

Taphonomy and Environmental Distribution of Helicoplacoid Echinoderms

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Helicoplacoids are Early Cambrian echinoderms with tri-radiate 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 tapho-

nomic 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).

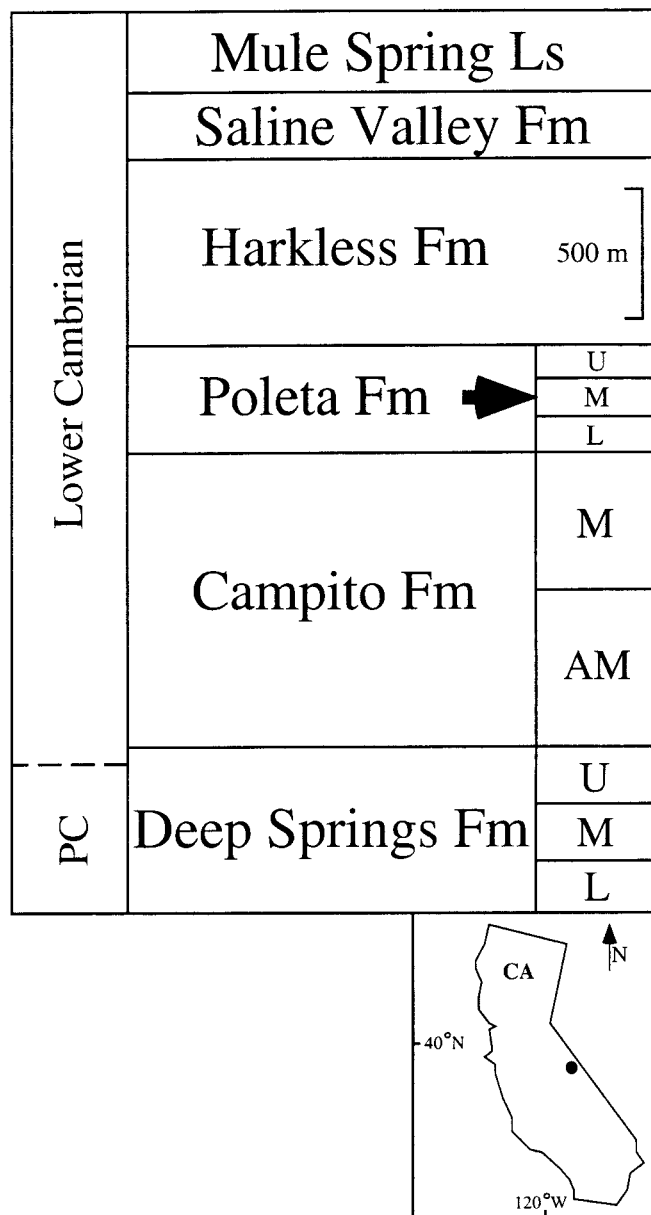
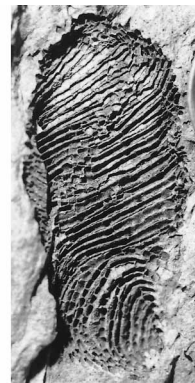


FIGURE 1—Regional Lower Cambrian and adjacent stratigraphy of the White-Inyo Mountains and location map of Westgard Pass in eastern central California. Occurrence of helicoplacoids, marked by large arrow, and location of Westgard Pass, indicated by black dot on map (Stewart, 1970; Nelson, 1976; Corsetti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

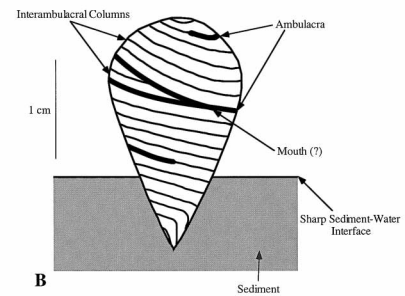
GEOLOGIC SETTING

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



A



B

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.

(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).

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

the other studies discussed above, have important implications for the study of fossil echinoderms because the length of time that an echinoderm decayed on the seafloor can be estimated based on the preservational condition of the specimen.

A particularly informative study on the taphonomy of fossil echinoderms was done by Brett et al. (1997a). They divided echinoderms into three different taphonomic grades based on the ease in which they became disarticulated. Then, they used these three taphonomic groups to define various "taphofacies" characteristic of certain sedimentary environments (Brett et al., 1997a).

The first taphonomic group (Type 1 echinoderms; Brett et al., 1997a) has plates that are held together only by soft tissues such as ligaments and muscles. It is not likely that Type 1 echinoderms will remain articulated for very long after death because their plates will be rapidly disarticulated by decay (Brett et al., 1997a). Examples of Type 1 echinoderms include asteroids, ophiuroids, eocrinoids, some edrioasteroids, and some homalozoans, as well as helicoplacoids. Naturally, Type 1 echinoderms rarely are preserved in the fossil record except as disarticulated skeletal ossicles, which are usually unidentifiable (Brett et al., 1997a). Only very rarely are Type 1 echinoderms preserved partially or wholly articulated (Brett et al., 1997a).

Portions of Type 2 echinoderm skeletons are more tightly articulated, whereas other portions are loosely articulated; examples include crinoids, cystoids, and many regular echinoids (Brett et al., 1997a). Because of the variation in their skeletal construction, Type 2 echinoderms are preserved in a wide range of taphonomic grades (Brett et al., 1997a).

Type 3 echinoderms have a skeleton that is almost entirely tightly articulated or sutured, as is typical of irregular echinoids and some crinoids and blastoids (Brett et al., 1997a). This group is very resistant to decay, which commonly entails breakage along sutures; hence, mostly disarticulated specimens indicate prolonged post-mortem seafloor exposure, probably in high energy environments (Brett et al., 1997a).

Given that the preservation of echinoderms, and, specifically, helicoplacoids, is dependent on the conditions of their physical burial, it is important to consider the burial, or obrution, events that are responsible for their preservation. Obrution deposits represent extremely rapid burial events during which the bodies of organisms are quickly and permanently buried by a large influx of sediment, not allowing for their decay on the seafloor (Brett et al., 1997b). There are four factors identified by Brett et al. (1997b) as necessary for an obrution deposit to form. First, numerous intact organisms, dead or alive, must be present on the seafloor during burial. Second, a relatively thick (1 mm to 1 cm) bed of sediment must be deposited rapidly. Third, there must be no later physical or biological reworking of the obrution layer. And, finally, there must be a favorable early diagenetic environment (Brett et al., 1997b).

Obrution events can have a variety of causes, including seismites, turbidites, and ash falls or flows (Seilacher, 1982; Clifton, 1988). In marine shelves, however, the most common initiators of obrution deposits are storms (Brett et al., 1997b). Storms cause erosional winnowing in coarse-grained nearshore settings, resulting in the basin-



FIGURE 3—Photograph of the new helicoplacoid locality utilized in this research in Westgard Pass, White-Inyo Mountains, California. All specimens were collected from the talus slope seen here, despite extensive outcrop excavation. Hammer handle is approximately 1 meter long.

ward transport of fine-grained suspended sediment (Aigner, 1985; Clifton, 1988). These suspended sediments blanket offshore areas with a layer of fine sediment, resulting in the preservation in obrution deposits of any organisms unfortunate enough to have been present and unable to escape (Aigner, 1985; Clifton, 1988).

METHODS

To study the taphonomy of helicoplacoids, 107 specimens collected at a new helicoplacoid locality in Westgard Pass (37°17'45" N, 118°08'15" W; Fig. 3) and 39 specimens from the Los Angeles County Museum of Natural History (LACMNH) were examined carefully. Specimens collected are deposited at both the LACMNH and the Peabody Museum of Natural History, Yale University. Because the shales in the Middle Member of the Poleta Formation typically weather into talus slopes with little exposed outcrop, all specimens collected during this study were found on pieces of talus. Unfortunately, although almost 2 stratigraphic meters of available outcrop were excavated for X-radiographic purposes, no helicoplacoid specimens were found in their original stratigraphic position. In fact, no other outcrops are currently known that contain *in situ* helicoplacoids.

Specimens were categorized into one of three groups based on the quality of their preservation: (1) well-preserved with a slight amount of disarticulation (Fig. 4A); (2) partially disarticulated (Fig. 4B); and (3) almost fully disarticulated (Fig. 4C). The percentage of total helicoplacoid specimens in each group was calculated, as well as the percentage of specimens that share a bedding plane with other individuals. These percentages were used to characterize helicoplacoid preservation.

It should be noted that there may be a bias towards reduction in occurrences of almost fully disarticulated (Group 3) helicoplacoid specimens. This bias results from the fact that during specimen collection almost fully disarticulated specimens would have been more difficult to locate and collect because of their lack of any distinct

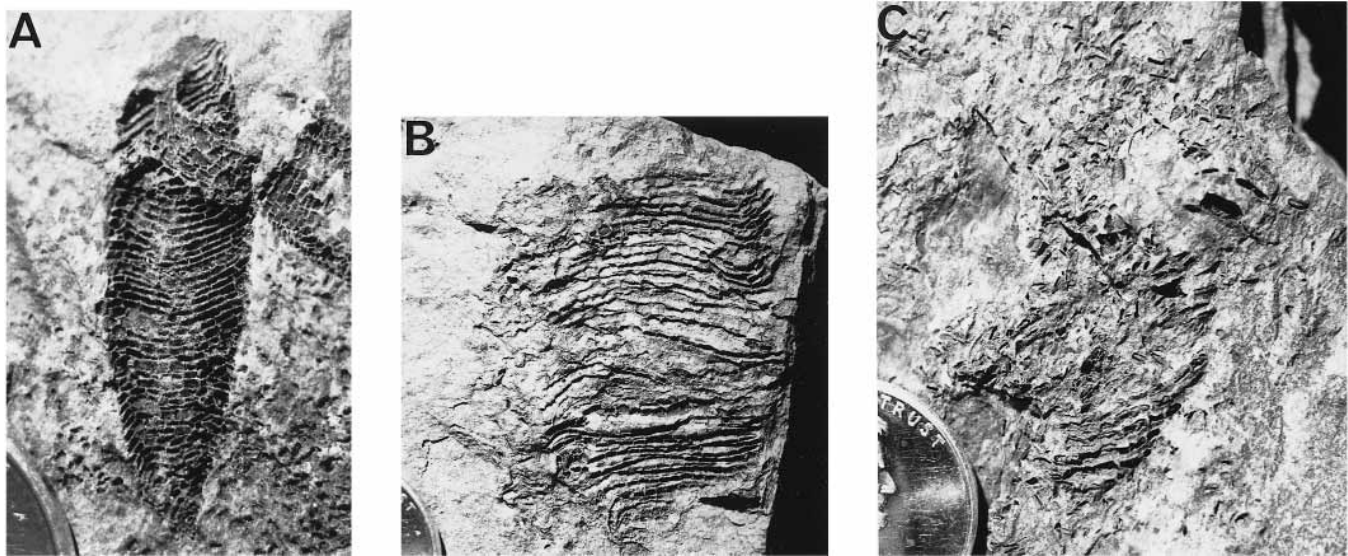


FIGURE 4—Examples of helicoplacoid taphonomic groups utilized in this study. (A) Photograph of a Group 1 (well-preserved with a slight amount of disarticulation) helicoplacoid specimen. This specimen is not disarticulated in the slightest, but is merely partially overlain by another specimen in its uppermost portion. Portion U.S. one cent coin for scale. (B) Photograph of a Group 2 (partially disarticulated) helicoplacoid specimen. Many interambulacral columns are partially preserved, but this specimen shows signs of decay in the loose plates around its edges. Portion of U.S. one cent coin for scale. (C) Photograph of a Group 3 (almost fully disarticulated) helicoplacoid specimen. Only a few vestiges of interambulacral columns are preserved in this specimen, the rest consisting of a scattering of loose plates. Portion of U.S. one cent coin for scale.

structure. As a result of this collection bias, a disproportionately low number of Group 3 helicoplacoids probably were collected.

To better examine helicoplacoid preservation, any original calcite in these specimens was dissolved in HCl to allow for closer examination of the resulting external molds, and latex casts were made of selected specimens. All specimens also were examined to search for evidence of preservational differences among regions of the helicoplacoid body, to test the hypothesis that the lower end of their body may have been constructed more rigidly because it was adapted for insertion into the substrate (Dornbos and Bottjer, 2000).

Because the limited natural outcrop exposure of the Middle Member of the Poleta Formation at this site did not allow for the measurement of a continuous stratigraphic section, a variety of sedimentological information on the rocks in which helicoplacoids were preserved was acquired by excavating 6 outcrops of the siltstone at this site. From these excavations 81 rock samples were collected for petrographic and X-radiographic studies. These rock samples were slabbed, placed in stratigraphic order, and X-radiographed, thereby creating an X-radiograph core of each sampled outcrop. These “cores” allowed for convenient mm-scale observation of sedimentary structures in 155.8 cm of the stratigraphic section in which helicoplacoids have been found preserved. In addition, all 44 rock samples containing helicoplacoid specimens also were slabbed vertically and X-radiographed to search for any sedimentological correlations between the three taphonomic groups.

The orientations of 33 specimens from three small slabs, totalling approximately 0.1 m² in area, were measured and plotted on rose diagrams to determine, with the aid of circular statistics, the level of alignment of these speci-

mens. In addition to the standard error from the mean vector, the statistical measure used in this study is the Rayleigh test of uniformity, which calculates the probability that the data in the rose diagram are uniformly distributed. Probabilities that are close to, or at, zero therefore indicate that the vectors are preferentially aligned. Fourteen of these 33 specimens are assigned to Group 1, while 19 are assigned to Group 2. No group 3 specimens were preserved on these slabs. Because these three slabs were found in a talus slope, the quadrants on the rose diagrams are meaningless; only the alignment of the specimens on individual slabs, and not their actual orientations, is significant.

HELICOPLACOID TAPHONOMY

Because helicoplacoids were Type 1 echinoderms, their plates probably became disarticulated under post-mortem seafloor exposure in a matter of days (Brett et al., 1997a). Combined with the observation that they commonly are found at the base of graded beds (Durham, 1967, 1993), these facts indicate that all helicoplacoid specimens most likely were preserved in obrution deposits (Dornbos and Bottjer, 2000). The majority of the specimens collected in this study (69%) and at LACMNH (62%) are assigned to Group 2 (partially disarticulated; Table 1).

The physical sedimentary structures visible in the X-radiograph cores from this site provide further insight into helicoplacoid preservation. They typically include: thin (generally <2 cm) beds that are commonly graded in thin section; laminations (generally <1 mm thick); and, more rarely, 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

TABLE 1—The percentages of helicoplacoid specimens at USC and the LACMNH in each taphonomic group. See text for explanation of taphonomic groups.

Taphonomic Group	USC %	LACMNH %
1	19	8
2	69	62
3	12	30

shelf environment that periodically received some slight disturbance by tempestites, an ideal setting for the formation and preservation of obrution deposits (Brett et al., 1997b).

Examination of X-radiographs from rocks in which these helicoplacoid specimens are preserved indicates that there are some sedimentological differences between lithologies that preserve Groups 1 and 3. Group 1 specimens generally are associated with thin (<2 cm), sometimes graded beds, but none of the 20 Group 1 specimens are associated with thick graded beds rich in bioclastic material. On the other hand, 46% (6 of 13) of Group 3 specimens are associated with thick (>2 cm) graded beds rich in bioclastic material. Group 2 specimens are associated with both of these end-members. It also is interesting to note that Group 1 and 3 specimens were never preserved together, but they were both preserved with Group 2 specimens.

X-radiographic evidence indicates that Group 3 specimens generally were preserved in higher energy regimes than Group 1 specimens, whereas Group 2 specimens were preserved in a broad range of energy regimes. An explanation for these observed differences may be that higher energy conditions aided in the almost complete disarticulation of many Group 3 specimens by further disarticulating them during transport (Kidwell and Baumiller, 1990). Many of the Group 3 specimens, for instance, probably would have been preserved as Group 2 specimens under lower energy conditions. Likewise, the Group 2 specimens preserved with the Group 3 specimens probably would have been preserved as Group 1 specimens under lower energy conditions. Hence, the fact that Group 1 and Group 3 specimens are not preserved together may simply be a function of their preservation in obrution events of differing energy levels, as supported by the sedimentological evidence.

The predominance of Group 2 specimens observed in this study is probably due to a combination of two factors: (1) many preserved helicoplacoid specimens may have undergone post-burial decay, and (2) many preserved helicoplacoid specimens may have already been dead and experienced some decay on the seafloor before their rapid burial in obrution events (Brett et al., 1997b). It is difficult to determine which of these two factors made a greater contribution towards this preservational pattern. It does seem likely, though, that some combination of pre-burial and post-burial decay contributed to the large percentage of Group 2 specimens observed in this study. Given the loosely articulated skeletal structure of helicoplacoids, it is not at all surprising that they are most commonly preserved partially disarticulated. Well-preserved specimens of Type 1 echinoderms are indeed extremely rare (Brett et al., 1997a).



FIGURE 5—Photograph of a portion of a bedding plane containing 17 helicoplacoid specimens, accompanied by numerous loose plates. Portion of a U.S. one cent coin for scale.

Not only were most helicoplacoid specimens assigned to Group 2, but 73% were preserved on the same bedding plane with at least one other individual, and 39% were found preserved on a bedding plane containing at least 10 individuals (Fig. 5). The fact that helicoplacoids most commonly are preserved with other individuals, and commonly with numerous other individuals, attests to both their gregarious nature and their frequent preservation in mass mortality events in which numerous individuals were killed either shortly before or during rapid burial (Brett et al., 1997b).

As discussed earlier, the specimens collected in this study were carefully examined to test the hypothesis that the lowermost region of the helicoplacoid body was more rigidly constructed than the rest of the organism. This examination revealed that 78% of the specimens had no preferential preservation; hence, no particular region of the body was better preserved than the rest of the individual. The lower region of the body was preserved preferentially in 15% of the specimens, whereas the upper region of the body was preserved preferentially in 7% of the specimens. Clearly, based on these numbers, there is no evidence that the lower region of the helicoplacoid body was constructed more rigidly than the rest of the individual. This result,

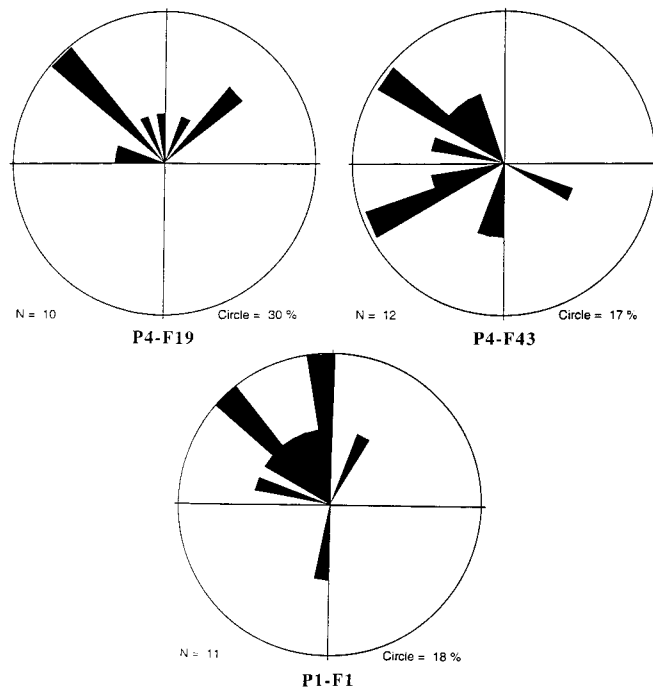


FIGURE 6—Rose diagrams of the orientations of complete helicoplacoid specimens on three separate slabs (samples P4-F19, P4-F43, and P1-F1). Only the alignment of the specimens within each slab is significant, not their orientations. Circle = percentage of specimens present in the largest vectors in each diagram. N = number of specimens in each diagram. See text for discussion of the circular statistics of these rose diagrams.

while informative, does not detract from the conclusion that helicoplacoids lived as sediment stickers, which is strongly supported by the presence of specimens preserved *in situ* with their lower ends inserted upright in the sediment (Dornbos and Bottjer, 2000).

The orientations of 33 specimens on 3 separate slabs have some alignment, within each slab, when plotted on rose diagrams (Fig. 6). Specimen orientations usually are concentrated in one quadrant of the rose diagrams, with a few outlying vectors. Furthermore, circular statistics show that the vector alignment visible in these diagrams is statistically significant. The three diagrams (from samples P4-F19, P4-F43, and P1-F1) have standard errors around the mean vector of only 5.1%, 7.6%, and 4.8%, respectively. The Rayleigh test of uniformity produces probabilities of 0.00, 0.02, and 0.00, respectively, signifying that the concentration of the vectors in these rose diagrams is statistically significant. This statistically significant alignment provides even more evidence for the preservation of helicoplacoids in obrution deposits.

There are several other factors that probably aided in the preservation of helicoplacoids. First, extensive X-radiography of helicoplacoid-bearing rocks reveals that bioturbation was both limited in extent and solely horizontal in nature (see fig. 2 in Dornbos and Bottjer, 2000). In fact, the majority of the stratigraphic section examined in this manner had no signs of bioturbation (Dornbos and Bottjer, 2000). The low levels of strictly horizontal bioturbation in the substrate on which the helicoplacoids were living, and in which they were preserved, allowed for helicoplacoids to

remain relatively undisturbed by bioturbators following burial (Brett et al., 1997b). These low levels of bioturbation also may have allowed for the microbial stabilization of the sediment in which helicoplacoids were buried, as evidenced by the presence of suspect-microbial structures such as wrinkle structures throughout the Middle Member of the Poleta Formation, including the fossil locality that is most abundant in helicoplacoids (Hagadorn and Bottjer, 1999).

The combination of minimal bioturbation and possible microbial stabilization of the substrate would have led to a redox boundary that was just below the sediment-water interface. This shallow redox boundary may have aided in helicoplacoid preservation because once individuals were buried to only a shallow depth, they would have been in a reducing environment (Brett et al., 1997b). This reducing environment would have slowed the further decay of these helicoplacoids.

The usually calm depositional environment in which the helicoplacoids lived also helped facilitate their preservation. While this may appear counterintuitive because they are preserved in higher energy obrution events caused by storms, the preservation of the resulting periodic obrution deposits is dependent on a relatively calm background depositional environment (Brett et al., 1997b). For example, in a nearshore environment where high-energy depositional events occur one after the other, their deposits are continually obliterated by subsequent high-energy depositional events, preventing the accumulation of obrution deposits (Brett et al., 1997b). On the other hand, in the offshore setting in which helicoplacoids are preserved, obrution deposits are infrequent and thereby preserved because they are not destroyed by subsequent high-energy depositional events.

A delicate balance of energy regimes thus is required to form obrution deposits like those in which the helicoplacoids are preserved. The ideal setting for the formation and preservation of these obrution deposits is a calm, low-energy environment punctuated by occasional higher-energy events such as storms (Brett et al., 1997b). This is precisely the paleoenvironment reconstructed from our X-radiographic evidence. Because the exquisite preservation of helicoplacoid specimens is restricted to the Middle Member of the Poleta Formation in the Westgard Pass area, it seems that the proper balance of energy regimes, in conjunction with the favorable factors discussed above, was achieved in this region, allowing for the development of a taphonomic window in which these helicoplacoids were preserved.

It is interesting to note that many of the attributes of the late Neoproterozoic biotope defined by Hagadorn and Bottjer (1999), such as low levels of bioturbation and microbial stabilization of the substrate, also probably aided in helicoplacoid preservation. Dornbos and Bottjer (2000) have demonstrated that helicoplacoids also were well-adapted to, and dependent on, these substrate conditions. Because of this dependence, helicoplacoids may have become extinct due to the increase in vertical bioturbation in shelf environments that accompanied the restriction of the late Neoproterozoic biotope during the Cambrian (Hagadorn and Bottjer, 1999; Bottjer et al., 2000). It appears, then, that the preservation of helicoplacoids was aided by some of the same substrate conditions on which they de-

pended for survival. As discussed previously, however, the proper balance of energy regimes is probably the dominant contributor to helicoplacoid preservation.

LOWER CAMBRIAN ECHINODERM PLATE BEDS AND HELICOPLAGOID OCCURRENCES

Considering that whole specimens of helicoplacoids are preserved in a taphonomic window exposed in the Westgard Pass area of California, it is reasonable to presume that they lived in other depositional environments but simply were not preserved therein. Because most helicoplacoids are preserved as beds of disarticulated plates (Durham, 1993), the presence of echinoderm plate beds in Lower Cambrian rocks may indicate their presence in these depositional environments, because they, along with a few edrioasteroids, are among the only skeletonized echinoderms present in the Early Cambrian. With this in mind, a search of the literature was undertaken to determine the facies distribution of Lower Cambrian echinoderm plate beds as well as individual helicoplacoids.

Li and Droser (1997) conducted a study of Cambrian shell beds but found none dominated by echinoderm plates in the Early Cambrian. This is probably because helicoplacoid plate beds are relatively rare during this time period and also because helicoplacoid plate beds are usually very thin (<5mm); hence, in outcrop they are virtually unrecognizable without close examination. Significant echinoderm plate beds do not appear until the Middle Cambrian (Li and Droser, 1997), when helicoplacoids are no longer present in the fossil record. The occurrence of Lower Cambrian echinoderm plate beds, therefore, provides little evidence for the facies distribution of helicoplacoids because none have been reported outside of localities where specimens have been found.

Durham (1993), while not dealing with echinoderm plate beds, does provide all known localities at which helicoplacoid specimens have been found prior to this study. Besides Westgard Pass, where the vast majority of helicoplacoid specimens have been recovered, helicoplacoids have been found in the Wood Canyon Formation in the Death Valley area of California, the Silver Peak area of Nevada, and at a locality in British Columbia, Canada (Durham, 1993). In these instances, except for the Wood Canyon Formation which contains shales and carbonates, Durham (1993) did not provide information on what facies these specimens are preserved in. Durham (1993) also mentioned that disarticulated helicoplacoid plates have been found in southwestern Nevada and northeastern Washington. But, again, no facies information was provided (Durham, 1993). It does seem clear, based on the distribution of helicoplacoid specimens throughout western North America, that helicoplacoids were distributed widely along the northern coast of Laurentia during the Early Cambrian.

Helicoplacoid specimens in the Poleta Formation most commonly are found in the shales of the Middle Member. However, rare specimens also have been found in the sandstone and bioclastic limestone facies of the Middle Member (Durham, 1993), indicating that helicoplacoids were not restricted to living in strictly muddy offshore environments. Although little data exist on the facies distribution of helicoplacoids and Lower Cambrian echinoderm

plate beds, the work that has been done thus far indicates that helicoplacoids had a relatively broad geographical distribution along the northern coast of Laurentia and, because they are preserved in shale, sandstone, and limestone facies of the Middle Member of the Poleta Formation, probably were not restricted to living in a single depositional environment. As discussed above, helicoplacoids were preserved in abundance in Westgard Pass, not because that is the only place in which they lived but because of a taphonomic window.

The fact that helicoplacoids may have lived in environments other than those represented in shales of the Middle Member of the Poleta Formation does not affect the hypothesis that their survival was dependent on the sharp sediment-water interface and firmer substrate provided by low levels of vertical bioturbation (Dornbos and Bottjer, 2000). As long as the above substrate conditions existed, helicoplacoids probably could have survived irregardless of the composition of the substrate on which they lived. In fact, they very likely were better adapted for living on coarser sediments because their water vascular systems probably were particularly sensitive to fine suspended sediment (Seilacher et al., 1985).

CONCLUSIONS

(1) Because their plates were held together only by soft tissue, allowing for their rapid decay and disarticulation on the seafloor, helicoplacoids were preserved in obrution (rapid burial) deposits.

(2) The majority of helicoplacoids collected in this study (69%) and those in the LACMNH (62%) are Group 2 (partially disarticulated) specimens.

(3) X-radiography indicates that Group 3 (almost completely disarticulated) specimens are commonly associated with higher-energy regimes than are Group 1 (well-preserved, with slight degree of disarticulation) specimens. This pattern may be due to the further disarticulation of Group 3 individuals during the transport associated with their burial in an obrution event.

(4) The predominance of Group 2 specimens probably is due to the combination of pre-burial decay of helicoplacoids on the seafloor and post-burial decay of helicoplacoids under the seafloor.

(5) Most (73%) helicoplacoid specimens are preserved on the same bedding plane as at least one other individual, while many (39%) are preserved on a bedding plane containing at least 10 individuals. These numbers indicate that helicoplacoids were gregarious and often preserved in mass mortality obrution events.

(6) The vast majority (78%) of specimens show no preferential preservation of any particular body region, suggesting that the lower region of helicoplacoids was not constructed more rigidly than other areas of the skeleton.

(7) The orientations of 33 specimens on 3 separate slabs show statistically significant alignment within each slab, providing additional evidence for the preservation of helicoplacoids in obrution deposits.

(8) The preservation of helicoplacoids also was aided by low levels of bioturbation, possible microbial stabilization of the substrate, a shallow redox boundary, and a low energy depositional environment capable of preserving the obrution deposits once they formed.

(9) It seems probable that the magnificent preservation of helicoplacoids is restricted to the Middle Member of the Poleta Formation of Westgard Pass because in the Early Cambrian it is in this region where the proper balance of energy regimes, in conjunction with the favorable factors discussed above, was achieved.

(10) The presence of helicoplacoids in shale, sandstone, and limestone facies of the Middle Member of the Poleta Formation suggests that helicoplacoids lived in other environments than offshore muds.

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