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-
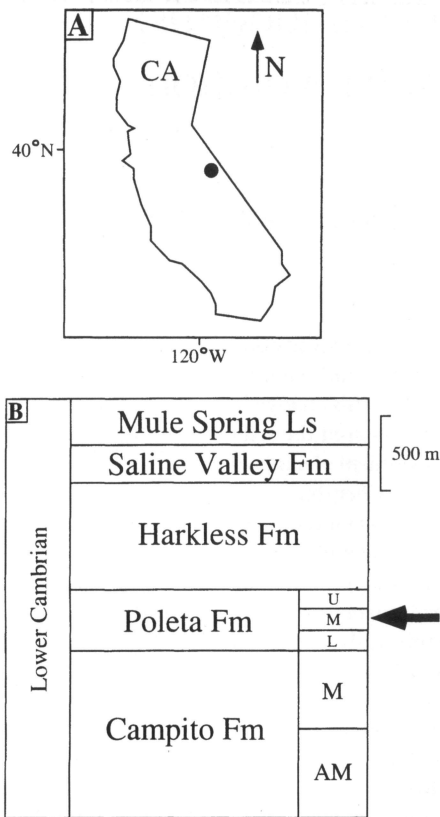
Figure 1. A: Location of Westgard Pass in (black circle) California. B: General Lower Cambrian stratigraphy of White-Inyo Mountains, east-central California. Arrow marks occurrence of helicoplacoids in Middle Member of Poleta Formation (stratigraphy based on Stewart, 1970).

nia Museum of Paleontology (UCMP) and 39 from the Los Angeles County Museum of Natural History (LACMNH), were examined. All of the specimens collected during this study were from talus, so the relative original stratigraphic positions of the specimens are unknown. These specimens were typically preserved as external molds, with only a few specimens still containing their original calcite plates. Original stratigraphic orientation of these pieces of talus was determined by using graded beds within the slabs. Specimens collected in this study are deposited at both the LACMNH and the Peabody Museum of Natural History at Yale University.

To more fully understand the environments in which helicoplacoids lived, six outcrops of the siltstone at this site were excavated in order to collect 81 rock samples for X-radiographic and petrographic studies. These rock samples were slabbed, and the resulting X-radiographs were placed in stratigraphic order for each outcrop, thereby creating what amounts to an X-radiograph core of each sampled outcrop. These cores allowed for convenient and detailed observation of bioturbation levels and sedimentary structures in almost 2 m of the sedimentary rock in which the helicoplacoids occurred. Rocks containing helicoplacoid specimens were also X-radiographed, and

thin sections were made of 49 of the slabbed and X-rayed samples. These thin sections served as the basis for a petrographic study of the deposition and diagenesis of these rocks and were also examined for any features suggestive of the presence of microbial mats (e.g., Schieber, 1999).

PALEOENVIRONMENTAL ANALYSIS

Field observations indicate that the shales of the Middle Member of the Poleta Formation, where almost all helicoplacoid specimens have been found (Durham, 1993), are only minimally bioturbated. Evidence for bioturbation was present on rare bedding plane exposures with horizontal *Planolites*, but outcrops at this site typically have an ichnofabric index (ii) (Droser and Bottjer, 1986) of 1.

Because some of the primary features in the X-radiograph cores were obscured by weathering or low-grade metamorphism, the level of bioturbation was interpretable in only 155.8 cm of the total 192 cm of the core. Over half of the interpretable core, 90.5 cm (58%), is unbioturbated (ii 1) (e.g., Fig. 2), whereas slight bioturbation (ii 2) is present in 39.1 cm (25%). Moderate bioturbation (ii 3) (e.g., Fig. 2) is in only 25 cm (16%) of the interpretable core, and relatively intense bioturbation (ii 4) is in only 1.2 cm (1%). None of the core is completely bioturbated (ii 5). This bioturbation is usually represented by cross sections of horizontal traces commonly less than 5 mm wide (ii 2) and by slightly mottled intervals (ii 3) (e.g., Fig. 2) of very limited vertical extent (0.7–5 cm). Some traces appear to be concentrated at the bases of laminated intervals, possibly indicating that if microbial mats were present these traces would have been formed by undermat miners (Seilacher, 1999). This bioturbation, with a few possible exceptions, is restricted to individual beds and sets of beds with sharp contacts. Such limited bioturbation and the sharp contacts between these thin beds indicate that a mixed layer was generally not present. The typically low levels (ii 2–ii 3) of horizontal bioturbation and the subsequent lack of the mixed layer would have created a relatively firm substrate with a low water content and a sharp sediment-water interface.

The physical sedimentary structures visible on outcrop and in these X-radiograph cores provide further insight into the paleoenvironment in which helicoplacoids lived. They typically include thin (generally <2 cm) beds that are commonly graded in thin section laminations (generally <1 mm thick), and relatively thick (generally 2–5 cm) graded beds rich in bioclastic material (either echinoderm plates, trilobite fragments, or archaeocyathids). These sedimentary structures are characteristic of a generally low energy outer shelf environment that periodically received some slight disturbance by tempestites (e.g., Brett et al., 1997).

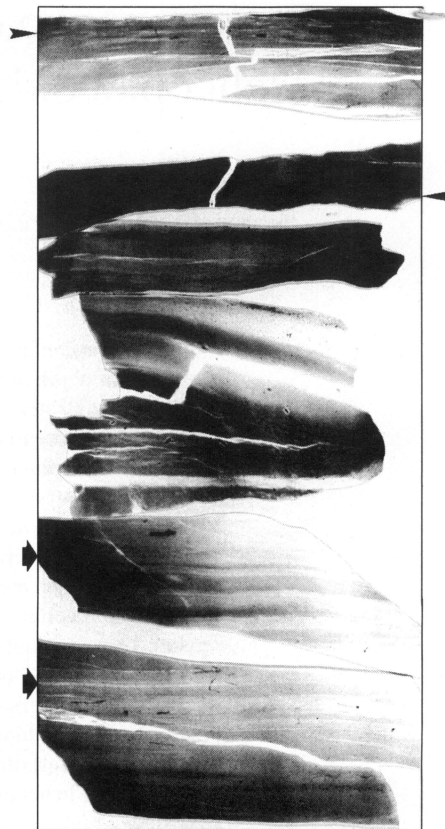Utilizing the criteria set by Schieber (1999) for indicating the presence of microbial mats in silici-

Figure 2. Photograph of typical 20 cm segment of X-radiograph core from shales of Middle Member of Poleta Formation. Note unbioturbated (ii 1) thin (<5 mm) beds and laminations with sharp contacts in lower two samples of segment (indicated by wide arrows), indicating lack of mixed layer. Small amount (ii 3) of vertically restricted, horizontal bioturbation is visible in two uppermost samples (indicated by thin arrows) of segment as gray ovals, cross sections of horizontal burrows. Core is 8 cm wide.

clastic rocks, there is only limited petrographic evidence, and some field evidence, to support the presence of microbial mats on substrates where the helicoplacoids were living. This evidence includes micaceous laminae, mat-decay mineralization, and wrinkle structures, which are suspect-microbial sedimentary structures (e.g., Hagadorn and Bottjer, 1999). Microbial mats were thus present but were most probably rather rare.

PALEOECOLOGICAL ANALYSIS

All of these helicoplacoid specimens are interpreted to have been preserved during rapid burial by thin obrution deposits. As would be expected in an obrution deposit, helicoplacoids are almost always preserved lying flat on their sides (e.g., Fig. 3A). However, two specimens were found with part of each individual preserved vertically, and these are interpreted to have been preserved in situ.

The first specimen that was preserved in situ has its lower end vertically inserted into the rock, and the upper portion is lying flat on the upper-
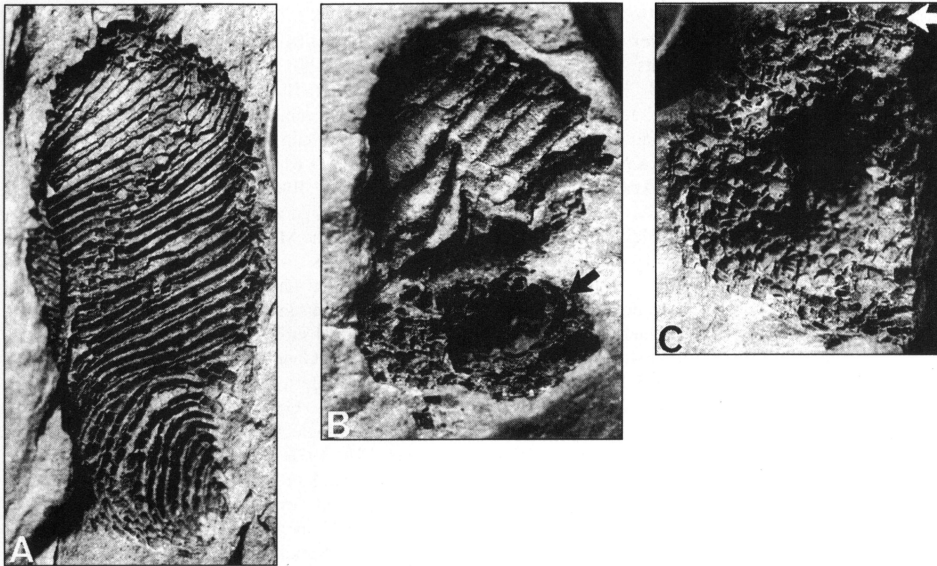
Figure 3. Helicoplacoid preservation and life habit. A: Well-preserved helicoplacoid specimen lying flat on its side as external mold. Edge of U.S. one cent coin (1.9 cm diameter) for scale in upper right. B: Helicoplacoid preserved in situ with its lower end inserted vertically into substrate, interambulacral columns spiraling upward out of depression (arrow), and upper end lying flat on bedding plane. Portion of U.S. one cent coin for scale in upper right corner. C: Second helicoplacoid preserved in situ. A few concentrically arranged interambulacral columns are preserved on fringe of depression (arrow). Edge of U.S. one cent coin for scale in upper left corner.

Figure 4. Generalized reconstruction of helicoplacoid echinoderm in life position based on fossil evidence.

most bedding plane (Fig. 3B). Well-preserved columns of plates spiral upward in the depression left by the lower end, indicating that the depression is not just a random accumulation of helicoplacoid plates. Loose plates surround the depression, evidence that the individual was partially ruptured or torn by the force of the burial. This specimen was apparently an upright sediment sticker (e.g., Seilacher, 1999) whose upper end was knocked over during a preservational obrution event, leaving the lower end vertically oriented in sediment.

The second specimen interpreted to have been preserved in life position is in a relatively large circular depression (Fig. 3C). Inside this depression, the body of the helicoplacoid spirals upward from the base. Most of the plates are rather chaotically arranged, indicating that this individual had decayed slightly before burial. Well-preserved columns of plates concentrically fringe some of the outer edges of the depression. This individual apparently was living upright as a sediment sticker and then, after death, collapsed upon itself shortly before rapid burial.

The functional morphology of helicoplacoids also indicates that they were living as suspension-feeding sediment stickers. The triradiate ambulacra are restricted to approximately the upper two-thirds of the helicoplacoid body, while the lowermost third contains no ambulacra and is commonly composed of interambulacral columns that are arranged straight upward as opposed to helical (Fig. 4). This arrangement of the ambulacra is ideally suited for both suspension feeding and sediment sticking. The ambulacra, by nature of their helical arrangement, are present on every

surface of the helicoplacoid that would have been in contact with the water column (Fig. 4). Assuming that these ambulacra played a central role in feeding, this arrangement would have been advantageous in suspension feeding. The length of these ambulacra is also maximized by their helical arrangement.

The lower third, with no ambulacra, was well adapted to insertion in the sediment (Fig. 4). The vertical interambulacral columns in this lower portion indicate that this part of the body grew upward, perhaps to lengthen itself for insertion into the sediment or to keep pace with slowly accumulating sediment. The lack of ambulacra in this body region also indicates that it was inserted in the sediment, because it is highly doubtful that ambulacra would be located in an area permanently inserted in the substrate.

Although helicoplacoids were apparently living on a muddy seafloor, they show none of the usual suspension-feeder adaptations for survival on typical Phanerozoic soft substrates with a mixed layer. There is no evidence that they encrusted or attached to hard substrates or had rootlike holdfasts to stabilize themselves in soft substrates (e.g., Thayer, 1975; Sprinkle and Guensburg, 1995). Their morphology also reveals that their body mass was centered over a single point, which would have caused them to easily sink into a soft substrate (Thayer, 1975). Clearly, the morphology of helicoplacoids is completely inconsistent with survival on soft substrates typical of the Phanerozoic. Therefore, the sediment on which they were living, regardless of its composition, had to have been relatively firm, like those that typified the Neoproterozoic.
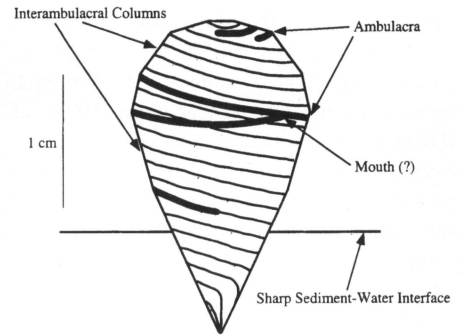
DISCUSSION

Helicoplacoids are not the only suspension-feeding echinoderms that were dependent on the firmer substrate provided by low levels of bioturbation characteristic of offshore siliciclastic settings during the Early to Middle Cambrian. Based on their small sizes and unique morphologies, several Cambrian stemless eocrinoids, including *Lichenoides*, *Cymbionites*, and *Periodinites*, were most likely also dependent on the lack of the mixed layer in these settings for survival (Ubaghs, 1968; Smith, 1982). The remaining Cambrian eocrinoid genera, such as *Gogia*, were able to attach to small pieces of hard substrate amidst the mud, such as trilobite fragments, by way of stems with varying morphologies (Sprinkle and Guensburg, 1995). The first true eocrinoid stems (those with columnals) appeared during the late Middle Cambrian, and by the middle Late Cambrian all eocrinoids had stems with columnals and lived attached to hard substrates (e.g., Sprinkle, 1976; Sumrall et al., 1997).

In contrast edrioasteroids, which along with helicoplacoids are the oldest undisputed echinoderms (Sprinkle and Guensburg, 1997), survived the Cambrian to become a part of the Paleozoic fauna (Sprinkle and Guensburg, 1995). Their success in comparison to helicoplacoids was most likely because they evolved the ability to attach to hard substrates, whereas helicoplacoids lived as unattached sediment stickers. The remainder of the undisputed Cambrian echinoderms, stylophorans, homosteleans, homoiosteleans, and ctenocystoids, are all interpreted as having had mobile life habits either as suspension or deposit feeders (e.g., Sprinkle, 1992). Thus, the mobility of these early echinoderms made them contributors to, rather than victims of, these Cambrian substrate changes.

The agronomic revolution for benthic organisms that burrow created a substrate revolution for those that did not. Whatever the initial cause of the increased vertical component to burrowing, it changed the ecological stage in benthic environments forever. This change led to the extinction of the helicoplacoids and the evolution of stems and attachment structures in other echino-

derms. It is likely that the Cambrian substrate revolution played a role in the evolutionary paleoecology of other members of the Cambrian fauna (e.g., Bottjer and Hagadorn, 1999), although other factors were also surely involved. Because the Cambrian was a time of transition in the substrate revolution, the co-occurrence during this time of metazoans adapted more to the late Neoproterozoic substrate style with those more adapted to the subsequent Paleozoic substrate style may have contributed to the seemingly unusual high disparity of morphologies present during the event that is known as the Cambrian explosion (e.g., Briggs et al., 1992; Foote and Gould, 1992).

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