Taphonomy and Environmental Distribution of Helicoplacoid Echinoderms

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Helicoplacoids are Early Cambrian echinoderms with triradiate ambulacra that are covered by helically-arranged columns of calcite plates. They are abundant only in shales of the Middle Member of the Lower Cambrian Poleta Formation (Atdabanian) at Westgard Pass in the White-Inyo Mountains of California. To identify and understand the unique taphonomic conditions that led to their preservation, 146 helicoplacoid specimens were examined along with the rocks in which they are preserved. Considering their loosely articulated skeletal construction, together with their common occurrence at the base of cm-scale graded beds, helicoplacoids most likely were preserved during obrution events. A majority (69%) of helicoplacoid specimens are partially disarticulated, probably indicating that most helicoplacoids underwent some combination of pre-burial and post-burial decay. Because most (73%) helicoplacoid specimens are preserved on the same bedding plane as at least one other individual, and many (39%) are preserved on bedding planes containing at least 10 individuals, it appears that helicoplacoids were gregarious and frequently were preserved in mass mortality obrution deposits. Low levels of bioturbation, possible microbial stabilization of the sediment, a shallow redox boundary, and a normally calm depositional environment capable of preserving obrution deposits are all factors that aided in the preservation of helicoplacoids. Additionally, the presence of helicoplacoids in several facies of the Middle Member of the Poleta Formation indicates that they lived in a wider range of paleoenvironments than those represented by the shales, where they are found most commonly. The exceptional preservation of helicoplacoids, therefore, is most likely narrowly restricted stratigraphically and geographically because the proper balance of energy regimes, together with the factors mentioned above, was achieved only rarely during the Early Cambrian, not because helicoplacoids were restricted to living in one paleoenvironment.

INTRODUCTION

Occurrence of abundant, well-preserved specimens of the Early Cambrian helicoplacoid echinoderms is narrowly restricted stratigraphically to the Middle Member of the Lower Cambrian Poleta Formation and geographically to Westgard Pass of the White-Inyo Mountains in eastern California, USA (Durham, 1993; Fig. 1). This occurrence of helicoplacoids could either indicate that helicoplacoids were specialists restricted to living in one paleoenvironment or, instead, that they lived in a range of paleoenvironments but only were preserved in an unique taphonomic window. Hence, by understanding the taphonomy of helicoplacoids it may be possible to determine the cause of their restricted occurrence.

Helicoplacoids, along with edrioasteroids, are the oldest undisputed skeletonized echinoderms and are covered by unusual helically-arranged columns of calcite plates (Fig. 2A). They are small in size (1–5 cm in height) and are the only known echinoderms with fully triradiate ambulacra. The calcite plates that comprise them only were held together by soft tissues, most likely negatively biasing their preservation potential (Durham and Caster, 1963; Durham, 1967; Derstler, 1982; Paul and Smith, 1984; Durham, 1993; Dornbos and Bottjer, 2000).

Dornbos and Bottjer (2000) recently have demonstrated that helicoplacoids lived as sediment stickers on fine-grained sediment (Fig. 2B). This conclusion is based on the combination of: (1) helicoplacoid specimens preserved *in situ* with their lower ends inserted upright in the sediment; and (2) extensive X-radiography of the rocks in which the helicoplacoids are preserved, which shows that the substrate on which they lived only underwent minimal horizontal bioturbation and generally lacked a mixed layer (Dornbos and Bottjer, 2000). These low-bioturbation conditions created a substrate that was relatively firm with a sharp sediment-water interface. Because of their small size and lack of typical Phanerozoic soft substrate adaptations, such as attachment structures or root-like holdfasts (Thayer, 1975; Sprinkle and Guensburg, 1995), helicoplacoids were very likely dependent on such substrate characteristics for survival. This dependence most likely led to their extinction due to increased depth and intensity of bioturbation through the Cambrian, which increased the water content and blurred the sediment-water interface of soft sediments in nearshore and shelf settings (Dornbos and Bottjer, 2000; Bottjer et al., 2000).

Whereas previous workers have considered the preservation of helicoplacoids (Durham and Caster, 1963; Durham, 1967; Derstler, 1982; Paul and Smith, 1984; Durham, 1993; Dornbos and Bottjer, 2000), none have attempted to determine if their limited occurrence reflects primary restriction to specific depositional environments or if it is merely the product of a taphonomic window. However, Durham (1993) did note that occurrence as disarticulated plates is the most common mode of preservation for helicoplacoids, because the soft parts that held together their helical skeletons probably decayed shortly after death, disaggregating the plates. Furthermore, rare specimens with plates in life position are found most commonly along bedding planes beneath graded beds, indicating that these helicoplacoids were buried during rapid depositional events (Durham, 1993).

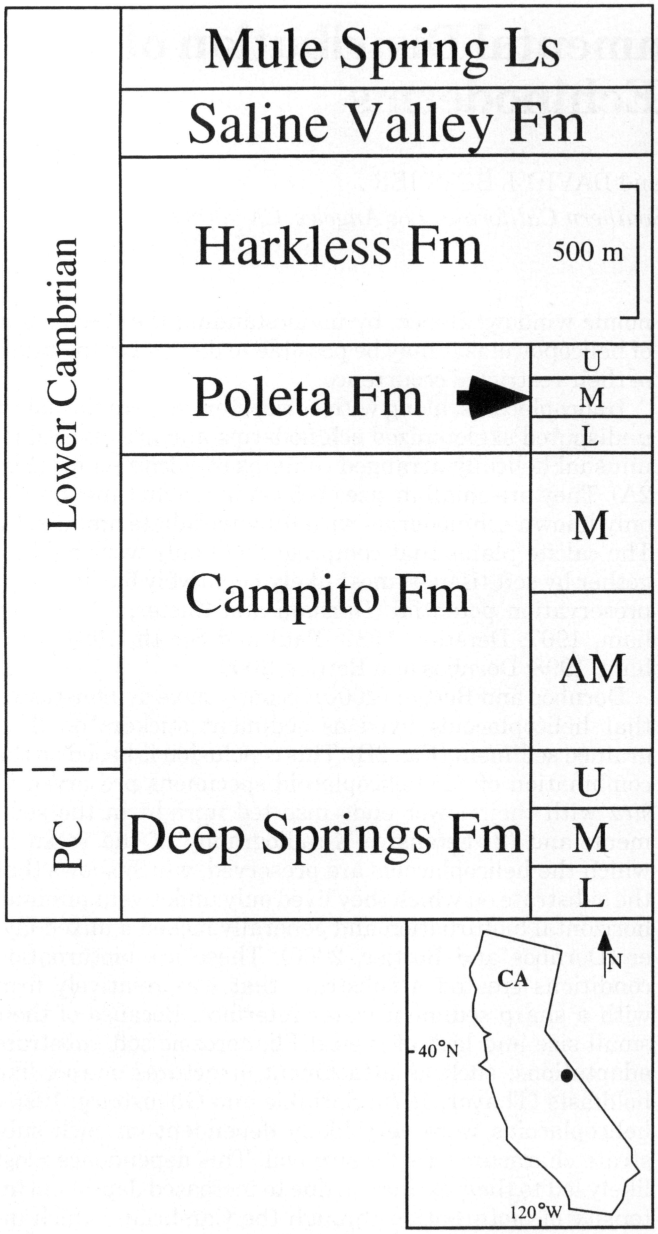

FIGURE 1—Regional Lower Cambrian and adjacent stratigraphy of the White-Inyo Mountains and location map of Westgard Pass in eastern central California. Occurrence of helicoplacoids, marked by large arrow, and location of Westgard Pass, indicated by black dot on map (Stewart, 1970; Nelson, 1976; Corsetti and Kaufman, 1994).

GEOLOGIC SETTING

The Lower Cambrian Poleta Formation, which is exposed throughout western central Nevada and eastern central California, consists of marine carbonates and siliciclastics. The Poleta is divided into three members (Nelson, 1966, 1971), which represent shifts within a shelf setting from a carbonate-bank-dominated environment (Lower Member) to a siliciclastic-dominated environment (Middle Member), and then back to a carbonate-bank-dominated environment (Upper Member; Moore, 1976a).

The Middle Member, in which helicoplacoids are preserved, ranges from 70 m to more than 230 m in thickness (Moore, 1976a) and is in the Upper Atdabanian *Nevadella* trilobite zone (Fritz, 1972; Nelson, 1976; Durham, 1993). In the White-Inyo Mountains, the Middle Member consists of four distinct units: the lower siltstone unit, the lower sandstone-siltstone unit, the middle limestone-siltstone unit, and the upper sandstone unit (Moore, 1976a, b). The lower siltstone usually comprises approximately two-thirds of the Middle Member in the White-Inyo Mountains (Moore, 1976a). This unit is divided into upper and lower parts by a limestone marker bed. Below this marker bed shales were deposited in a subtidal environment (Moore, 1976a, b). These shales contain abundant beds of trilobite fragments, archaeocyathids, and echinoderm plates, which were most likely storm-deposited. This part of the Middle Member is where the helicoplacoid site reported here is located, and where almost all helicoplacoid individuals have been preserved (Durham, 1993; Dornbos and Bottjer, 2000).

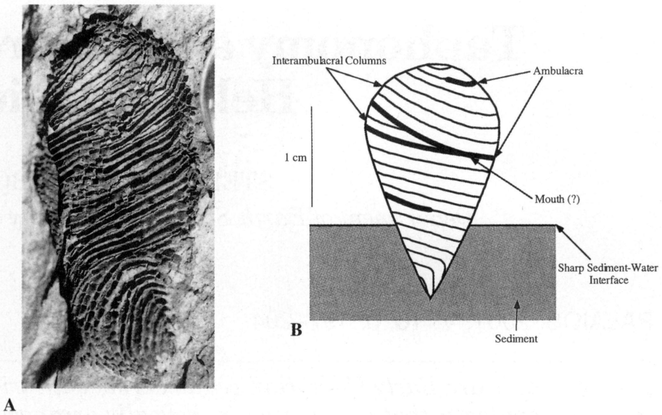

FIGURE 2—Helicoplacoid preservation and life position. (A) Photograph of a typical well-preserved helicoplacoid specimen, preserved as an external mold. Portion of U.S. one cent coin (1.9 cm in diameter) for scale. (B) Generalized reconstruction of a helicoplacoid in life position based on fossil evidence.

TAPHONOMY OF ECHINODERMS

Studies have shown that echinoderms in normal marine conditions usually disarticulate into individual ossicles within one to two weeks, depending on their construction and environmental factors (Meyer, 1971; Liddell, 1975; Kidwell and Baumiller, 1990; Greenstein, 1991; Donovan, 1991). More specifically, the arms and cirri of modern crinoids become disarticulated within three days of death; six days after death only the calyx and certain arm segments are still articulated (Meyer, 1971; Liddell, 1975; Lewis, 1986). The spines of echinoids are the first skeletal elements lost, followed by the disarticulation of the lantern and the breaking apart of the corona, after the decay of the connecting tissues holding them together (Kidwell and Baumiller, 1990; Greenstein, 1991).

The effects of physical disturbance on the decay of modern echinoids have been studied by Kidwell and Baumiller (1990). These were laboratory studies, and their results indicate that freshly killed echinoids remain articulated through hours of physical disturbance, whereas decayed echinoids disarticulate rapidly when physically disturbed (Kidwell and Baumiller, 1990). These results, and those of