Supporting information

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

By Philip M. Novack-Gottshall, Jack Purcell, Ali Sultan, Isa Ranjha, Bradley Deline *and* Colin D. Sumrall

Appendix S2: Supplementary notes on methods, statistical tests, and ancillary results and discussion

Additional details on coding functional traits, body size, and tiering height

The codings used herein are a subset of a larger database of Phanerozoic marine life habits for 4,511 genera (all but 10 of which are animals, and 570 of which are other echinoderms not presented here, but which allow for increased sampling coverage when inferring missing character states for tip genera). This broader database is occasionally referenced herein when discussing the broader evolutionary context of echinoderm ecology.

To better distinguish the diversity of filter-feeding echinoderms, a new characters was added to the framework of Novack-Gottshall (2007). “Filter density” describes the density of the filter-feeding organ (when present). The character has three states: low density (such as observed in edrioasteroids, plesiomorphic glyptocystitoid rhombiferans, and gogiid eocrinoids), intermediate density (as observed in most ‘homocrinid’ crinoids), and high density (as observed in most iocrinid crinoids).

Body size is its own character in the database (Table 1), but also helps inform the codings of other characters (see below). For each genus, we measured the three cardinal body axes (anteroposterior [A/P], dorsoventral [D/V], and transverse lengths) of the dominant body part (e.g., calyx or theca) of the best-preserved adult specimen for the type or best-studied species,

following the protocol of Novack-Gottshall (2008). For stalked echinoderms, these lengths were measured to generally correspond to the calyx/theca height, width, and depth, with transverse arbitrarily chosen as the maximal diameter when the actual body axis could not be confirmed. Orientations for free-living (stalk-less) echinoderms were made of the oral-aboral plane with D/V length (usually) oriented orthogonally to substratum, and with transverse along the remaining orthogonal plane. For asterozoans, the entire body (including arms) was typically measured, placing each specimen in bilaterally symmetrical orientation with ventral mouth and with single arm at top. Because arms of such taxa are often incompletely preserved, preserved in a bent death posture, or only partially illustrated, missing or bent arms were digitally reconstructed to form a complete reconstruction prior to measurement. Columns (stems/pelmata), holdfasts, aulacophores, and other appendages, attachment, or feeding organs were excluded from body-size measurements, but recorded separately because they are helpful for coding tiering height, attachment, and other characters. When one or more body axes were not available, the missing measurement(s) was estimated by isometrically rescaling the known length of the closest taxonomic relative with nearest stratigraphic range in the larger echinoderm life-habit database. The body sizes were converted to body volume using a standardized equation (Novack-Gottshall 2008), and then $\log_{10}$-transformed to produce discrete, ordered body-size bins (Table 1). Overall, 72% of data set genera have body sizes measured at genus level, 91% at family-or-better, and 96% at order-or-better level.

Several characters (e.g., characters 2–4 in Table 1) code the typical maximum distance that an adult specimen of a taxon inhabits from the seafloor (or immediate substrate) when resting, as well as the equivalent location of where its food is located. These distances—and an estimate of tiering height (referred to here as “absolute stratification distance” [AbsStratDist]

instead of tiering height so that it not limited conceptually to filter feeders)—were obtained by reconstructing the measured specimen in typical resting and feeding postures (and often illustrated in the literature cited above) with stems, arms, or other appendicular or accessory organs attached in resting and feeding orientations. Complete stems (pelmata) are used in these estimates, when available (which is frequently; cf., Brett 1984; Guensburg 1992; Brower 1994; Brett *et al.* 2008; Brower 2011; Cole *et al.* 2018); however, because these are not always available and many echinoderms are described with only partial stems, the resulting AbsStratDist distances should in many cases be treated as a conservative estimate (but likely to be within the same order of magnitude, such as for characters 2–4, and these characters were coded to the next higher state if the available partial estimate was close to the distance for the realistic, next higher state). When the genus lives epibiotically or attaches to a substantial substrate (such as edrioasteroids resting atop strophomenid valves or perched atop conulariids or tall crinoids), these distances also include the height of their typical substrate (which are also often documented in the literature). For consistency, taxa that are raised atop living strophomenids are raised 5.53 mm (the average dorsoventral height across 24 genera in the larger database), those that specifically live atop living *Rafinesquina* are raised 14.5 mm, and those living atop "orthocerid" cephalopod conchs are raised 14.9 mm (half the average across 11 genera to account for the skeleton being half buried in sediment). In all such cases, these substrate additions are documented (Appendix 1). When the body-size algorithm infers missing body sizes, it also estimates AbsStratDist when taxonomically close relatives with such values are available, but only when their AbsStratDist is based on a cardinal body axis (typically D/V height for asterozoans, benthic edrioasteroids, cinctans, and stylophorans, or A/P length for crinoids, diploporitans, and others that live recumbently with their calyx/theca oriented vertically along

the sea floor). Stem lengths and heights of living of shelly substrates are never propagated by this algorithm. The database includes 194 estimates of AbsStratDist (or 53% of tip genera), 167 of which are filter feeders that are included for analyses of tiering below.

Relative food stratification (RelFoodStrat, character 5, Table 1) describes the distance that food is located away from the foraging animal. (In contrast, character 4 [absolute food stratification] describes where the food is located with regard to the sea floor, which may or may not correspond to where the animal forages). Because filter-feeding echinoderms are passive suspension feeders (Labarbera 1984), distance from food can be approximated by flow rate (quantity of food passing the feeding organ in one second), which depends on ambient flow velocity and height in water column. Best (1988) documented ambient water velocity at various distances above the sea floor in a 10-metre-deep subtidal habitat. Generalizing her observations provides the following regression equation: ambient velocity [mm/s] = -0.001 x (height [mm])^2 + 0.694 (height [mm]) + 0.5). This can be simplified to code the smallest passive filter-feeders (those feeding less than 0.7 mm above the sea floor) in state 0 for character 5, those feeding 0.7–14 mm above the sea floor in state 1, those 14–191 mm above in state 2, and those greater than 191 mm above in state 3. We generally follow this convention for consistency for the 90% of Cambrian–Ordovician echinoderms that are filter feeders. For scavengers and hunting predators, RelFoodStrat will usually be proportional to the speed at which the animal can move, or slightly modified depending on inferred sensory abilities (i.e., whether tactile or chemosensory). For such echinoderms, we use the observation that four extant asteroid species moved 1.3–7.7 mm/s, regardless of body size (Mueller *et al.* 2011); therefore, we assign such asterozoans state 1 for character 5 (1–10 mm from forager, Table 1). For deposit feeders, RelFoodStrat will usually refer to the length of the feeding organ. We code such epifaunal and infaunal nonselective

detrital mass-feeders (e.g., asteroid *Cnemidactis*, Blake and Guensburg 1993; Blake and Rozhnov 2007) with state 0 for this character, on the basis that their mouth is in contact with food; for selective deposit feeders (e.g., holothuroid *Palaeocucumaria*, Kerr and Kim 2001), we use the inferred length of the food-gathering podia to estimate this state.

Like for body size (character 1, Table 1), these four distance-based microhabitat characters are converted to $\log_{10}$ bins when coded for characters 2–5. Because the bins each span an order of magnitude, they also limit the impact of over-simplications made when converting complex, continuous measurements into discrete states, or sampling errors made when measuring specimens or assigning AbsStratDist tiering heights. Relevant notes used to guide such codings are noted in Appendix 1 for individual genera. When life-habit character states, body-size measurements, or AbsStratDist distances are estimated algorithmically for tip genera, such propagations are also documented separately in the database for transparency, as well as to allow the estimates to be updated during future implementations as the database continues to grow.

Trends for several characters are not described because they are invariant across all early echinoderms. These include sexual reproduction (character 7, Table 1), fluidic substrate (11), insubstantial substrate consistency (14), incorporeal food (37), and autotrophic (33) and herbivorous diets (35). Mode of reproduction is not unambiguously known for any fossil echinoderm, but the ‘mode’ character state propagation algorithm infers that all fossil echinoderms were able to do meiosis and shed gametes because all extant echinoderms are known to do so. Autotrophy and incorporeal food generally require photoautotrophic feeding habits, which no echinoderms have the ability to do. Fluidic and insubstantial habits involve swimming or pelagic habitats, which are only known to occur among rare holothuroids and

Mesozoic roveacrinids (briefly discussed below). Herbivory (here defined as feeding on plants *sensu strictu* and not seaweeds, which are coded instead here as a form of bulk-feeding microbivory; *sensu* Novack-Gottshall 2007) among echinoderms first only evolves in the Mesozoic, and is restricted to the crown group echinoids.

Combinations of characters and their states can describe commonly used ecological strategies (e.g., the widely used ones of Bush *et al.* 2007). When foraging habits and diets are described, they refer directly to taxa coded as having state 1 for characters 27–31 and 33–36, respectively (Table 1). Exceptions include the low-, medium-, and high-density filter feeders, for which character 32 (filter density) is joined to states 0, 1, and 2, respectively, with character 28 (filter feeder). If no state is specified (or propagated) for character 32, then such filter feeders are placed in category "unknown-density filter feeder." When habitat trends are described, the following character-state combinations are specified [with character number from table 1 in brackets]:

Pelagic: [11] fluidic substrate composition = 1.

Epibiotic: [9] biotic substrate = 1 and [17] above primary substrate = 1 and [19] above immediate substrate = 1.

Tall epifaunal: [17] above primary substrate = 1 and [18] within primary substrate = 0 and [10] lithic substrate = 1 and [2] primary distance > 2.

Intermediate epifaunal: [17] above primary substrate = 1 and [18] within primary substrate = 0 and [10] lithic substrate = 1 and [2] primary distance = 2.

Short epifaunal: [17] above primary substrate = 1 and [18] within primary substrate = 0 and [10] lithic substrate = 1 and [2] primary distance <= 1.

Semi-infaunal: [17] above primary substrate = 1 and [18] within primary substrate = 1 and [10] lithic substrate = 1.

Infaunal: [17] above primary = 0 and [18] within primary = 1 + [10] lithic substrate = 1.

Statistical analysis of body size and tiering height

Tests of body size and tiering height trends are conducted independently for each of the time-scaled phylogenies, using 100 "continuous" time-scale bins. During intervals when sample variance equals zero, the variance is replaced with the pooled variance across intervals. Model support is represented using Akaike weight, with weight greater than 0.5 signifying majority support and weight greater than 0.9 signifying overwhelming support. In the case of tiering, an additional test is conducted to determine whether the distribution of tiering heights is consistent with a mixture of lognormal distributions—that is, whether the tiering heights consist of discrete multimodal tiers. The test uses the mclust R package (Fraley and Raftery 2002, 2007; Fraley *et al.* 2022) to identify the most likely parameters—for each sample of tiering heights within a given epoch—across 18 mixture models (allowing 1 to 9 discrete lognormal distributions that all have equal or unequal variances), using Bayesian information criteria to identify the best-supported model.

Maximum-likelihood analyses (Hunt 2006; Hunt 2022) support that Cambrian–Ordovician echinoderm body-size evolution (Fig. 3A) is best fit by a model of an unbiased random walk (Fig. S2A), although we cannot rule out a weakly driven model. Only three of the 100 time-scaled phylogenies provide majority support (Akaike weight < 0.53) for a driven model, with the remainder supporting an unbiased random-walk model (median Akaike weight = 0.733 across all phylogenies). Although the overall mean body size is relatively constant (Fig.

3A), the large variance and sporadic deviations are sufficiently common so that no trees provide any support for a model of stasis.

Using the same methods as conducted for body size, average tiering height during the Cambrian–Ordovician (Fig. 3B) 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). 78% of the 100 time-scaled phylogenies provide better support for an unbiased random walk model (median Akaike weight = 0.647 across all phylogenies). As was the case for body size, there is no support for a model of stasis.

Likelihood-based statistical analysis of the distribution of epifaunal tiering heights provide little evidence that discrete tiers existed during these periods. For each of the seven epochs, across all 100 time-scaled phylogenies, 449 (75%) of the 600 post-Terreneuvian tiering distributions are best fit by unimodal lognormal distributions (albeit with means and variances that increased through time, Fig. 3B). There is some support for discrete, bimodal tiers during Series 2 (in 70% of the 100 phylogenies), Miaolingian (25%), and Early and Middle Ordovician (27% and 18% respectively), whose means are centered in the 0.5–0.8 and 1.5–2.0 $\log_{10}$ tiering heights with equal variances around each mean (and which is evident in figure 3B by the absence of intermediate raised tiers between clusters of genera with smaller and larger heights). However, the majority of phylogenies during these three epochs remain best supported by unimodal distributions, which also retain close second-best likelihood values.

Interpretation of Cambrian–Ordovician ecospace using the "ecocube" approach

Figure S7 illustrates the life habits for 87 Cambrian and 274 Ordovician echinoderm tip genera, using the "ecocube" framework (Bambach *et al.* 2007; Bush, *et al.* 2007) that characterizes life

habits according to feeding habit, mode of locomotion (including attachment and activity), and tiering habitat. Four Ordovician cyclocystoid genera (surficial suspension-feeders), whose attachment could not be determined with confidence (Appendix 1) are excluded, as are four post-Ordovician genera. Echinoderms coded as intermittently and habitually mobile (character 6, Table 1) are coded here as "fully motile, slow." Epibionts that are raised substantially above the seafloor are coded as "erect." Carnivorous scavengers are coded as "predatory." The sole instance of an erect, sedentary predator is the Ordovician taxocrinid *Protaxocrinus*, which is coded as raptorial given its large, robust, and nonpinnulate arms (Meyer and Lane 1976).

Echinoderms inhabit eight ecocubes during the Cambrian, increasing to 13 during the Ordovician, a 62.5% increase. Most of the expansion is caused by the origins of asterozoans (somasteroids, stenuroids, ophiuroids, and asteroids) and echinozoans (echinoids and stem-holothuroid ophiocistioids). These clades add novel carnivorous, predatory, scavenging, grazing, deposit-feeding, and generally more mobile habits, but their impact is limited because of their low genus richness.

Genera are very unevenly distributed in most ecocubes. Three Cambrian ecocubes include only one genus in each, and six Ordovician ecocubes have less than five genera in each. Two Cambrian ecocubes alone (erect, sedentary suspension feeders and surficial, facultatively mobile suspension feeders) include nearly 70% of Cambrian genera. Surficial, sedentary, suspension feeders are common during both periods, accounting for 11.5% and 7.9% of genera, respectively.The frequency of surficial facultatively mobile suspension feeders declines substantially by the Ordovician, when it accounts for less than 5% of habits. Occurring among members of several classes in each period, the decline is primarily caused by the Miaolingian extinction of cinctans and decreased importance of Ordovician ctenocystoids (represented solely

by the genus *Conollia*), although the habit continues among some Ordovician rhombiferans, solutes, and stylophorans. In contrast, the dominant Ordovician habit is the erect, sedentary suspension feeders, accounting for 68% of genera, mostly crinoids but including many other classes. While the expansion in early life habits is accurately portrayed using this framework, it hides the enormous fecundity that early Palaeozoic echinoderms invented in terms of ecological variation among and within these generalized strategies.

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