# Title: Evolution and Development at the Origin of a Phylum

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**Abstract:**

Quantifying morphological evolution is key in determining the patterns and processes underlying the origin of phyla. We constructed a hierarchical morphological character matrix to characterize the radiation and establishment of echinoderm body plans during the early Paleozoic. This showed that subphylum-level clades diverged gradually through the Cambrian, and the distinctiveness of the resulting body plans was amplified by the extinction of transitional forms and obscured by convergent evolution during the Ordovician. Higher-order characters that define these body plans were not fixed at the origin of the phylum, countering hypotheses regarding developmental processes governing the early evolution of animals. Instead, these burdened

characters were flexible enabling continued evolutionary innovation throughout the clades' history.

**Main Text:**

Developmental and evolutionary mechanisms underpinning the origin of phyla[1] are vital for understanding the nature of the Cambrian explosion and subsequent major radiations of animal life. Many hypotheses have been proposed regarding the triggers[2-4] (or lack thereof[5]), evolutionary drivers[6-8], and morphologic patterns of the Cambrian explosion[8-10], but there are still conspicuous gaps in our knowledge. Foremost is a lack of studies documenting higher-order patterns of morphological evolution through the early Paleozoic Era. Previous studies were limited in taxonomic breadth[11,12] or coarsely compared morphologic diversity between the Cambrian and the Recent[8,13-14]. Hypotheses of maximum initial disparity (diversity of organismal form or characteristics) are prevalent, based on phylum- and class-level taxonomic diversity[9], but this long-standing view has yet to be tested directly because of difficulties quantifying disparity at higher-taxonomic levels. Additionally, it has been proposed that the evolutionary mechanisms crucial to the early evolution and establishment of phyla were non-uniformitarian, and that developmental and genetic processes underlying character evolution at the origins of bodyplans[6,7,15] differed from mechanisms operating later in evolutionary time. However, these results might reflect byproducts of our current taxonomic framework paired with insufficient sampling across the tree of life[16,17].

The rapid appearance and distinctiveness of animal phyla in the fossil record suggest testable hypotheses regarding the variability of higher-order morphological characters that are vital in establishing body plans. The hierarchical nature of animal body plans suggests that characters with a high morphological burden (i.e. a high number of characters contingent on

them) are integral in establishing body regions that characterize higher taxonomic groups and have been retained through evolutionary time[18]. This phenotypic model has been expanded with new discoveries in gene regulatory networks (GRNs) providing a genomically-encoded underpinning to body plan evolution[6,7]. GRNs are hierarchical nested and recursively re-wired. GRN subcircuits have been hypothesized to underlie constraint in body plan evolution and result in morphological characters that are relatively impervious to evolutionary change[6,7]. As a result, the rate of evolution of morphological traits may be dependent on the hierarchical position of the GRN subcircuits that direct their development[6]. However, GRN networks mediate complicated processes that may not be directly analogous to observed patterns in body plan construction[19,20]. Moreover, the constraint in morphology from the evolution of these hierarchical systems has been suggested to be routinely broken and thus not an increasing curtailment of evolutionary potential[18].

Therefore, the distinctiveness of animal body plans could result from the establishment of rigid and hierarchical developmental systems increasing morphological distance between clades. Alternatively, the large morphological separation among modern body plans may result from preferential extinction of intermediaries[8,21], along with the progressive and flexible evolution of higher-order morphological characters. Unfortunately, the evolution of gene regulatory networks in deep time can only be studied with reference to extant taxa[22,23], which are over 500 million years removed from phylum origination. Direct testing is thus restricted to studying the phenotypic expression of these networks within the fossil record.

To examine the evolutionary patterns and processes surrounding the origination and subsequent diversification of a major phylum, the Echinodermata (e.g. sea stars and sea urchins), we compiled an extensive database of early Paleozoic echinoderm morphology to test hypotheses

regarding the patterns of morphological diversification and evolutionary mechanisms underlying the establishment of body plans within a phylum.

## Quantification of Echinoderm Morphology

Echinoderms were ecologically, taxonomically, and morphologically diverse during the Cambrian and Ordovician periods, about 541 to 444 million years ago[24] (Fig 1). During the early Paleozoic, they encompassed more than 30 distinctive clades[25]. This extreme diversity in form presents both an ideal model for exploring evolutionary dynamics and a distinctive challenge for quantifying their morphology. Echinoderms are characterized by a mineralized skeleton that is rich in morphological characters[11], such that the loss of data associated with the degradation of soft tissues during fossilization is minor compared to other taxonomic groups[8,26,27]. Therefore, the recovered trends are not subject to significant preservational biases[28], and skeletal features have been vital for reconstructing evolutionary relationships in early echinoderms. The wide diversity of forms among early echinoderms necessitates character-based studies to accurately quantify morphology. Character-based analyses can also converge on evolutionary patterns inferred by geometric-based studies[29,30]. Furthermore, the interdependence and non-uniform value of information contained within characters allows for direct testing of developmental and evolutionary hypotheses.

We constructed a novel character matrix comprising 413 characters incorporating the range of morphologies in early Paleozoic echinoderms (Table S1). This character suite was constructed hierarchically and attempted to avoid overt phylogenetic signal by including autapomorphies and obviously homoplastic characters. Elements of broad homology schemes such as the universal elemental homology model[31,32] and the extraxial-axial model[33] were used to recognize similar features in disparate body plans. This character suite was used to code 366

early Paleozoic echinoderm genera (Table S2), including a nearly comprehensive sampling of Cambrian and Ordovician echinoderms along with representatives from classes in which definitive articulated body fossils are first recorded from the middle Paleozoic (e.g. holothuroids and ophiocistioids). Morphologic patterns were visualized using principal coordinates analysis (PCO) with Gower's similarity metric[34]. Analyses at a higher taxonomic level necessitate character-based methods, which are valuable exploratory tools although they often have affine properties[35,36]. Furthermore, pairing patterns of morphologic evolution with phylogenetic hypotheses provides an evolutionary context and perspective to anatomical dynamics[37,38]. The echinoderm morphological data were thus combined with an independently constructed phylogenetic hypothesis based on previously published cladistic analyses (Figure S1) in order to map character evolution through the early Paleozoic. Analyses were conducted using the phytools[39], paleotree[40], and ape[41] packages in R version 3.5.1[42].

**Echinoderm Morphological Evolution**

The resulting morphospace (Fig. 2a,b) recovered four major body plans within echinoderms based on k-means clustering. These include non-radial (homalozoans, Fig. 1a), pentaradial directly attached and mobile (edrioasteroids, Fig. 1b and eleutherozoans, Fig. 1c), and two pentaradial groups with stalks (Crinoids, Fig. 1d and blastozoans, Fig. 1e,f), which differ in the area of morphospace they occupy as well as their distinctiveness (i.e. their proximity to other body plans). As expected, the first two axes explain a low proportion of the variance (7.4%, Table S4). However, k-means clustering returned roughly the same four body plans based on 3 (9.5%) and 100 (39.5%) axes (Fig. S5). Later axes reflect lower taxonomic signals differentiating orders and families, particularly among crinoids (Fig. S4). The apparent proximity of these body plans (i.e. overlapping envelopes) within morphospace partially results from the presence of

intermediate forms such as eocrinoids (Fig. 1F), which occupy an area medial to edrioasteroids and pelmatozoans (Fig. 2A). The subsequent extinction of these transitionary forms, therefore, accentuated body plan distinctiveness through time. Alternatively, forms can be extremely morphologically distant early and converge in body plans later in evolutionary time (e.g. blastozoans, such as gomphocysitid diploporitans, Fig. 4e converging on edrioasteroids, Fig. 4b). The distinctiveness of echinoderm body plans is thus emphasized by the extinction of transitional forms and confounded by subsequent convergent evolution.

This pattern is inconsistent, however, with the morphological dynamics observed between non-radial and radial echinoderms. There is little overlap in morphological space between early non-radial body plans and pentaradial forms (Fig. 2b). This distinctiveness is apparent from the first appearance of these body plans in the Cambrian and is largely maintained through the early Paleozoic (Fig. 2c). This may be the result of an incomplete fossil record in which transitional forms have yet to be recovered or recognized. Alternatively, symmetry may inherently be a strongly burdened character such that the transition from bilateral or asymmetrical to pentaradial required significant shifts in developmental or constructional constraints that resulted in rapid morphological change. As subsequent paedomorphic evolution of pentaradial forms during the Ordovician resulted in taxa bearing triradial and bilateral ambulacra[25], the vestige of pentaradial symmetry remained such that the morphological gap between the major body plans persisted despite similarities in ambulacral symmetry.

The distribution of classes within each of the four major body plans also varies. The four classes in the non-radial cluster (Ctenocystoidea, Cincta, Stylophora, and Soluta) are all distinctive and non-overlapping (Fig. 2a). Their early appearance, early extinction within some groups, basal phylogenetic position, and the lack of overarching control on symmetry (building

morphological separation in morphospace) may have accentuated the morphological differences between their bodies, which are present in distinctive clusters in morphospace. In contrast, stalked echinoderms mostly diversified during the Ordovician following the evolution of several key features (e.g. erect feeding appendages and structured theca), while ensuing morphological diversification and iterative evolution produced many similar forms within a particular ecologic niche.

Patterns of morphologic disparity differ according to the metric used (Fig. 2e,f), and these metrics highlight different aspects of early Paleozoic echinoderm evolution. The variance (i.e. preordination distance) steadily increased through the Cambrian, despite low generic richness (Fig. 2d), as major body plans appeared, separated, and intermediates became extinct (Fig. 2e). The variance then plateaued during the Ordovician despite a dramatic increase in generic richness (i.e. the Great Ordovician Biodiversification Event), reflecting morphologic expansion within rather than between major body plans. The ratio of generalized variance avoids the non-metric properties of character-based ordination, providing a meaningful measure of the relative spread of taxa within morphospace[36]. The ratio of generalized variances based on the first three axes indicates little expansion through the Cambrian, followed by a dramatic increase into the Ordovician. As more axes are included in the analysis, the expansion in the Late Ordovician is amplified (Sup. Fig. S3), consistent with the later axes capturing within group diversification. The establishment of the three major body plans is captured by the variance, but their spacing is static, such that the metric plateaus throughout the Ordovician. However, the ratio of generalized variance captures the spread within the body plans (e.g. class-level expansions), including a large increase during the Early Ordovician capturing the appearance and diversification of extant groups such as crinoids and asterozoans. This indicates that the opportunity for morphologic

innovation was not restricted to the initial burst of body plan evolution, but continued through the phylum's history with the staggered appearance of class-level characteristics emphasizing the high plasticity of echinoderms. Whether this capacity is later diminished following major extinctions, as has been suggested in class-level studies[44, 45], or with increasing developmental constraint[46], could be addressed by extending the temporal coverage of the current dataset.

**Constraints, Modularity, and Evolutionary Processes**

Elucidating patterns of phylum-level morphologic evolution provides insight into the mechanistic underpinning of these macroevolutionary patterns. Morphological characters that determine body plan-level anatomical structures have been proposed to carry a heavy burden and, thus, have a lower chance of evolutionary change or loss[18]. It has been suggested that the evolutionary constraint on these more heavily burdened characters is underlain by the evolvability of their underlying GRNs, with body plan-level characters underlain by recursively wired networks of regulatory genes higher up in a GRN hierarchy[7]. To test this pattern, characters were mapped onto an independently constructed phylogenetic hypothesis (Figure S2). The phylogenetic signal[47] was calculated for each character and compared with that character's burden, i.e. the number of contingent characters. There is no trend between morphologic burden and phylogenetic signal (Fig. 3), countering the predicted model[17].

This pattern suggests that body plan-level characters were not static during the establishment of Echinodermata and retained the ability to change during the progressive evolution of individual classes. This result is consistent with the steady expansion of morphologic space occupied by echinoderms during the early Paleozoic, as well as the breakability of functional constraint[19,20]. For example, crinoids occupied a new area of morphospace when they evolved during the Ordovician, through a novel combination of

191 character suites that all appeared in earlier echinoderm groups (e.g. structured theca, arms, and
192 columnal-based pelma), rather than the evolution of new, fixed, and burdened characters.
193 Furthermore, these higher-order character suites can be altered, lost, or reacquired. For example,
194 the Middle Ordovician crinoid *Tripatocrinus*[48] lost a heavily burdened character (arms) and
195 reacquired a previously lost module (recumbent ambulacra). Heavily burdened features may
196 become developmentally constrained over time, as has been observed in extant taxa[18], but the
197 appearance of burdened features is not establishing the body plan characteristics of higher
198 taxonomic groups. The tightly wired GRNs present in extant taxa may result from subsequent
199 additionally recursive rewiring during the hundreds of millions of years since phyla were
200 established, but these processes are unlikely to be directly correlated with the initial evolution of
201 higher-order traits[47]. In addition, many simple (unburdened) traits have high levels of
202 phylogenetic significance and are strongly conserved, such that the complexity of GNRs might
203 be independent of the complexity of morphological characters.

204 The wiring of GRNs may play a role in the establishment and maintenance of very high
205 order characters (e.g. cell or tissue types[50]), but anatomical characters such as symmetry and
206 skeletal architecture as explored in the current study are not consistent with this evolutionary
207 model. Although parts of GRNs may be directly homologous between organisms, particular
208 regulatory genes can be co-opted and changed to control the development of new characters.
209 Furthermore, developmental systems drift, where evolutionarily divergent GRNs control the
210 development of morphologically homologous structures, which may result in an unclear
211 relationship between morphological characters and the genomic regulatory basis of their
212 development[50,52]. These concepts, paired with our analyses, necessitate a more flexible
213 evolutionary system than a model of character evolution underlain explicitly by the hierarchical

nature of GRNs. Our results suggest regulatory genes and character suites are decoupled, but the modular nature of GRN subcircuits may be responsible for the flexible nature of character suites[19,52]. This potentially supports deep homology[52] of some of these reoccurring modules in our character set and prolonged plasticity in echinoderm evolution. For instance, calcitic stereom is a fundamental synapomorphy of the echinoderm body plan and the suite of transcription factors and signaling molecules underlying echinoderm biomineralization is conserved across wide phylogenetic distance[49], and likely follows this model. Within crinoids, entire body regions such as anal structures[53] or the mouth frame[32] decalcify, indicating a modular regulation of skeletogenesis. The modular plasticity is further illustrated by the reappearance of a calcified oral region in a Mississippian crinoid within a lineage that lost it a hundred million years previously[32].

To further investigate morphologic evolution and constraint, we constructed a theoretical morphospace[54]. Given the size of the full character set, the number of possible character combinations is immense (~$9.55 \times 10^{212}$). Thus, we reduced the morphological dataset to 35 characters (Table S3) that capture body plan-level features (e.g. broad or heavily burdened). We then randomly modeled 5000 theoretical echinoderms with and without including character contingencies and missing data consistent with the level of preservation of particular characters. These theoretical echinoderms were then analyzed with actual early Paleozoic genera to compare theoretical and realized morphologic space (Fig. 4).

The theoretical echinoderms modeled without character contingencies occupy a broad and continuous area in morphospace. However, when contingencies are added this space fragments into four non-overlapping regions within morphospace. These gaps represent character combinations that are impossible given the constructional relationships among characters, thus

237 the addition of morphological constraint (e.g. character contingencies) both restricts morphology
238 in the area surrounding these basic body plans and creates empty pockets of theoretically
239 impossible forms. However, the diversity of modeled forms overall is not constricted, thus the
240 constraint fragments without limiting evolutionary potential. The overall distribution of early
241 Paleozoic echinoderms is retained within this reduced character set, but differs in having
242 increased distance between some non-radial echinoderm classes (homalozoans). The
243 phylogenetic path traversed by early Paleozoic echinoderms crosses the space that is
244 constructionally unoccupied and likely improbable. Therefore, the paths are not continuous and
245 linear, representing bursts of evolution rather than continuous change. This also implies that
246 transitions in burdened characters can underlie significant jumps across morphospace and that
247 large gaps in morphospace, such as the one between non-radial and pentaradial forms, might
248 represent the evolution of new modules rather than an increase in evolutionary rate or a gap in
249 preservation.

250 The explored region of the modeled theoretical space is fairly minimal, which is likely a
251 product of the character contingencies, developmental processes, as well as selection, ecology,
252 and random events. The extent of exploration differs between the various body plans. Stalked
253 echinoderms occupy a wide range of morphospace and abut the edge of the theoretical area,
254 whereas other groups such as edrioasteroids or lepidocystoids never explore more distal and
255 theoretically plausible forms. This is evident in the broad morphology of these two groups;
256 stalked echinoderms vary with respect to many burdened characters such as the organization of
257 the theca, symmetry, feeding appendages, stalks, ambulacral structures, and respiratory
258 structures, whereas edrioasteroids either lack these structures or lack any variation in them and
259 thus appear more constrained. Ecology-driven morphological evolution likely plays a lesser role

in these patterns given that edrioasteroids and stalked echinoderms, which are both attached suspension-feeders, are contained within the same broad niche. In addition, shared ancestral plating[29,30] and observed morphologically transitional forms indicate that their two body plans likely had a similar underlying developmental toolkit. Therefore, the differences in disparity and complexity between these groups may indicate a loss in developmental potential following the divergence of the echinoderm body plans. This may suggest a staggered establishment of constrained GRN circuits, such that different lineages become more constrained at different intervals within their history. The continued flexibility of higher-ordered characters and potential staggered constraints highlights the importance of the evolutionary dynamics beyond the initial morphological diversitification of the phylum.

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**Data and materials availability:** All data is available in the main text or the supplementary materials.

**Supplementary Information** is available for this paper.

**Fig. 1.** Representative early Paleozoic echinoderms showing the range of body plans. (A.) The Cambrian ctenocystoid *Ctenocystis*, non-radial (NHMUK E63150)[55]. (B.) The Ordovician edrioasteroid *Edrioaster*, pentaradial attached (CMC IP51986)[56]. (C.) The Ordovician echinoid *Bromidechinus*, mobile (NHMUK EE6632a). (D.) The Ordovician crinoid *Anomalocrinus*, pentaradial stalked (CMC 55140). (E.) The Ordovician diploporitan *Gomphocystites*, pentaradial stalked (FMNH 19708)[57]. (F.) the Cambrian eocrinoid *Sinoeocrinus*; pentaradial stalked (GM 9-3-1382)[53]. *Abbreviations:* NHMUK, Natural History Museum (UK); CMC, Cincinnati Museum Center (USA), FMNH, Field Museum of Natural History (USA); GM, The Paleontological Museum, Guizhou University (China).

**Fig. 2.** Morphological evolution in early Paleozoic echinoderms. (A.) Morphospace of early Paleozoic echinoderms grouped by taxonomic class as well as the major clades (B.) Phylomorphospace of early Paleozoic Echinoderms, colors match those used in (A). Ancestral positions based on stochastic character mapping. (C.) Exploration and morphospace occupation of early Paleozoic echinoderms through time: orange: non-radial; green: pentaradial with stalks; blue: pentaradial with stalks, crinoids; purple: pentaradial attached; and red: mobile. (D.) Echinoderm generic richness. (E, F.) Morphologic disparity through time as measured as the pre-ordination average squared Gower distance between taxa (E) and the ratio of generalized variance (F) based on the first three PCO axes binned by epoch.

**Fig.3.** Comparison between phylogenetic signal and character burden. Phylogenetic signal is calculated as a stochastic mapping variation of the δ-value (Sup. Materials). Highly burdened characters are shown on *Sinoeocrinus* (bottom right) and *Edrioaster* (top right).

**Fig. 4.** Theoretical and actual morphospace occupation of Paleozoic echinoderms based on a subset of 35 morphological characters. Light Gray: 5000 modeled echinoderms in which the character states are based on those observed in early Paleozoic echinoderms. Dark Gray: 5000 modeled echinoderms in which the character states are based on those observed in early Paleozoic echinoderms with contingencies between characters included. Colors of the body plans match those used in Fig. 2.

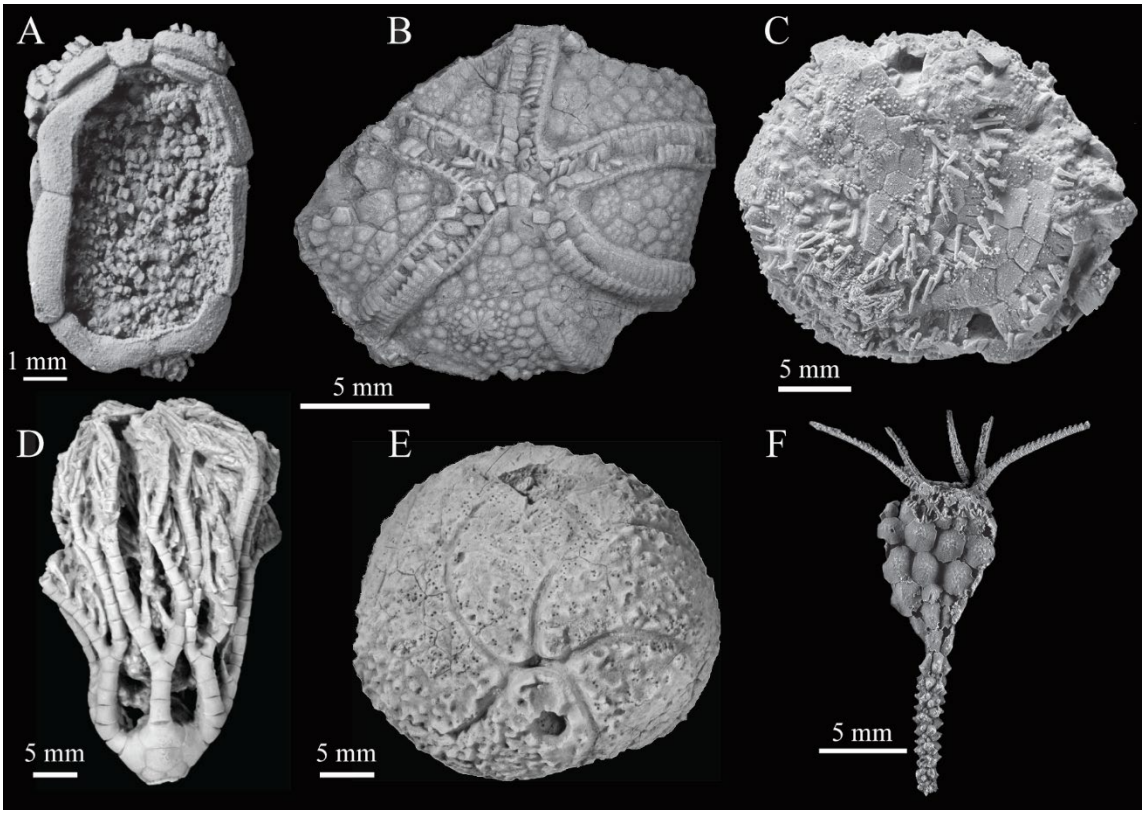



**Figure 1**

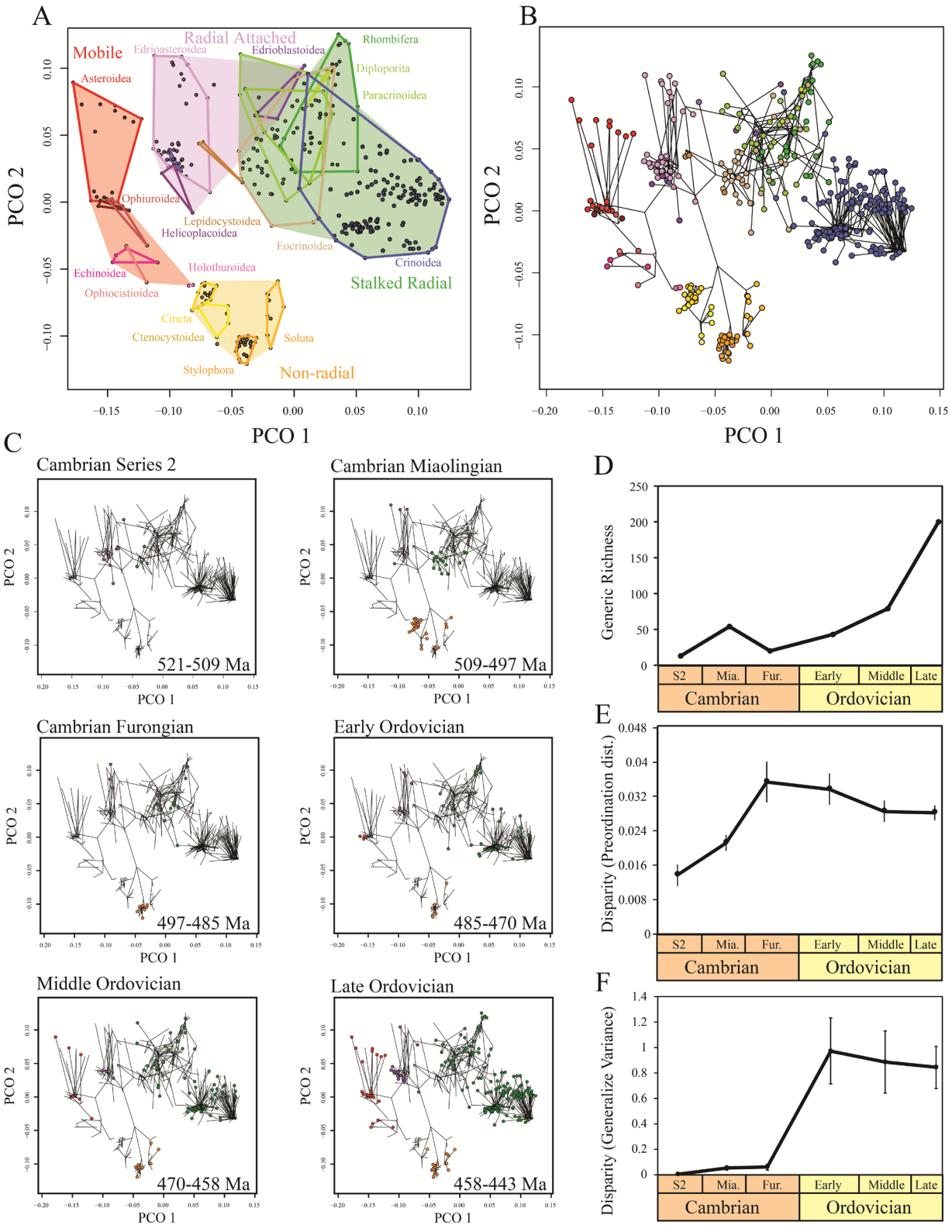

A
Mobile
Radial Attached
Stalked Radial
Non-radial
Asteroidea
Edrioasteroidea
Edrioblastoidea
Rhombifera
Diploporita
Paracrinoidea
Ophiuroidea
Lepidocystoidea
Helicoplacoidea
Eocrinoidea
Crinoidea
Echinoidea
Holothuroidea
Ophiocistioidea
Cincta
Ctenocystoidea
Soluta
Stylophora
PCO 1
PCO 2
B
C
Cambrian Series 2
521-509 Ma
Cambrian Miaolingian
509-497 Ma
Cambrian Furongian
497-485 Ma
Early Ordovician
485-470 Ma
Middle Ordovician
470-458 Ma
Late Ordovician
458-443 Ma
D
Generic Richness
E
Disparity (Preordination dist.)
F
Disparity (Generalize Variance)
S2
Mia.
Fur.
Early
Middle
Late
Cambrian
Ordovician

**Figure 2**

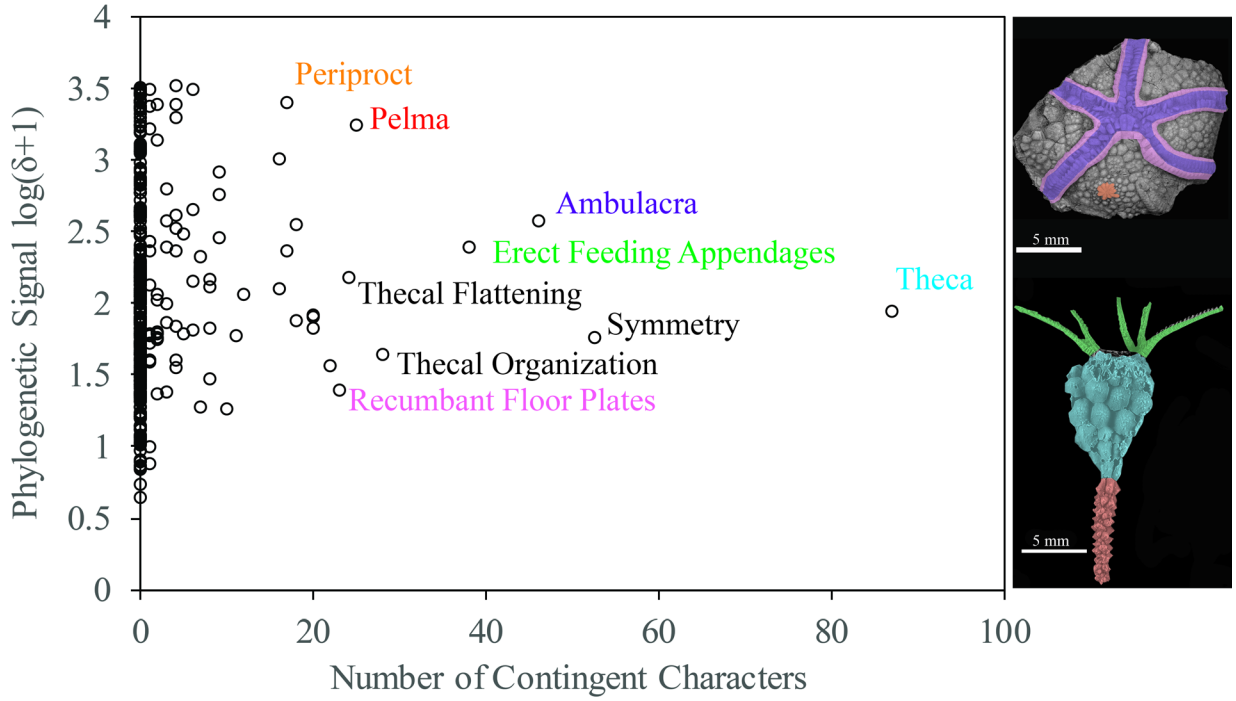
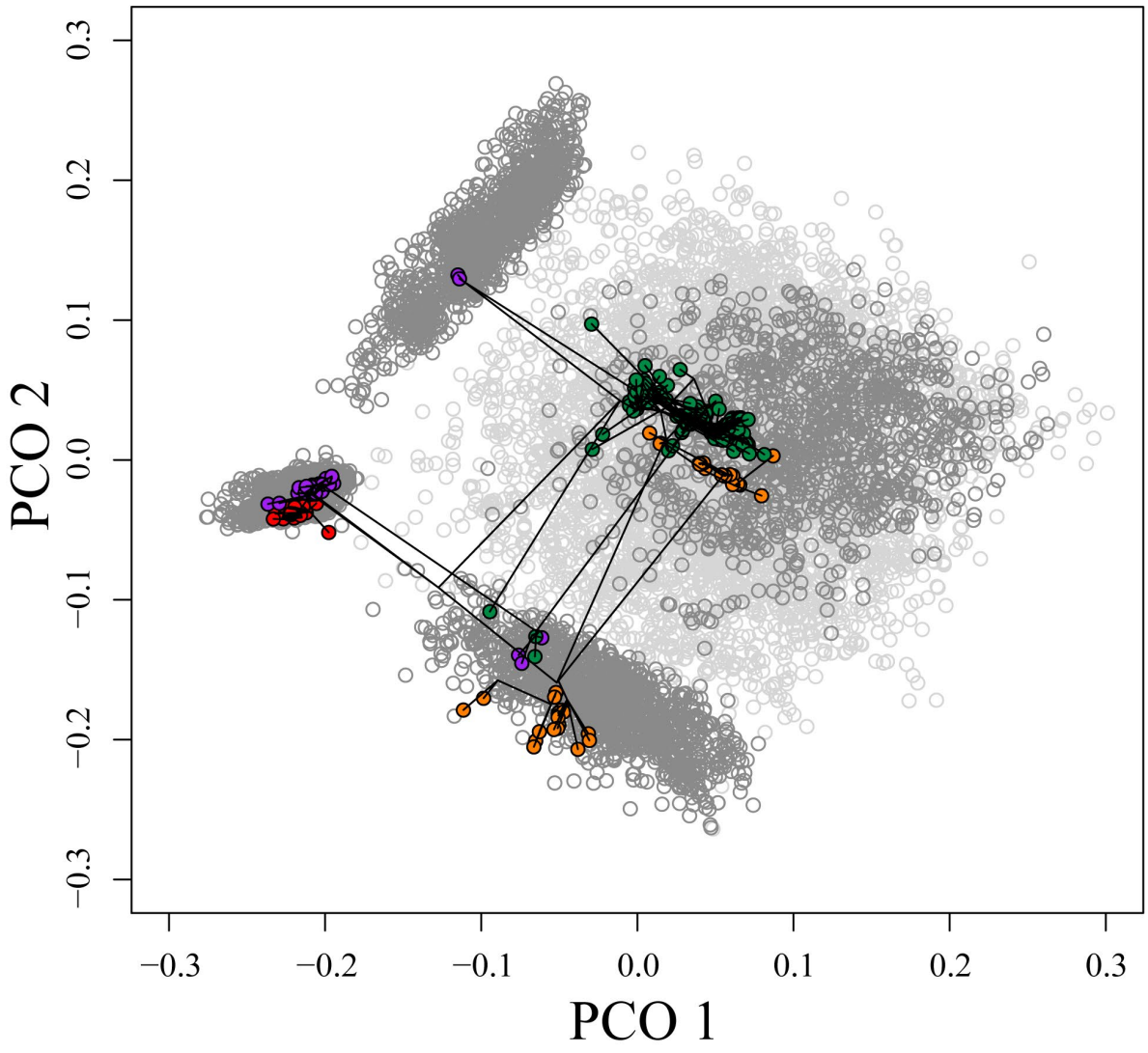

Phylogenetic Signal log(δ+1)
Number of Contingent Characters
Periproct
Pelma
Ambulacra
Erect Feeding Appendages
Thecal Flattening
Symmetry
Thecal Organization
Recumbant Floor Plates
Theca
5 mm
5 mm

**Figure 3**




453

454 **Figure 4.**
455