Evolutionary paleoecology of the earliest echinoderms: Helicoplacoids and the Cambrian substrate revolution

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ABSTRACT

Bioturbation in neritic siliciclastic settings during the Proterozoic-Phanerozoic transition increased in depth and intensity, causing a change in substrates from the matgrounds characteristic of the Proterozoic to the mixgrounds characteristic of the Phanerozoic. This change in bioturbation increased the water content of surficial layers of sediment and blurred the sediment-water interface, leading to the first appearance of a mixed layer. Development of a mixed layer throughout neritic environments would have had a strong impact on any benthic metazoans, particularly sessile suspension feeders, that were well adapted for survival on relatively unbioturbated Proterozoic substrates. The impact of this substrate transition on benthic metazoans has been termed the "Cambrian substrate revolution." The unusual Early Cambrian helicoplacoid echinoderms were well adapted for survival on typical Proterozoic-style substrates. The examination of new helicoplacoid specimens collected during this study, combined with extensive study of the rocks in which they are preserved, indicate that helicoplacoids lived as sediment stickers on a muddy substrate that underwent only low to moderate levels of strictly horizontal bioturbation and did not have a mixed layer. The significant increase of bioturbation through the Cambrian in neritic siliciclastic settings is likely to have led to the extinction of the helicoplacoids. Other similarly adapted sessile suspension-feeding echinoderms may have also been driven to extinction by the effects of the Cambrian substrate revolution. The co-existence during the Cambrian of organisms adapted to the variety of substrates characteristic of this transitional period may also have contributed to the high degree of perceived morphological disparity during the Cambrian "explosion."

Keywords: helicoplacoids, Cambrian, echinoderms, bioturbation.

INTRODUCTION

The Cambrian is characterized by a variety of benthic animals with morphologies that seem strange to the modern eye (e.g., Gould, 1989). In particular, Cambrian echinoderms have long intrigued paleontologists. Perhaps the strangest are the helicoplacoids, small benthic animals covered with unusual helically arranged columns of calcite plates and triradiate ambulacra, which occur only in the Lower Cambrian of North America (Durham, 1993). Along with edrioasteroids they are the earliest undisputed echinoderms in the fossil record (Sprinkle and Guensburg, 1997). Molecular data indicate, however, that echinoderms may have first evolved as long ago as 1000 Ma (e.g., Wray et al., 1996), so that ancestors of helicoplacoids with unmineralized skeletons likely had a history before the Early Cambrian.

While previous workers (Durham and Caster, 1963; Durham, 1967, 1993; Derstler, 1982; Paul and Smith, 1984) have studied the phylogenetic relationships, functional morphology, and life mode of helicoplacoids, they never closely considered characteristics of the environments in which they and their ancestors lived and evolved or possible causes for their extinction. Recent studies have shown that the Cambrian was a time of profound environmental change for organisms living on soft substrates. During this time soft subtidal seafloors in neritic environments were undergoing a transition from nonactualistic earlier substrate conditions dominated by surficial microbial mats and/or horizontal surface bioturbation, characteristic of the late Neoproterozoic, to substrates more characteristic of the post-Cambrian, which lacked microbial mats but included both horizontally and vertically directed bioturbation and the first appearance of a well-developed mixed layer (e.g., Droser, 1987; Droser and Bottjer, 1988; Droser et al., 1999; Hagadorn and Bottjer, 1999; Seilacher, 1999; Seilacher and Pflüger, 1994). Mixed layers constitute the soupy upper few centimeters of the substrate that are homogenized by bioturbation and are characteristic of later Phanerozoic fine-grained substrates (e.g., Ekdale et al., 1984).

These more typically late Neoproterozoic substrate conditions were characterized by a fairly stable, relatively low water content sediment surface and by a sharp water-sediment interface. The transition to the new substrate style, due to further evolution of bioturbating organisms, was termed the "agronomic revolution" by Seilacher and Pflüger (1994). These substrates, because of the development of the mixed layer, are characterized by a blurry sediment-water interface, greater water content, and lack of a well-developed microbial mat covering. The effects on nonburrowing benthic organisms of this change in seafloor conditions have been termed the "Cambrian substrate revolution" (Bottjer and Hagadorn, 1999). This research was undertaken to characterize helicoplacoid paleoecology and paleoenvironments, to understand what role they played in the Cambrian substrate revolution, and to determine if the fate of the helicoplacoids was linked to the evolutionary and ecological histories of other echinoderms in the Cambrian fauna.

METHODS

The Lower Cambrian Poleta Formation, which is exposed throughout west-central Nevada and east-central California (Fig. 1A), consists of marine carbonates and siliciclastics and is divided into three members (Fig. 1B) (e.g., Moore, 1976). All field observations, specimen collecting, and rock sampling took place at a new helicoplacoid-rich locality from a 12-m-thick interval of the Middle Member of the Poleta Formation in Westgard Pass (Fig. 1A) (37°17′45″N 118°08′15″W). Field observations were made to determine the depositional environment in which the helicoplacoids lived as well as type of bioturbation and ichnofabric index (Droser and Bottjer, 1986) for intervals in which helicoplacoids were found.

The 107 specimens collected at the new locality, along with 29 from the University of Califor-