PALAEOECOLOGY

Early echinoderms decouple form and function

Rapid morphological evolution in early echinoderms was later outpaced by increases in ecological diversification, indicating the phylum exhibited morphological volatility and ecological constraints at its origin.

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Evolutionary radiations at the origins of phyla and other higher taxa are typically characterized by increases in both morphological and ecological diversity. Such diversifications may be adaptive radiations, where ecological opportunity is responsible for the generation of morphological novelty and the emergence of new taxa, or alternatively, ecological and taxonomic diversity may be driven by limits on the evolution of novel morphological forms (for example, developmental constraints)[1,2]. While ecological and morphological innovations are not mutually exclusive drivers of diversification, the nature, interaction and relative roles of each are key to understanding how and why clades successfully diversify. The two are difficult to disentangle, however, and while morphological disparity has been investigated extensively at the origins of major clades[3], ecological disparity has received comparatively less attention. Writing in *Nature Ecology & Evolution*, Novack-Gottshall and co-authors[4] directly investigate this topic by evaluating the early morphological and ecological dynamics of phylum Echinodermata during the Cambrian and Ordovician periods (around 540–440 million years ago). By using separate morphological and ecological datasets for over 360 taxa (encompassing all echinoderm lineages known from the study interval) in combination with a phylogenetic framework, they are able to independently evaluate morphological and ecological dynamics in parallel during the phylum's origin. Within this remarkably detailed framework, their findings show that ecological and morphological disparity follow markedly dissimilar evolutionary trajectories, with many implications for understanding the nature of ecological versus morphological diversification during evolutionary radiations.

Fossil echinoderms are particularly suited to this study due to their skeletal construction of individual calcium carbonate plates ranging in number from dozens into the thousands depending on the clade. This multi-elemental skeleton provides a rich source of character data that has made fossil echinoderms a model group for studies of morphological evolution[5,6] and facilitates a well-understood phylogeny for the group[7–9]. Recently, these strengths were leveraged to characterize patterns of morphological disparity during the radiation of Cambrian to Ordovician echinoderms[10].

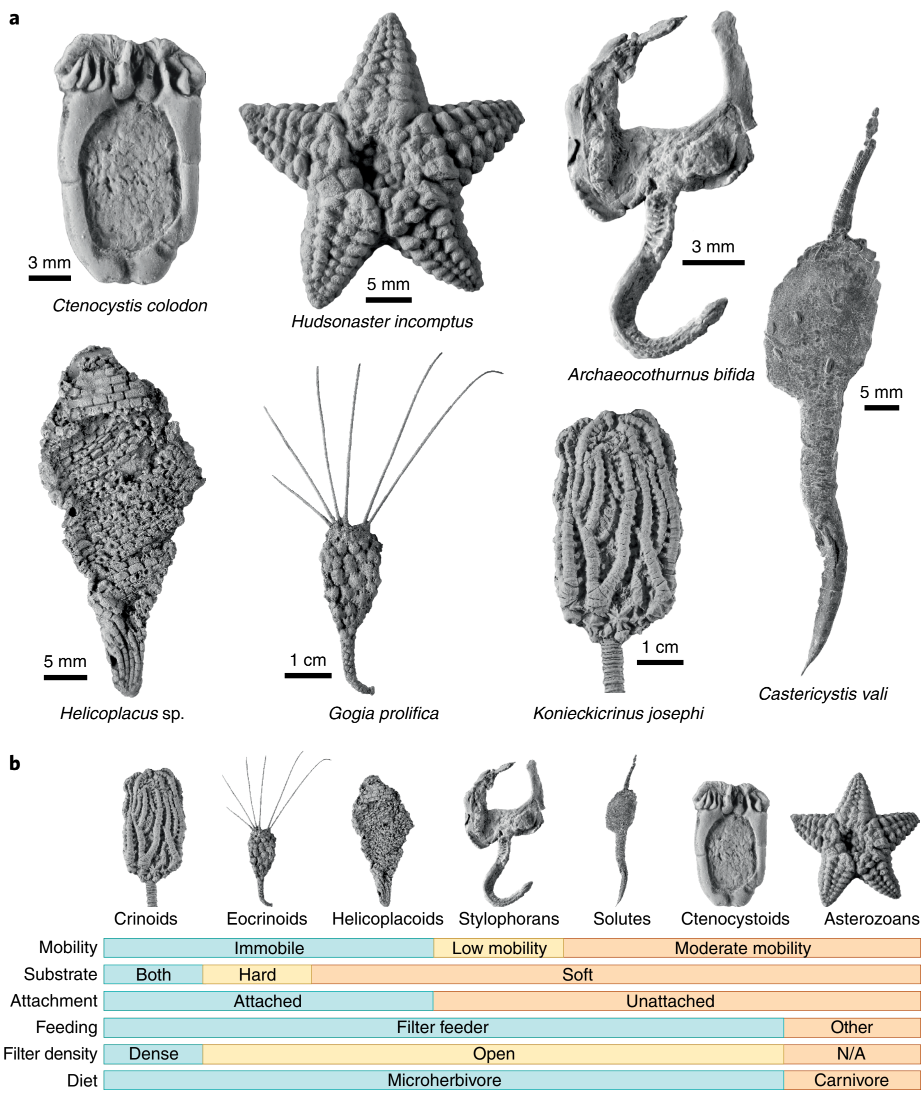

Fig. 1 | Examples of morphological and ecological disparity in Cambrian and Ordovician echinoderms. **a**, Representative echinoderms showing the breadth of body plans, including extreme variations on symmetry. **b**, Examples of functional ecological strategies that are common within major groups of echinoderms, highlighting the presence of extensive overlap of certain ecological strategies between distantly related groups (variations on ecological strategies within groups are not shown).

The phylum reached peak class-level diversity and morphological disparity during this time and experimented with extreme variations in body plans[10] (Fig. 1a).

Building off this existing framework for morphological disparity, which comprises over 400 anatomical traits, Novack-Gottshall et al[4]. add an important new source of data: functional ecology. Although summarizing ecological traits of hundreds of wildly disparate fossil taxa is no small feat, they accomplish this by applying a previously developed framework to the echinoderm fossil record that quantifies the positions of taxa in ecospace using a series of taxonomically independent life-habit traits[11]. The resulting novel ecological dataset for echinoderms includes 40 characters reflecting a wide range of factors that describe how echinoderms interact with their environment and with other organisms, including body size, mobility, reproduction, substrate preference, foraging habit, diet and microhabitat (Fig. 1b). As a result, their study is able to contrast dynamics of morphological disparity with those of ecological disparity. This approach is particularly notable because few palaeontological studies to date have evaluated morphological and ecological disparity using separate datasets[12,13], especially for higher taxonomic ranks such as phyla. Novack-Gottshall and colleagues take an analytically rigorous approach to evaluating diversification dynamics, including the use of multiple disparity indices to capture different aspects of trait space occupation and methods that account for character dependence[14]. Likewise, patterns were evaluated within a phylogenetic context to examine how ecology and morphology differ with regards to relationships among echinoderm lineages, and care was taken to establish results were robust to many potential biases.

The most prominent result emerging from this investigation is that morphological and ecological disparity exhibit dramatically different dynamics during the early history of echinoderms. The authors demonstrate that morphological disparity quickly increased and exceeded ecological disparity by the middle Cambrian, consistent with previous investigations[10]. They show that this was possible in part because rates of morphological evolution were substantially faster overall than those of ecological diversification. By contrast, ecological innovation continued at a slower, steadier pace during the Cambrian and eventually outpaced morphological disparity around the beginning of the Ordovician. This establishes that peak morphological novelty preceded peak ecological diversification by about 11 million years, refuting the idea that ecological success is an essential precursor to morphological diversification (at least at broad taxonomic scales). It further demonstrates that ecological evolution was subject to greater constraints than morphological evolution was during the early diversification history of echinoderms.

During the Late Cambrian to Early Ordovician, two echinoderm classes went extinct and at least eight others evolved. This class-level turnover event resulted in dramatic changes in the total amount of morphospace occupied as several new asterozoan, crinoid and echinozoan body plans evolved. Conversely, the trajectory of ecological diversification remained relatively unaffected because few novel ecological strategies were lost or evolved during this time. Instead, gradual ecological diversification arose from tinkering with existing strategies rather than the evolution of novel modes of life, resulting in repeated convergence of phylogenetically distant taxa on similar ecological strategies, such as filter-feeding (Fig. 1b). Fundamental differences between ecological and morphological evolution are further revealed by the significantly higher phylogenetic signal for morphological characters than for ecological characters, and much lower rates of convergence in morphology compared with ecology.

In addition to these findings, this study raises many intriguing areas for further study, such as the discovery that the tempo of ecological innovation is much slower than that of morphological evolution. This is somewhat surprising, as it is widely (though not universally) held that ecological traits tend to have higher evolutionary rates than morphological traits[15,16]. This may, in part, represent an issue of scale in how ecology is characterized. Although Novack-Gottshall et al. used sample standardization to account for differences in the number of morphological versus ecological characters, a more detailed ecological dataset might recover nuances in ecological strategies that are masked at higher levels yet fundamental for niche partitioning, such as has been shown for early crinoid echinoderms[17]. While such a dataset may be impractical to construct for a phylum-level investigation, it would be a valuable future study area for echinoderm subclades.

Overall, the study presented by Novack-Gottshall and co-authors[4] provides a welcome large-scale investigation of morphological and ecological dynamics and should stimulate many subsequent analyses of evolutionary diversification. For example, adapting the methods used by the authors to characterize functional ecology[11] for other fossil groups would allow future investigations into how ecological and morphological dynamics differ between clades and across ecological and taxonomic scales. These studies could help to establish whether there are fundamental commonalities or 'rules' to diversification dynamics, or whether each clade's evolutionary history is dictated by its own unique set of intrinsic and extrinsic conditions. ❐

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Published online: 10 February 2022

https://doi.org/10.1038/s41559-022-01664-8

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Competing interests

The author declares no competing interests.