

## ENVIRONMENTAL CONTROLS OF RAPIDLY DIVERSIFYING ECHINODERMS DURING THE EARLY PALEOZOIC

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Echinoderms were among the earliest phyla to exploit global environmental shifts leading to the rise of the Paleozoic Evolutionary Fauna during the Ordovician. Echinoderms including crinoids and rhombiferans diversified more rapidly and actually precede other groups such as bryozoans, corals, and many articulate brachiopods in the record. We argue that preadaptive morphologic strategies among the echinoderms coupled with newly available and widespread living space led to this success.

Sessile attached echinoderms, especially crinoids and some blastozoans, dominate echinoderm faunas generally throughout the Paleozoic. These organisms were rheophilic suspension feeders with elongate stalked morphologies capable of attaining high feeding levels above competitors. However, this morphology required firm attachment. Suitable sites were relatively rare in Early and especially Middle Cambrian time when shelf and slope sedimentation was dominated by fine siliciclastics and nonbiogenic carbonates resulting in extensive soft substrates. Sea level was relatively low during the Middle Cambrian, restricting shallow shelf living space. Stalked echinoderms then lived attached to scattered bioclastic fragments but had low diversity and were a relatively minor component of the faunal record. Mode of occurrence and morphologic features suggest they were generally unable to cope with soft and unstable substrates. Nearshore shelf sedimentation styles changed during the Late Cambrian and Early Ordovician to bioclastic-dominated carbonates and organic buildups. These were often subject to intermittent storm events and rapid submarine cementation of the seafloor because of changes in global atmospheric and seawater chemistry. This resulted in formation of hardgrounds on intraformational conglomerates, grainstones, and buildups. Gradual sea level rise beginning in the Late Cambrian and continuing through the Early Ordovician was a major contributing cause for these changes. The widespread lithified substrates provided ideal attachment sites for the preadapted echinoderms and greatly expanded the total habitable area, resulting in rapidly increasing diversity.

Among crinoids, disparid inadunates were the first to extensively exploit this situation and they dominated throughout the Early Ordovician. Attached blastozoans were also common both in the Late Cambrian and Early Ordovician. Later, many camerate and cladid inadunate crinoids and a few blastozoans developed attachment styles suitable to soft substrates, continuing and expanding this diversification. Some previous authors have misidentified life modes of these Cambro-Ordovician echinoderms because they used forced scenarios based on phylogenetic analysis alone. In contrast, we argue that life modes and paleoecologic settings are basic field-derived data that should be used along with morphologic character analysis to determine phylogenetic relationships. Both the fossils and their environmental settings must be studied together to reconstruct the adaptive history and phylogeny of a rapidly-radiating group.