerozoic history of marine animal biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **52**, 269-289.

BUSH, A. M. and PRUSS, S. B. 2013. Theoretical ecospace for ecosystem paleobiology: energy, nutrients, biominerals, and macroevolution. 1-20. *In* BUSH, A. M., PRUSS, S. B. and PAYNE, J. L. (eds). *Ecosystem paleobiology and geobiology*. Paleontological Society & Paleontological Research Institute, Short Courses in Paleontology, **19**.

BUSH, A. M., BAMBACH, R. K. and DALEY, G. M. 2007. Changes in theoretical ecospace utilization in marine fossil assemblages between the mid-Paleozoic and late Cenozoic. *Paleobiology*, **33**, 76-97.

Author Manuscript

BUTTERFIELD, N. J. 2011. Animals and the invention of the Phanerozoic Earth system. *Trends in Ecology & Evolution*, **26**, 81-87.

CANFIELD, D. E., POULTON, S. W. and NARBONNE, G. M. 2007. Late-Neoproterozoic deep-ocean oxygenation and the rise of animal life. *Science*, **315**, 92-95.

CHATTERTON, B. D. E., JOHANSON, Z. and SUTHERLAND, G. 1994. Form of the trilobite digestive system: alimentary structures in *Pterocephalia*. *Journal of Paleontology*, **68**, 294-305.

CLAUSEN, S. 2004. New Early Cambrian eocrinoids from the Iberian Chains (NE Spain) and their role in nonreefal benthic communities. *Eclogae Geologicae Helvetiae*, **97**, 371-379.

COHEN, K. M., FINNEY, S. C., GIBBARD, P. L. and FAN, J.-X. 2013. The ICS International Chronostratigraphic Chart. *Episodes*, **36**, 199-204.

COLE, S. R. and HOPKINS, M. J. 2021. Selectivity and the effect of mass extinctions on disparity and functional ecology. *Science Advances*, **7**, eabf4072.

COLE, S. R., AUSICH, W. I., WRIGHT, D. F. and KONIECKI, J. M. 2018. An echinoderm Lagerstätte from the Upper Ordovician (Katian), Ontario: taxonomic re-evaluation and description of new dicyclic camerate crinoids. *Journal of Paleontology*, **92**, 488-505.

COLE, S. R., WRIGHT, D. F. and AUSICH, W. I. 2019. Phylogenetic community paleoecology of one of the earliest complex crinoid faunas (Brechin Lagerstätte, Ordovician). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **521**, 82-98.

CORDIE, D. R., DORNBOS, S. Q., MARENCO, P. J., OJI, T. and GONCHIGDORJ, S. 2019. Depauperate skeletonized reef-dwelling fauna of the early Cambrian: Insights from archaeocyathan reef ecosystems of western Mongolia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **514**, 206-221.

Author Manuscript

DALEY, P. E. J. 1995. Anatomy, locomotion and ontogeny of the solute *Castericystis vali* from the Middle Cambrian of Utah. *Geobios*, **28**, 585-614.

DALEY, P. E. J. 1996. The first solute which is attached as an adult: a Mid-Cambrian fossil from Utah with echinoderm and chordate affinities. *Zoological Journal of the Linnean Society*, **117**, 405-440.

DARROCH, S. A. F., SMITH, E. F., LAFLAMME, M. and ERWIN, D. H. 2018. Ediacaran extinction and Cambrian explosion. *Trends in Ecology & Evolution*, **33**, 653-663.

DAVID, B., LEFEBVRE, B., MOOI, R. and PARSLEY, R. 2000. Are homalozoans echinoderms? An answer from the extraxial-axial theory. *Paleobiology*, **26**, 529-555.

DEAKER, D. J., AGÜERA, A., LIN, H.-A., LAWSON, C., BUDDEN, C., DWORJANYN, S. A., MOS, B. and BYRNE, M. 2020. The hidden army: corallivorous crown-of-thorns seastars can spend years as herbivorous juveniles. *Biology Letters*, **16**, 20190849.

DEAN, J. 1999. What makes an ophiuroid? A morphological study of the problematic Ordovician stelleroid *Stenaster* and the palaeobiology of the earliest asteroids and ophiuroids. *Zoological Journal of the Linnean Society*, **126**, 225-250.

DELINE, B., THOMPSON, J. R., SMITH, N. S., ZAMORA, S., RAHMAN, I. A., SHEFFIELD, S. L., AUSICH, W. I., KAMMER, T. W. and SUMRALL, C. D. 2020. Evolution and development at the origin of a phylum. *Current Biology*, **30**, 1672-1679.

DONOVAN, S. K. and SCHMIDT, D. A. 2001. Survival of crinoid stems following decapitation: evidence from the Ordovician and palaeobiological implications. *Lethaia*, **34**, 263-270.

Author Manuscript

DORNBOS, S. Q. 2006. Evolutionary palaeoecology of early epifaunal echinoderms: Response to increasing bioturbation levels during the Cambrian radiation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **237**, 225-239.

DORNBOS, S. Q. 2008. Tiering history of early epifaunal suspension-feeding echinoderms. 132-143. *In* AUSICH, W. I. and WEBSTER, G. D. (eds). *Echinoderm paleobiology*. Indiana University Press.

DORNBOS, S. Q. and BOTTJER, D. J. 2000. Evolutionary paleoecology of the earliest echinoderms: Helicoplacoids and the Cambrian substrate revolution. *Geology*, **28**, 839-842.

DU, M., LI, H., TAN, J., WANG, Z. and WANG, W. 2023. The bias types and drivers of the Furongian Biodiversity Gap. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **612**, 111394.

DURHAM, J. W., CASTER, K. E., EXLINE, H., FELL, H. B., FISCHER, A. G., FRIZZELL, D. L., KESLING, R. V., KIER, P. M., MELVILLE, R. V., MOORE, R. C., PAWSON, D. L., REGNÉLL, G., SPENCER, W. K., UBAGHS, G., WAGNER, C. D. and WRIGHT, C. W. 1966. *Treatise on Invertebrate Paleontology. Part U. Echinodermata 3, Asterozoa–Echinozoa, vols 1–2*. Geological Society of America & University of Kansas Press, 695 pp.

DZIK, J. and ORŁOWSKI, S. 1993. The Late Cambrian eocrinoid *Cambrocrinus*. *Acta Palaeontologica Polonica*, **38**, 21-34.

ERWIN, D. H. 2015. Novelty and innovation in the history of life. *Current Biology*, **25**, 930-940.

ERWIN, D. H. 2021. A conceptual framework of evolutionary novelty and innovation. *Biological Reviews*, **96**, 1-15.

Author Manuscript

ERWIN, D. H. and TWEEDT, S. 2011. Ecological drivers of the Ediacaran–Cambrian diversification of Metazoa. *Evolutionary Ecology*, **26**, 417-433.

ERWIN, D. H., LAFLAMME, M., TWEEDT, S. M., SPERLING, E. A., PISANI, D. and PETERSON, K. J. 2011. The Cambrian conundrum: early divergence and later ecological success in the early history of animals. *Science*, **334**, 1091-1097.

EWIN, T. A. M., MARTIN, M., ISOTALO, P. and ZAMORA, S. 2020. New rhenopyrgid edrioasteroids (Echinodermata) and their implications for taxonomy, functional morphology, and paleoecology. *Journal of Paleontology*, **94**, 115-130.

FANG, X., KRÖGER, B., ZHANG, Y.-D., ZHANG, Y.-B. and CHEN, T.-E. 2019. Palaeogeographic distribution and diversity of cephalopods during the Cambrian–Ordovician transition. *Palaeoworld*, **28**, 51-57.

FATKA, O. and KORDULE, V. 1985. *Etoctenocystis bohemica* gen. et sp. nov.--new ctenocystoid from Czechoslovakia (Echinodermata, Middle Cambrian). *Věstník Ústředního ústavu geologického*, **60**, 225-229.

FERGUSON, J. C. 1982. A comparative study of the net metabolic benefits derived from the uptake and release of free amino acids by marine invertebrates. *The Biological Bulletin*, **162**, 1-17.

FOOTE, M. 1994. Morphological disparity in Ordovician-Devonian crinoids and the early saturation of morphological space. *Paleobiology*, **20**, 320-344.

FOOTE, M. and RAUP, D. M. 1996. Fossil preservation and the stratigraphic ranges of taxa. *Paleobiology*, 121-140.

FORTEY, R. A. and OWENS, R. M. 1999. Feeding habits in trilobites. *Palaeontology*, **42**, 429-465.

Author Manuscript

FRALEY, C. and RAFTERY, A. E. 2002. Model-based clustering, discriminant analysis, and density estimation. *Journal of the American Statistical Association*, **97**, 611-631.

FRALEY, C. and RAFTERY, A. E. 2007. Bayesian regularization for normal mixture estimation and model-based clustering. *Journal of Classification*, **24**, 155-181.

FRALEY, C., RAFTERY, A. E. and SCRUCCA, L. 2022. mclust: Gaussian mixture modelling for model-based clustering, classification, and density estimation. R package 6.0.0. https://cran.r-project.org/package=mclust.

FRIEDRICH, W.-P. 1993. Systematik und Funktionsmorphologie mittelkambrischer Cincta (Carpoidea, Echinodermata). *Beringeria*, **7**, 1-190.

GOLDBERG, S. L., PRESENT, T. M., FINNEGAN, S. and BERGMANN, K. D. 2021. A high-resolution record of early Paleozoic climate. *Proceedings of the National Academy of Sciences*, **118**, e2013083118.

GOLDBERG, W. M. 2013. *The biology of reefs and reef organisms*. University of Chicago Press, 401 pp.

GORZELAK, P. and ZAMORA, S. 2016. Understanding form and function of the stem in early flattened echinoderms (pleurocystitids) using a microstructural approach. *PeerJ*, **4**, e1820.

GORZELAK, P., KOŁBUK, D., SALAMON, M. A., ŁUKOWIAK, M., AUSICH, W. I. and BAUMILLER, T. K. 2020. Bringing planktonic crinoids back to the bottom: Reassessment of the functional role of scyphocrinoid loboliths. *Paleobiology*, **46**, 104-122.

GOULD, S. J. 1988. Trends as changes in variance: a new slant on progress and directionality in evolution. *Journal of Paleontology*, **62**, 319-329.

Author Manuscript

GOULD, S. J. and CALLOWAY, C. B. 1980. Clams and brachiopods: ships that pass in the night. *Paleobiology*, **6**, 383-396.

GROSSMAN, E. L. and JOACHIMSKI, M. M. 2022. Ocean temperatures through the Phanerozoic reassessed. *Scientific Reports*, **12**, 8938.

GUBANOV, A. P. and PEEL, J. S. 2000. Cambrian monoplacophoran molluscs (Class Helcionelloida). *American Malacological Bulletin*, **15**, 139-145.

GUENSBURG, T. E. 1988. Systematics, functional morphology, and life modes of Late Ordovician edrioasteroids, Orchard Creek Shale, southern Illinois. *Journal of Paleontology*, **62**, 110-126.

GUENSBURG, T. E. 1991. The stem and holdfast of *Amygdalocystites florealis* Billings, 1854 (Paracrinoidea): lifestyle implications. *Journal of Paleontology*, **65**, 693-695.

GUENSBURG, T. E. and SPRINKLE, J. 1992. Rise of echinoderms in the Paleozoic evolutionary fauna: significance of paleoenvironmental controls. *Geology*, **20**, 407-410.

GUENSBURG, T. E. and SPRINKLE, J. 1994. Revised phylogeny and functional interpretation of the Edrioasteroidea based on new taxa from the Early and Middle Ordovician of western Utah. *Fieldiana (Geology)*, **29**, 1-43.

GUENSBURG, T. E. and SPRINKLE, J. 2001. Ecologic radiation of Cambro-Ordovician echinoderms. 428-444. *In* ZHURAVLEV, A. I. U. and RIDING, R. (eds). *The ecology of the Cambrian radiation*. Columbia University Press.

GUENSBURG, T. E. and SPRINKLE, J. 2003. The oldest known crinoids (Early Ordovician, Utah) and a new crinoid plate homology system. *Bulletins of American Paleontology*, **264**, 1-43.

Author Manuscript

GUENSBURG, T. E., SPRINKLE, J., MOOI, R., LEFEBVRE, B., DAVID, B., ROUX, M. and DERSTLER, K. 2020. Athenacrinus n. gen. and other early echinoderm taxa inform crinoid origin and arm evolution. *Journal of Paleontology*, **94**, 311-333.

GUILLERME, T. and COOPER, N. 2018. Time for a rethink: time sub-sampling methods in disparity-through-time analyses. *Palaeontology*, **61**, 481-493.

GUILLERME, T., COOPER, N., BRUSATTE, S. L., DAVIS, K. E., JACKSON, A. L., GERBER, S., GOSWAMI, A., HEALY, K., HOPKINS, M. J., JONES, M. E. H., LLOYD, G. T., O'REILLY, J. E., PATE, A., PUTTICK, M. N., RAYFIELD, E. J., SAUPE, E. E., SHERRATT, E., SLATER, G. J., WEISBECKER, V., THOMAS, G. H. and DONOGHUE, P. C. J. 2020. Disparities in the analysis of morphological disparity. *Biology Letters*, **16**, 20200199.

HAGDORN, H. and WANG, X.-F. 2015. The pseudoplanktonic crinoid *Traumatocrinus* from the Late Triassic of Southwest China -- Morphology, ontogeny, and taphonomy. *Palaeoworld*, **24**, 479-496.

HAGDORN, H., WANG, X. and WANG, C. 2007. Palaeoecology of the pseudoplanktonic Triassic crinoid *Traumatocrinus* from Southwest China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **247**, 181-196.

HARMON, L. J., LOSOS, J. B., DAVIES, T. J., GILLESPIE, R. G., GITTLEMAN, J. L., JENNINGS, W. B., KOZAK, K. H., MCPEEK, M. A., MORENO-ROARK, F. and NEAR, T. J. 2010. Early bursts of body size and shape evolution are rare in comparative data. *Evolution*, **64**, 2385–2396.

Author Manuscript

HARPER, D. A. T., TOPPER, T. P., CASCALES-MIÑANA, B., SERVAIS, T., ZHANG, Y.-D. and AHLBERG, P. 2019. The Furongian (late Cambrian) biodiversity gap: real or apparent? *Palaeoworld*, **28**, 4-12.

HEIM, N. A., KNOPE, M. L., SCHAAL, E. K., WANG, S. C. and PAYNE, J. L. 2015. Cope's rule in the evolution of marine animals. *Science*, **347**, 867-870.

HESS, H. 2010. Part T, revised, Vol. 1, Ch. 19: Paleoecology of pelagic crinoids. 1-33. *Treatise Online*, **16**, 1–33.

HESS, H. and ETTER, W. 2011. Life and death of *Saccocoma tenella* (Goldfuss). *Swiss Journal of Geosciences*, **104**, 99-106.

HESS, H., AUSICH, W. I., BRETT, C. E. and SIMMS, M. J. (eds) 1999. *Fossil crinoids*. Cambridge University Press, 300 pp.

HESS, H., MESSING, C. G. and AUSICH, W. I. 2011. *Treatise on Invertebrate Paleontology. Part T. Echinodermata 2 (revised), Crinoidea, vol. 3*. Geological Society of America & University of Kansas Press, 261 pp.

HOLLOWAY, D. J. and JELL, P. A. 1983. Silurian and Devonian Edrioasteroids from Australia. *Journal of Paleontology*, **57**, 1001-1016.

HOPKINS, M. J. and SMITH, A. B. 2015. Dynamic evolutionary change in post-Paleozoic echinoids and the importance of scale when interpreting changes in rates of evolution. *Proceedings of the National Academy of Sciences*, **112**, 3758-3763.

HOPKINS, M. J. and ST JOHN, K. 2018. A new family of dissimilarity metrics for discrete character matrices that include inapplicable characters and its importance for disparity studies. *Proceedings of the Royal Society B*, **285**, 20181784.

Author Manuscript

HUNT, G. 2006. Fitting and comparing models of phyletic evolution: random walks and beyond. *Paleobiology*, **32**, 578-601.

HUNT, G. 2007. The relative importance of directional change, random walks, and stasis in the evolution of fossil lineages. *Proceedings of the National Academy of Sciences*, **104**, 18404-18408.

HUNT, G. 2022. paleoTS: Modeling evolution in paleontological time-series. R package 0.5.3. https://cran.r-project.org/package=paleoTS.

JABLONSKI, D. 2017. Approaches to macroevolution: 1. General concepts and origin of variation. *Evolutionary Biology*, **44**, 427-450.

KAMMER, T. W., SUMRALL, C. D., ZAMORA, S., AUSICH, W. I. and DELINE, B. 2013. Oral region homologies in Paleozoic crinoids and other plesiomorphic pentaradial echinoderms. *PLoS One*, **8**, e77989.

KLOSS, T. J., DORNBOS, S. Q. and CHEN, J. 2015. Substrate adaptations of sessile benthic metazoans during the Cambrian radiation. *Paleobiology*, **41**, 342-352.

KNOPE, M. L., HEIM, N. A., FRISHKOFF, L. O. and PAYNE, J. L. 2015. Limited role of functional differentiation in early diversification of animals. *Nature Communications*, **6**, 6455-6461.

KOKORIN, A. 2015. What can *Aganaster* vertebrae tell about its ecology? 83-85. *In* ZAMORA, S. and RÁBANO, I. (eds). *Progress in echinoderm paleobiology*. Instituto Geológico y Minero de España, 292 pp.

KOLATA, D. R., STRIMPLE, H. L. and LEVORSON, C. O. 1977. Revision of the Ordovician carpoid family Iowacystidae. *Palaeontology*, **20**, 529-557.

Author Manuscript

KOWALEWSKI, M. and NOVACK-GOTTSHALL, P. 2010. Resampling methods in paleontology. 19-54. *In* ALROY, J. and HUNT, G. (eds). *Quantitative methods in paleobiology*. Paleontological Society & Paleontological Research Institute, Short Courses in Paleontology, **16**, 316 pp.

KRAFT, P., VAŠKANINOVÁ, V., MERGL, M., BUDIL, P., FATKA, O. and AHLBERG, P. E. 2023. Uniquely preserved gut contents illuminate trilobite palaeophysiology. *Nature*, **622**, 545–551.

KRÖGER, B., DESROCHERS, A. and ERNST, A. 2017. The reengineering of reef habitats during the Great Ordovician Biodiversification Event. *PALAIOS*, **32**, 584-599.

KRÖGER, B., SERVAIS, T. and ZHANG, Y. 2009. The origin and initial rise of pelagic cephalopods in the Ordovician. *PLoS One*, **4**, e7262.

LAIBL, L., SALEH, F. and PÉREZ-PERIS, F. 2023. Drifting with trilobites: the invasion of early post-embryonic trilobite stages to the pelagic realm. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **613**, 111403.

LANE, N. G. 1963. The Berkeley Crinoid Collection from Crawfordsville, Indiana. *Journal of Paleontology*, **37**, 1001-1008.

LAWRENCE, J. M., HERRERA, J. and COBB, J. 2004. Vertical posture of the clypeasteroid sand dollar *Encope michelini*. *Journal of the Marine Biological Association of the United Kingdom*, **84**, 407-408.

LEE, M. S. Y., SOUBRIER, J. and EDGECOMBE, G. D. 2013. Rates of phenotypic and genomic evolution during the Cambrian explosion. *Current Biology*, **23**, 1889-1895.

LEFEBVRE, B. 2003. Functional morphology of stylophoran echinoderms. *Palaeontology*, **46**, 511-555.

Author Manuscript

LEFEBVRE, B. 2005. Stylophoran supertrees revisited. *Acta Palaeontologica Polonica*, **50**, 477–486.

LEFEBVRE, B. 2007. Changes in Late Ordovician (pre-Hirnantian) echinoderm assemblages: palaeoenvironmental and palaeobiogeographical implications. *Acta Palaeontologica Sinica*, **46**, 241-248.

LEFEBVRE, B. and FATKA, O. 2003. Palaeogeographical and palaeoecological aspects of the Cambro–Ordovician radiation of echinoderms in Gondwanan Africa and peri-Gondwanan Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **195**, 73-97.

LEFEBVRE, B., NOAILLES, F., FRANZIN, B., REGNAULT, S., NARDIN, E., HUNTER, A. W., ZAMORA, S., VAN ROY, P., EL HARIRI, K. and LAZREQ, N. 2010. Les gisements à échinodermes de l'Ordovicien supérieur de l'Anti-Atlas oriental (Maroc): un patrimoine scientifique exceptionnel à préserver. *Bulletin de l'Institut Scientifique, Rabat*, **32**, 1-17.

LEFEBVRE, B., SUMRALL, C. D., SHROAT-LEWIS, R. A., REICH, M., WEBSTER, G. D., HUNTER, A. W., NARDIN, E., ROZHNOV, S. V., GUENSBURG, T. E., TOUZEAU, A., NOAILLES, F. and SPRINKLE, J. 2013. Palaeobiogeography of Ordovician echinoderms. 173-198. *In* HARPER, D. A. T. and SERVAIS, T. (eds). *Early Palaeozoic biogeography and palaeogeography*. Geological Society, London, Memoirs, **38**, 490 pp.

LIU, F., SKOVSTED, C. B., TOPPER, T. P. and ZHANG, Z. 2021. Revision of *Triplicatella* (Orthothecida, Hyolitha) with preserved digestive tracts from the early Cambrian Chengjiang Lagerstätte, South China. *Historical Biology*, **33?**, 1-15.

Author Manuscript

LLOYD, G. T. 2016. Estimating morphological diversity and tempo with discrete character-taxon matrices: implementation, challenges, progress, and future directions. *Biological Journal of the Linnean Society*, **118**, 131-151.

LLOYD, G. T. 2018. Journeys through discrete-character morphospace: synthesizing phylogeny, tempo, and disparity. *Palaeontology*, **61**, 637-645.

LLOYD, G. T., WANG, S. C. and BRUSATTE, S. L. 2012. Identifying heterogeneity in rates of morphological evolution: discrete character change in the evolution of lungfish (Sarcopterygii; Dipnoi). *Evolution*, **66**, 330-348.

LLOYD, G. T., GUILLERME, T., SHERRATT, E. and WANG, S. C. 2020. Claddis: Measuring morphological diversity and evolutionary tempo. R package 0.6.3. https://cran.r-project.org/package=Claddis.

LYONS, T. W., REINHARD, C. T. and PLANAVSKY, N. J. 2014. The rise of oxygen in Earth's early ocean and atmosphere. *Nature*, **506**, 307-315.

MANCOSU, A. and NEBELSICK, J. H. 2013. Multiple routes to mass accumulations of clypeasteroid echinoids: a comparative analysis of Miocene echinoid beds of Sardinia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **374**, 173-186.

McCLAIN, C. R. and BOYER, A. G. 2009. Biodiversity and body size are linked across metazoans. *Proceedings of the Royal Society B*, **276**, 2209-2215.

MERGL, M. and PROKOP, R. J. 2006. Lower Ordovician cystoids (Rhombifera, Diploporita) from the Prague Basin (Czech Republic). *Bulletin of Geosciences*, **81**, 1-15.

MEYER, D. L. and LANE, N. G. 1976. The feeding behaviour of some Paleozoic crinoids and Recent basketstars. *Journal of Paleontology*, **50**, 473-480.

Author Manuscript

MILLER, A. K., KERR, A. M., PAULAY, G., REICH, M., WILSON, N. G., CARVAJAL, J. I. and ROUSE, G. W. 2017. Molecular phylogeny of extant Holothuroidea (Echinodermata). *Molecular Phylogenetics and Evolution*, **111**, 110-131.

MONGIARDINO KOCH, N. 2021. Exploring adaptive landscapes across deep time: A case study using echinoid body size. *Evolution*, **75**, 1567-1581.

MOOI, R. and DAVID, B. 1997. Skeletal homologies of echinoderms. *The Paleontological Society Papers*, **3**, 305-335.

MUELLER, B., BOS, A. R., GRAF, G. and GUMANAO, G. S. 2011. Size-specific locomotion rate and movement pattern of four common Indo-Pacific sea stars (Echinodermata; Asteroidea). *Aquatic Biology*, **12**, 157-164.

NANGLU, K., COLE, S. R., WRIGHT, D. F. and SOUTO, C. 2022. Worms and gills, plates and spines: the evolutionary origins and incredible disparity of deuterostomes revealed by fossils, genes, and development. *Biological Reviews*, **98**, 316-351.

NOAILLES, F. 2016. Life on the seafloor: adaptations and strategies in Stylophora (Echinodermata). *Lethaia*, **49**, 365-378.

NOVACK-GOTTSHALL, P. M. 2007. Using a theoretical ecospace to quantify the ecological diversity of Paleozoic and modern marine biotas. *Paleobiology*, **33**, 273-294.

NOVACK-GOTTSHALL, P. M. 2008. Ecosystem-wide body-size trends in Cambrian–Devonian marine invertebrate lineages. *Paleobiology*, **34**, 210-228.

NOVACK-GOTTSHALL, P. M. 2016a. General models of ecological diversification. I. Conceptual synthesis. *Paleobiology*, **42**, 185-208.

NOVACK-GOTTSHALL, P. M. 2016b. General models of ecological diversification. II. Simulations and empirical applications. *Paleobiology*, **42**, 209-239.

Author Manuscript

NOVACK-GOTTSHALL, P. M., SULTAN, A., SMITH, N. S., PURCELL, J., HANSON, K. E., LIVELY, R., RANJHA, I., COLLINS, C., PARKER, R., SUMRALL, C. D. and DELINE, B. 2022. Morphological volatility precedes ecological innovation in early echinoderms. *Nature Ecology & Evolution*, **6**, 1-10.

Novack-Gottshall, P.M., Purcell, J., Sultan, A., Ranjha, I. Deline, B. and Sumrall, C.D. 2023. Data from: Ecological novelty at the start of the Cambrian and Ordovician radiations of echinoderms. Harvard Dataverse. https://dataverse.harvard.edu/dataverse/CamOrdEchinoEcology

NÜTZEL, A., LEHNERT, O. and FRÝDA, J. Í. 2006. Origin of planktotrophy—evidence from early molluscs. *Evolution & Development*, **8**, 325-330.

PARRY, L., TANNER, A. and VINTHER, J. 2014. The origin of annelids. *Palaeontology*, **57**, 1091-1103.

PARSLEY, R. 2015. Flume studies using 1:1 scale models of Series 2 and basal Series 3 Cambrian gogiid eocrinoids from Guizhou Province, China to determine feeding posture and mode of attachment. *Palaeoworld*, **24**, 400-407.

PARSLEY, R. L. and PROKOP, R. J. 2004. Functional morphology and paleoecology of some sessile Middle Cambrian echinoderms from the Barrandian region of Bohemia. *Bulletin of Geosciences*, **79**, 147-156.

PATERSON, J. R., EDGECOMBE, G. D. and LEE, M. S. Y. 2019. Trilobite evolutionary rates constrain the duration of the Cambrian explosion. *Proceedings of the National Academy of Sciences*, **116**, 4394-4399.

PAUL, C. 1968. *Macrocystella* Callaway, the earliest glyptocystitid cystoid. *Palaeontology*, **11**, 580-600.

Author Manuscript

PISANI, D., FEUDA, R., PETERSON, K. J. and SMITH, A. B. 2012. Resolving phylogenetic signal from noise when divergence is rapid: a new look at the old problem of echinoderm class relationships. *Molecular Phylogenetics and Evolution*, **62**, 27-34.

PLOTNICK, E. R. and BAUER, J. 2014. Crinoids aweigh: experimental biomechanics of *Ancyrocrinus* holdfasts. 3-20. *In* HEMBREE, I. D., PLATT, F. B. and SMITH, J. J. (eds). *Experimental approaches to understanding fossil organisms: Lessons from the living*. Springer, 437 pp.

POHL, A., HARPER, D. A. T., DONNADIEU, Y., HIR, G. L., NARDIN, E. and SERVAIS, T. 2018. Possible patterns of marine primary productivity during the Great Ordovician Biodiversification Event. *Lethaia*, **51**, 187-197.

PRICE, S. A., HOPKINS, S. S. B., SMITH, K. K. and ROTH, V. L. 2012. Tempo of trophic evolution and its impact on mammalian diversification. *Proceedings of the National Academy of Sciences*, **109**, 7008-7012.

RAHMAN, I. A., ZAMORA, S., FALKINGHAM, P. L. and PHILLIPS, J. C. 2015a. Cambrian cinctan echinoderms shed light on feeding in the ancestral deuterostome. *Proceedings of the Royal Society B*, **282**.

RAHMAN, I. A., STEWART, S. E. and ZAMORA, S. 2015b. The youngest ctenocystoids from the Upper Ordovician of the United Kingdom and the evolution of the bilateral body plan in echinoderms. *Acta Palaeontologica Polonica*, **60**, 39-48.

RAHMAN, I. A., THOMPSON, J. R., BRIGGS, D. E. G., SIVETER, D. J., SIVETER, D. J. and SUTTON, M. D. 2019. A new ophiocistioid with soft-tissue preservation from the Silurian Herefordshire Lagerstätte, and the evolution of the holothurian body plan. *Proceedings of the Royal Society B*, **286**, 20182792.

Author Manuscript

RAHMAN, I. A., O'SHEA, J., LAUTENSCHLAGER, S. and ZAMORA, S. 2020. Potential evolutionary trade-off between feeding and stability in Cambrian cinctan echinoderms. *Palaeontology*, **63**, 689-701.

RASMUSSEN, C. M. Ø., KRÖGER, B., NIELSEN, M. L. and COLMENAR, J. 2019. Cascading trend of Early Paleozoic marine radiations paused by Late Ordovician extinctions. *Proceedings of the National Academy of Sciences*, **116**, 7207-7213.

REICH, M. 2009a. The early evolution and diversification of holothurians (Echinozoa). 55-59. *In* HARRIS, L. G., BÖTTGER, S. A., WALKER, C. W. and LESSER, M. P. (eds). *Proceedings of the 12th International Echinoderm Conference*. Taylor & Francis.

REICH, M. 2009b. How many species of fossil holothurians are there? 5-9. *In* JOHNSON, C. (ed.) *Echinoderms in a changing world: Proceedings of the 13th International Echinoderm Conference*. Routledge, 318 pp.

REICH, M., SPRINKLE, J., LEFEBVRE, B., RÖSSNER, G. E. and ZAMORA, S. 2017. The first Ordovician cyclocystoid (Echinodermata) from Gondwana and its morphology, paleoecology, taphonomy, and paleogeography. *Journal of Paleontology*, **91**, 735-754.

ROZHNOV, S. V. 2002. Morphogenesis and evolution of crinoids and other pelmatozoan echinoderms in the Early Paleozoic. *Paleontological Journal*, **36**, S525-S674.

ROZHNOV, S. 2019. The onset of the Ordovician evolutionary radiation of benthic animals in the Baltic Region: Explosive diversity of attachment structures of stalked echinoderms, substrate revolution and the role of cyanobacterial communities. *Palaeoworld*, **28**, 110-122.

Author Manuscript

SALAMON, M. A., BRACHANIEC, T., KOŁBUK, D., SAHA, A. and GORZELAK, P. 2021. Shared patterns in body size declines among crinoids during the Palaeozoic extinction events. *Scientific Reports*, **11**, 20351.

SALTZMAN, M. R., EDWARDS, C. T., ADRAIN, J. M. and WESTROP, S. R. 2015. Persistent oceanic anoxia and elevated extinction rates separate the Cambrian and Ordovician radiations. *Geology*, **43**, 807-810.

SCHNEIDER, H. L. 1989. Zur Morphologie und Ontogenese von *Roveacrinus geinitzi* n. sp.(Crinoidea, Oberkreide). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **178**, 167-181.

SCHNEIDER, H. L. 1995. Crinoidea (Roveacrinidae) aus dem Unter-Turon von Wüllen (Münsterländer Kreidebecken/Nordrhein-Westfalen). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **198**, 35-46.

SEPKOSKI, J. J. Jr 1978. A kinetic model of Phanerozoic taxonomic diversity: I. Analysis of marine orders. *Paleobiology*, **4**, 223-251.

SERVAIS, T. and HARPER, D. A. T. 2018. The Great Ordovician Biodiversification Event (GOBE): definition, concept and duration. *Lethaia*, **51**, 151-164.

SERVAIS, T., PERRIER, V., DANELIAN, T., KLUG, C., MARTIN, R., MUNNECKE, A., NOWAK, H., NÜTZEL, A., VANDENBROUCKE, T. R. A., WILLIAMS, M. and RASMUSSEN, C. M. Ø. 2016. The onset of the 'Ordovician Plankton Revolution' in the late Cambrian. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **458**, 12-28.

SESLAVINSKI, K. B. and MAIDANSKAYA, I. D. 2001. Global facies distributions from late Vendian to Mid-Ordovician. 47-68. *In* ZHURAVLEV, A. I. U. and RIDING, R. (eds). *The ecology of the Cambrian radiation*. Columbia University Press.

Author Manuscript

SEVASTOPULO, G. D. 2008. Paleobiology of Carboniferous microcrinoids. 54-69. *In* AUSICH, W. I. and WEBSTER, G. D. (eds). *Echinoderm paleobiology*. Indiana University Press.

SHEFFIELD, S. L. and SUMRALL, C. D. 2019. The phylogeny of the Diploporita: a polyphyletic assemblage of blastozoan echinoderms. *Journal of Paleontology*, **93**, 740-752.

SIGNOR, P. W. and VERMEIJ, G. J. 1994. The plankton and the benthos: origins and early history of an evolving relationship. *Paleobiology*, **20**, 297-319.

SIMAKOV, O., KAWASHIMA, T., MARLÉTAZ, F., JENKINS, J., KOYANAGI, R., MITROS, T., HISATA, K., BREDESON, J., SHOGUCHI, E., GYOJA, F., YUE, J.-X., CHEN, Y.-C., FREEMAN, R. M., SASAKI, A., HIKOSAKA-KATAYAMA, T., SATO, A., FUJIE, M., BAUGHMAN, K. W., LEVINE, J., GONZALEZ, P., CAMERON, C., FRITZENWANKER, J. H., PANI, A. M., GOTO, H., KANDA, M., ARAKAKI, N., YAMASAKI, S., QU, J., CREE, A., DING, Y., DINH, H. H., DUGAN, S., HOLDER, M., JHANGIANI, S. N., KOVAR, C. L., LEE, S. L., LEWIS, L. R., MORTON, D., NAZARETH, L. V., OKWUONU, G., SANTIBANEZ, J., CHEN, R., RICHARDS, S., MUZNY, D. M., GILLIS, A., PESHKIN, L., WU, M., HUMPHREYS, T., SU, Y.-H., PUTNAM, N. H., SCHMUTZ, J., FUJIYAMA, A., YU, J.-K., TAGAWA, K., WORLEY, K. C., GIBBS, R. A., KIRSCHNER, M. W., LOWE, C. J., SATOH, N., ROKHSAR, D. S. and GERHART, J. 2015. Hemichordate genomes and deuterostome origins. *Nature*, **527**, 459-465.

SLATER, G. J. and FRISCIA, A. R. 2019. Hierarchy in adaptive radiation: a case study using the Carnivora (Mammalia). *Evolution*, **73**, 524-539.

Author Manuscript

SLATER, G. J., PRICE, S. A., SANTINI, F. and ALFARO, M. E. 2010. Diversity versus disparity and the radiation of modern cetaceans. *Proceedings of the Royal Society B*, **277**, 3097-3104.

SMITH, A. B. and REICH, M. 2013. Tracing the evolution of the holothurian body plan through stem-group fossils. *Biological Journal of the Linnean Society*, **109**, 670-681.

SMITH, A. B. and ZAMORA, S. 2009. Rooting phylogenies of problematic fossil taxa; a case study using cinctans (stem-group echinoderms). *Palaeontology*, **52**, 803-821.

SMITH, A. B. and ZAMORA, S. 2013. Cambrian spiral-plated echinoderms from Gondwana reveal the earliest pentaradial body plan. *Proceedings of the Royal Society B*, **280**, 20131197.

SMITH, A. B., ZAMORA, S. and ÁLVARO, J. J. 2013. The oldest echinoderm faunas from Gondwana show that echinoderm body plan diversification was rapid. *Nature Communications*, **4**, 1385.

SMITH, F. A., PAYNE, J. L., HEIM, N. A., BALK, M. A., FINNEGAN, S., MICHAL, K., LYONS, S. K., MCCLAIN, C. R., MCSHEA, D. W., NOVACK-GOTTSHALL, P. M., ANICH, P. S. and WANG, S. C. 2016. Body size evolution across the Geozoic. *Annual Review of Earth and Planetary Sciences*, **44**, 523-553.

SPRINKLE, J. and COLLINS, D. 2006. New eocrinoids from the Burgess Shale, southern British Columbia, Canada, and the Spence Shale, northern Utah, USA. *Canadian Journal of Earth Sciences*, **43**, 303-322.

SPRINKLE, J. and GUENSBURG, T. E. 1995. Origin of echinoderms in the Paleozoic Evolutionary Fauna: the role of substrates. *PALAIOS*, **10**, 437-453.

STANLEY, S. M. 1973. An explanation for Cope's rule. *Evolution*, **27**, 1-26.

Author Manuscript

STIGALL, A. L., EDWARDS, C. T., FREEMAN, R. L. and RASMUSSEN, C. M. Ø. 2019. Coordinated biotic and abiotic change during the Great Ordovician Biodiversification Event: Darriwilian assembly of early Paleozoic building blocks. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **530**, 249-270.

SUMRALL, C. D. 2000. The biological implications of an edrioasteroid attached to a pleurocystitid rhombiferan. *Journal of Paleontology*, **74**, 67-71.

SUMRALL, C. D. and WATERS, J. A. 2012. Universal elemental homology in glyptocystitoids, hemicosmitoids, coronoids and blastoids: steps toward echinoderm phylogenetic reconstruction in derived Blastozoa. *Journal of Paleontology*, **86**, 956-972.

SUMRALL, C. D. and ZAMORA, S. 2011. Ordovician edrioasteroids from Morocco: faunal exchanges across the Rheic Ocean. *Journal of Systematic Palaeontology*, **9**, 425-454.

SUMRALL, C. D., SPRINKLE, J. and GUENSBURG, T. E. 1997. Systematics and paleoecology of Late Cambrian echinoderms from the western United States. *Journal of Paleontology*, **71**, 1091-1109.

SUMRALL, C. D., SPRINKLE, J. and GUENSBURG, T. E. 2001. Comparison of flattened blastozoan echinoderms: insights from the new Early Ordovician eocrinoid *Haimacystis rozhnovi*. *Journal of Paleontology*, **75**, 985-992.

SUMRALL, C. D., HEREDIA, S., RODRÍGUEZ, C. M. and MESTRE, A. I. 2013. The first report of South American edrioasteroids and the paleoecology and ontogeny of rhenopyrgid echinoderms. *Acta Palaeontologica Polonica*, **58**, 763-776.

SUTCLIFFE, O. E., SÜDKAMP, W. H. and JEFFERIES, R. P. S. 2000. Ichnological evidence on the behaviour of mitrates: two trails associated with the Devonian mitrate *Rhenocystis*. *Lethaia*, **33**, 1-12.

Author Manuscript

SYVERSON, V. J. and BAUMILLER, T. K. 2014. Temporal trends of predation resistance in Paleozoic crinoid arm branching morphologies. *Paleobiology*, **40**, 417-427.

TARHAN, L. G. and DROSER, M. L. 2014. Widespread delayed mixing in early to middle Cambrian marine shelfal settings. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **399**, 310-322.

TARHAN, L. G., DROSER, M. L., PLANAVSKY, N. J. and JOHNSTON, D. T. 2015. Protracted development of bioturbation through the early Palaeozoic Era. *Nature Geoscience*, **8**, 865-869.

THOMAS, R. D. K., RUNNEGAR, B. and MATT, K. 2020. *Pelagiella exigua*, an early Cambrian stem gastropod with chaetae: lophotrochozoan heritage and conchiferan novelty. *Palaeontology*, **63**, 601-627.

THOMPSON, J. R., COTTON, L. J., CANDELA, Y., KUTSCHER, M., REICH, M. and BOTTJER, D. J. 2021. The Ordovician diversification of sea urchins: systematics of the Bothriocidaroida (Echinodermata: Echinoidea). *Journal of Systematic Palaeontology*, **19**, 1395-1448.

THUY, B., KNOX, L., NUMBERGER-THUY, L. D., SMITH, N. S. and SUMRALL, C. D. 2023. Ancient deep ocean as a harbor of biotic innovation revealed by Carboniferous ophiuroid microfossils. *Geology*. https://doi.org/10.1130/G50596.1

TOPPER, T. P., STROTZ, L. C., HOLMER, L. E. and CARON, J.-B. 2015. Survival on a soft seafloor: life strategies of brachiopods from the Cambrian Burgess Shale. *Earth-Science Reviews*, **151**, 266-287.

Author Manuscript

TOPPER, T. P., ZHANG, Z., GUTIÉRREZ-MARCO, J. C. and HARPER, D. A. T. 2018. The dawn of a dynasty: life strategies of Cambrian and Ordovician brachiopods. *Lethaia*, **51**, 254-266.

TOPPER, T. P., GUO, J., CLAUSEN, S., SKOVSTED, C. B. and ZHANG, Z. 2019. A stem group echinoderm from the basal Cambrian of China and the origins of Ambulacraria. *Nature Communications*, **10**, 1366.

TOPPER, T. P., GUO, J., CLAUSEN, S., SKOVSTED, C. B. and ZHANG, Z. 2020. Reply to 'Re-evaluating the phylogenetic position of the enigmatic early Cambrian deuterostome *Yanjiahella*'. *Nature Communications*, **11**, 1287.

TORSVIK TROND, H. and COCKS, L. R. M. 2013. New global palaeogeographical reconstructions for the Early Palaeozoic and their generation. *Geological Society, London, Memoirs*, **38**, 5-24.

UBAGHS, G. 1998. Échinodermes nouveauxdu Cambrien supérieur de la Montagne noire (France méridionale). *Geobios*, **31**, 809-829.

UBAGHS, G., MOORE, R. C., RASMUSSEN, H. W., LANE, N. G., BREIMER, A., STRIMPLE, H. L., BROWER, J. C., JEFFORDS, R. M., SPRINKLE, J., PECK, R. E., D.B. MACURDA, JR., MEYER, D. L., ROUX, M., SIEVERTS-DORECK, H., FAY, R. O. and ROBISON, R. A. 1978. *Treatise on Invertebrate Paleontology. Part T. Echinodermata 2, Crinoidea, vols 1–3*. Geological Society of America & University of Kansas Press, 1027 pp.

WANG, X., HAGDORN, H. and WANG, C. 2006. Pseudoplanktonic lifestyle of the Triassic crinoid *Traumatocrinus* from Southwest China. *Lethaia*, **39**, 187-193.

Author Manuscript

WEBBY, B. D., PARIS, F., DROSER, M. L. and PERCIVAL, I. G. (eds) 2004. *The Great Ordovician Biodiversification Event*. Columbia University Press, 484 pp.

WHALEN, C. D. and BRIGGS, D. E. G. 2018. The Palaeozoic colonization of the water column and the rise of global nekton. *Proceedings of the Royal Society B*, **285**, 20180883

WILLS, M. A. 1998. Crustacean disparity through the Phanerozoic: comparing morphological and stratigraphic data. *Biological Journal of the Linnean Society*, **65**, 455-500.

WOOD, R. and ERWIN, D. H. 2018. Innovation not recovery: dynamic redox promotes metazoan radiations. *Biological Reviews*, **93**, 863-873.

WOOD, R. and PENNY, A. 2018. Substrate growth dynamics and biomineralization of an Ediacaran encrusting poriferan. *Proceedings of the Royal Society B*, **285**, 20171938.

WRIGHT, D. F. 2017. Bayesian estimation of fossil phylogenies and the evolution of early to middle Paleozoic crinoids (Echinodermata). *Journal of Paleontology*, **91**, 799-814.

YANG, J., LAN, T., ZHANG, X.-G. and SMITH, M. R. 2023. *Protomelission* is an early dasyclad alga and not a Cambrian bryozoan. *Nature*, **615**, 468-471.

YUAN, X., XIAO, S., PARSLEY, R. L., ZHOU, C., CHEN, Z. and HU, J. 2002. Towering sponges in an Early Cambrian Lagerstätte: Disparity between nonbilaterian and bilaterian epifaunal tierers at the Neoproterozoic-Cambrian transition. *Geology*, **30**, 363-366.

ZAMORA, S. and RAHMAN, I. A. 2014. Deciphering the early evolution of echinoderms with Cambrian fossils. *Palaeontology*, **57**, 1105-1119.

ZAMORA, S. and SMITH, A. B. 2010. The oldest isorophid edrioasteroid (Echinodermata) and the evolution of attachment strategies in Cambrian edrioasteroids. *Acta Palaeontologica Polonica*, **55**, 487-494.

Author Manuscript

ZAMORA, S., CLAUSEN, S. B., ÁLVARO, J. J. and SMITH, A. B. 2010. Pelmatozoan echinoderms as colonizers of carbonate firmgrounds in mid-Cambrian high energy environments. *PALAIOS*, **25**, 764-768.

ZAMORA, S., RAHMAN, I. A. and SMITH, A. B. 2012. Plated Cambrian bilaterians reveal the earliest stages of echinoderm evolution. *PLoS One*, **7**, e38296.

ZAMORA, S., LEFEBVRE, B., ÁLVARO, J. J., CLAUSEN, S., ELICKI, O., FATKA, O., JELL, P., KOUCHINSKY, A., LIN, J.-P., NARDIN, E., PARSLEY, R., ROZHNOV, S., SPRINKLE, J., SUMRALL, C. D., VIZCAÏNO, D. and SMITH, A. B. 2013. Cambrian echinoderm diversity and palaeobiogeography. 157-171. *In* HARPER, D. A. T. and SERVAIS, T. (eds). *Early Palaeozoic biogeography and palaeogeography*. Geological Society, London, Memoirs, **38**, 490 pp.

ZAMORA, S., DELINE, B., ÁLVARO, J. J. and RAHMAN, I. A. 2017. The Cambrian Substrate Revolution and the early evolution of attachment in suspension-feeding echinoderms. *Earth-Science Reviews*, **171**, 478-491.

ZAMORA, S., WRIGHT, D. F., MOOI, R., LEFEBVRE, B., GUENSBURG, T. E., GORZELAK, P., DAVID, B., SUMRALL, C. D., COLE, S. R., HUNTER, A. W., SPRINKLE, J., THOMPSON, J. R., EWIN, T. A. M., FATKA, O., NARDIN, E., REICH, M., NOHEJLOVÁ, M. and RAHMAN, I. A. 2020. Re-evaluating the phylogenetic position of the enigmatic early Cambrian deuterostome *Yanjiahella*. *Nature Communications*, **11**, 1286.

ZHANG, Z., ZHANG, Z., MA, J., TAYLOR, P. D., STROTZ, L. C., JACQUET, S. M., SKOVSTED, C. B., CHEN, F., HAN, J. and BROCK, G. A. 2021. Fossil evidence unveils an early Cambrian origin for Bryozoa. *Nature*, **599**, 251-255.

Author Manuscript

ZHAO, Y. L., SUMRALL, C. D., PARSLEY, R. L. and PENG, J. 2010. *Kailidiscus*, a new plesiomorphic edrioasteroid from the basal Middle Cambrian Kaili biota of Guizhou Province, China. *Journal of Paleontology*, **84**, 668-680.

ZHURAVLEV, A. Y. and WOOD, R. 2020. Dynamic and synchronous changes in metazoan body size during the Cambrian Explosion. *Scientific Reports*, **10**, 6784.

ZHURAVLEV, A. Y. and WOOD, R. A. 2018. The two phases of the Cambrian Explosion. *Scientific Reports*, **8**, 16656.

ZHURAVLEV, A. Y., WOOD, R. A. and PENNY, A. M. 2015. Ediacaran skeletal metazoan interpreted as a lophophorate. *Proceedings of the Royal Society B*, **282**, 20151860.

Author Manuscript

Author Manuscript

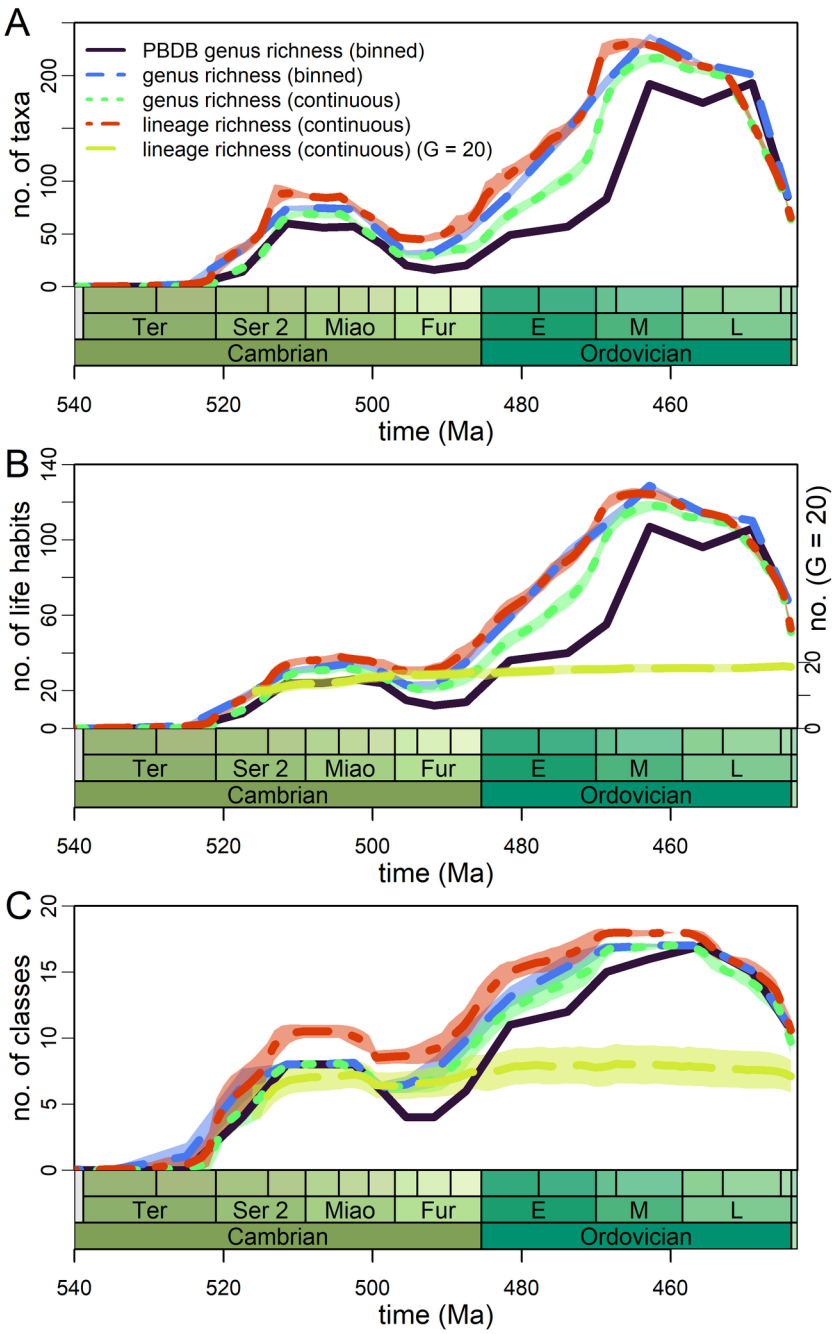


Fig1_Diversity_110.tif

Author Manuscript

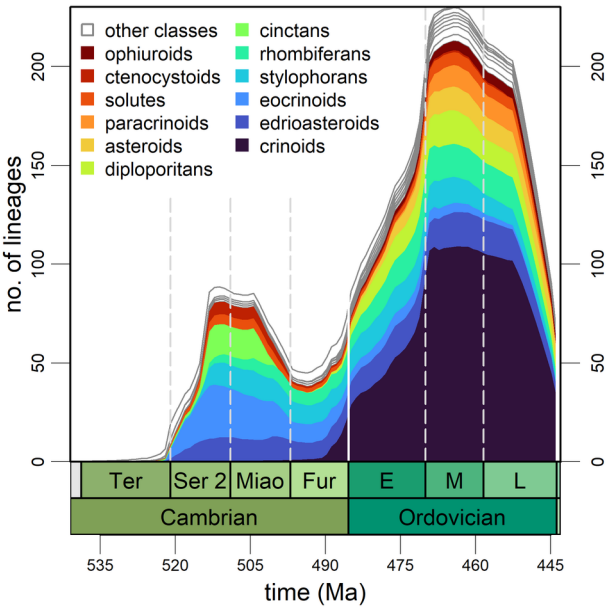


Fig2_StackedClasses_80.tif

Author Manuscript

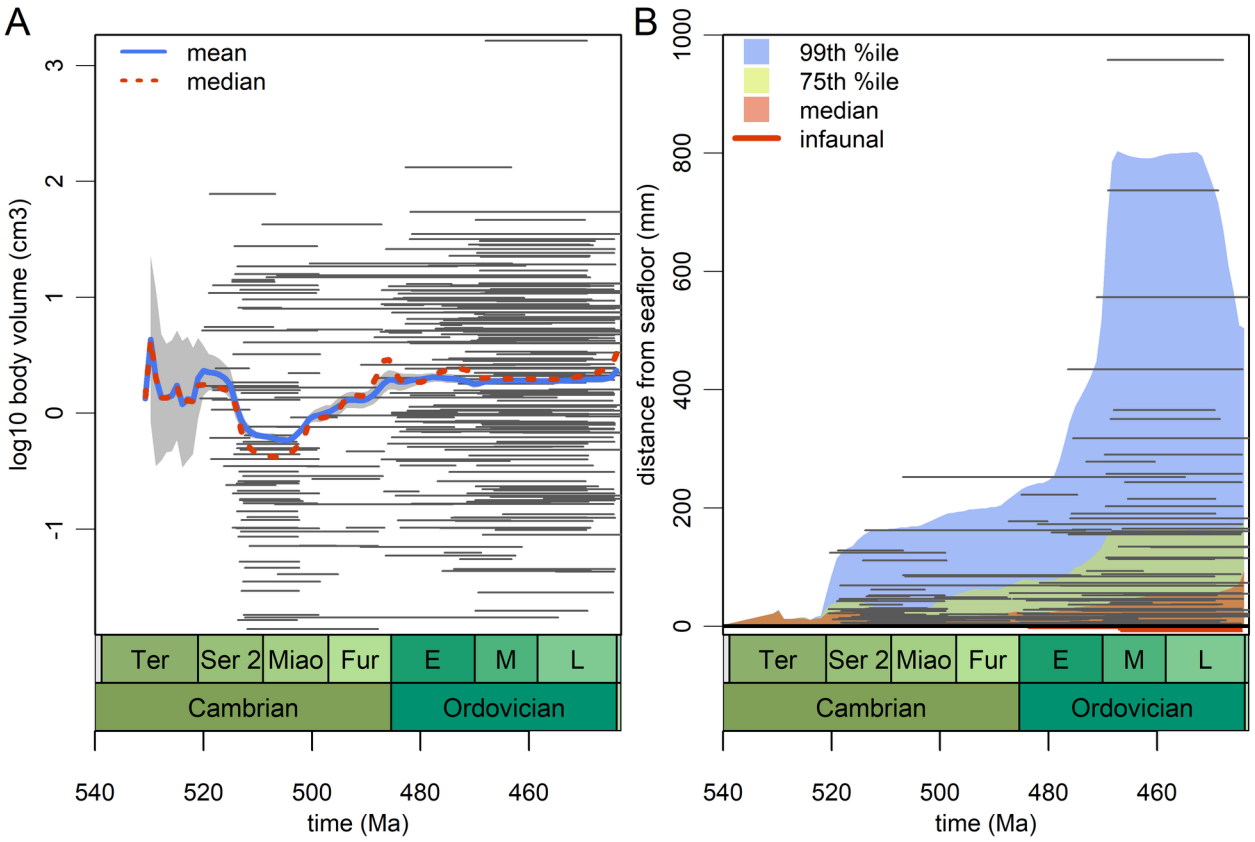


Fig3_Size&Tiering_166.tif

Author Manuscript

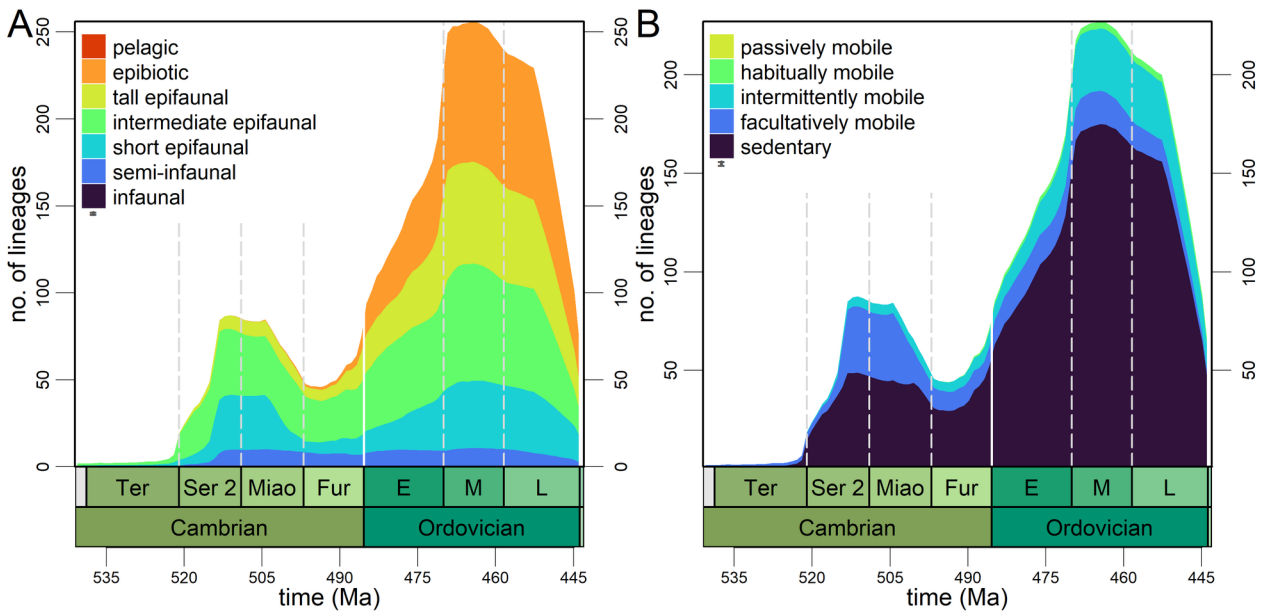


Fig4_Habitats&Mobility_166.tif

Author Manuscript

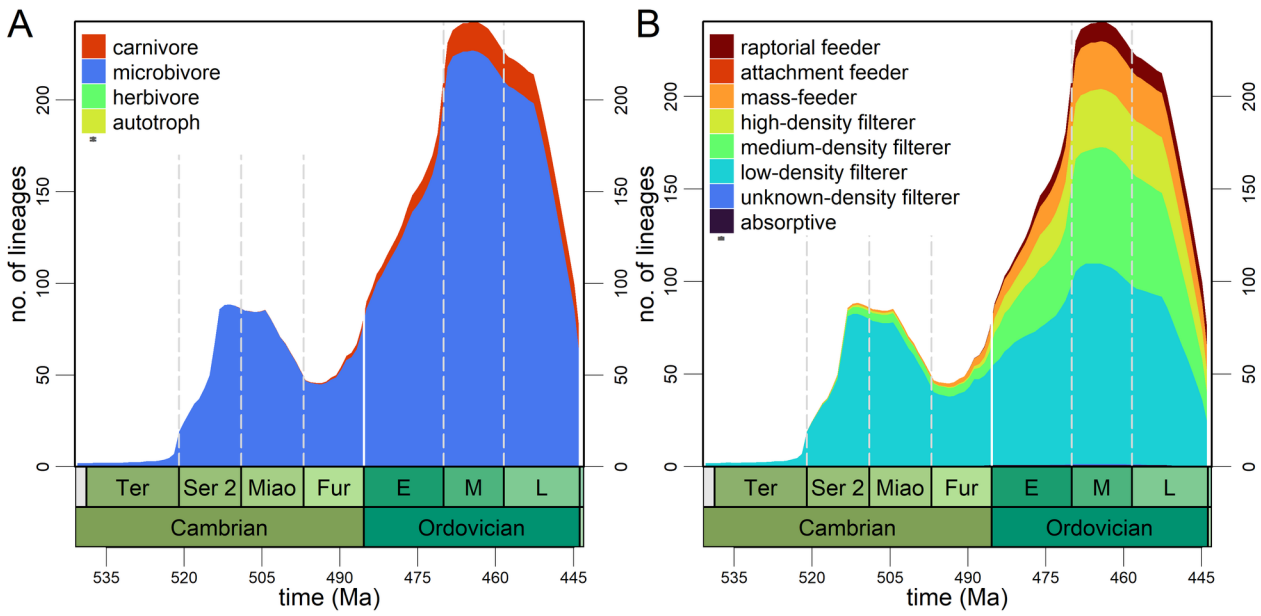


Fig5_Diet&Foraging_166.tif

Author Manuscript

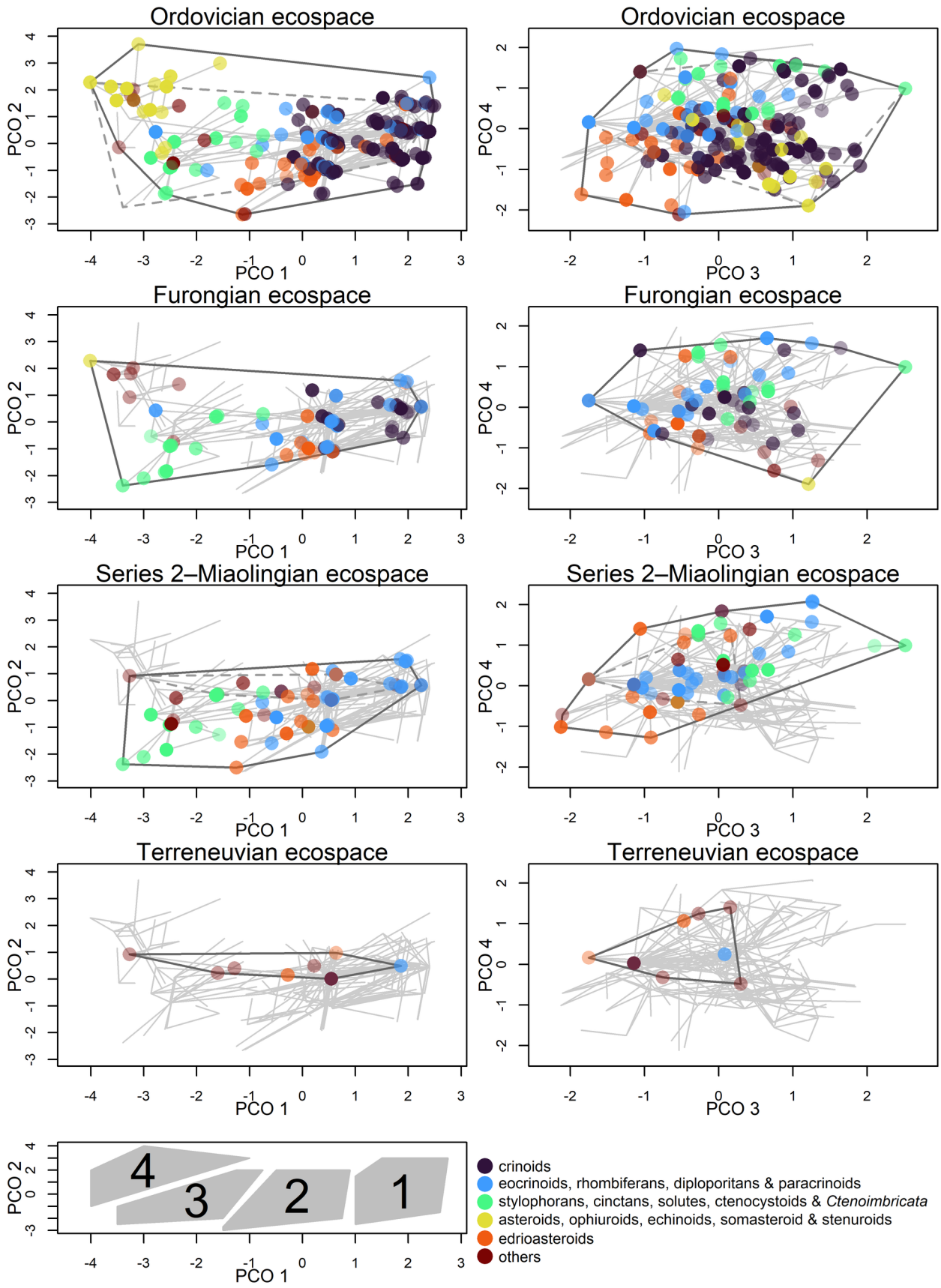


Fig6_Phyloecospace_166.tif