



Causes and consequences of ecospace colonization on the diversification of Early Palaeozoic echinoderms

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Marine communities can be characterized by their occupation of ecospace and its evolution through time. The ecospace gives an account of the vertical tiering, the motility level, and feeding mechanisms. At least two of these aspects are directly related to substrate properties. In Early to Middle Cambrian times, the dramatic increase of bioturbation in soft substrates caused a major palaeoecological transition from relatively firm, non-bioturbated to poorly bioturbated Proterozoic-type sea-bottoms, sealed by microbial mats, with a sharp water sediment interface, to much soupier, vertically highly bioturbated Phanerozoic-type sea-floors, with higher water content in the sediment. From late Middle Cambrian to Middle Ordovician times hard substrates became increasingly frequent by consolidation of cobbles or large shells or by early diagenesis of soft substrates. Marine benthic communities were strongly affected by this Cambrian substrate revolution. The evolution of the position in the ecospace of Cambro-Ordovician echinoderms is a good example to illustrate the impact of this dramatic palaeoenvironmental shift on a major group of benthic metazoans.

The morphology of Early Cambrian echinoderms suggests that most of them were adapted to Proterozoic-type substrates (e.g., *Camptostroma*, edrioasteroids, helicoplacoids, lepidocystids). Middle Cambrian echinoderms (e.g., early gogiids, lepidocystids) first experienced the expansion towards Phanerozoic-type substrates. The associated morphological innovations correspond to the acquisition of peduncles, which *i*) ease the attachment on hard skeletal part and/or on large algae (e.g., primitive eocrinoids and solutes), and *ii*) slightly increase their vertical tiering. In the Middle

Cambrian - Middle Ordovician time interval, the colonisation of soft Phanerozoic-type substrates may be at the origin of *i*) the variations observed in the motility level of early echinoderms (non-motile attached to free, vagile mode of life), and *ii*) many substantial morphological transformations, expressed by the convergent acquisition of an aboral appendage and a deep modification of the original body wall shape. In the Upper Cambrian, the progressive development of hard substrates could have driven the transformation of peduncle to stem, and thus, significantly, contributed to the increase of the vertical tiering in echinoderms (from surficial to erect at a high level). The resulting variations of ecospace occupation in early echinoderms could be related with their diversity dynamics. Periods of strong ecospace colonisation could correspond to periods of high evolutionary rates and phylogenetic diversification (Cambrian).