



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.

ACKNOWLEDGMENTS

This research was supported by grants to SQD from the Geological Society of America, the Paleontological Society, and the University of Southern California Department of Earth Sciences. We thank A. Fischer and A. Seilacher for helpful discussions, as well as two anonymous reviewers for their insightful comments.

REFERENCES

- AIGNER, T., 1985, Storm depositional systems: Dynamic stratigraphy in modern and ancient shallow-marine sequences: *Lecture Notes in the Earth Sciences*, v. 3, 174 p.
- BOTTJER, D.J., HAGADORN, J.W., and DORNBOS, S.Q., 2000, The Cambrian substrate revolution: *GSA Today*, v. 10, p. 1–8.
- BRETT, C.E., BAIRD, G.C., and SPEYER, S.E., 1997b, Fossil lagerstätten: Stratigraphic record of paleontological and taphonomic events: *in* BRETT, C.E., and BAIRD, G.C., eds., *Paleontological events: Stratigraphic, ecological, and evolutionary implications*: Columbia University Press, New York, p. 3–40.
- BRETT, C.E., MOFFAT, H.A., and TAYLOR, W.L., 1997a, Echinoderm taphonomy, taphofacies, and Lagerstätten: *in* WATERS, J.A., and MAPLES, C.G., eds., *Geobiology of echinoderms: The Paleontological Society Papers*, v. 3, p. 147–190.
- CLIFTON, H.E., ed., 1988, Sedimentological consequences of convulsive geologic events: *Geological Society of America Special Paper No. 229*, 157 p.
- CORSETTI, F.A., and KAUFMAN, A.J., 1994, Chemostratigraphy of Neoproterozoic units, White-Inyo region, eastern California and western Nevada: Implications for global correlation and faunal distribution: *PALAIOS*, v. 9, p. 211–219.
- DERSTLER, K., 1982, Helicoplacoids reinterpreted as triradiate edriasteroids: *Geological Society of America Abstracts with Programs*, v. 14, n. 4, p. 159.
- DONOVAN, S.K., 1991, The taphonomy of echinoderms: *in* DONOVAN, S.K., ed., *The Processes of Fossilization*, p. 241–269.
- DORNBOS, S.Q., and BOTTJER, D.J., 2000, Evolutionary paleoecology of the earliest echinoderms: Helicoplacoids and the Cambrian substrate revolution: *Geology*, v. 28, p. 839–842.
- DURHAM, J.W., and CASTER, K.E., 1963, Helicoplacoida: A new class of echinoderms: *Science*, v. 140, p. 820–822.
- DURHAM, J.W., 1967, Notes on the Helicoplacoida and early echinoderms: *Journal of Paleontology*, v. 41, p. 97–102.
- DURHAM, J.W., 1993, Observations on the Early Cambrian helicoplacoid echinoderms: *Journal of Paleontology*, v. 67, p. 590–604.
- FRITZ, W.H., 1972, Lower Cambrian trilobites from the Sekwi Formation type section, Mackenzie Mountains, northwestern Canada: *Bulletin of the Geological Survey of Canada*, v. 212, p. 1–58.
- GREENSTEIN, B.J., 1991, An integrated study of echinoid taphonomy: Predictions for the fossil record of four echinoid families: *PALAIOS*, v. 6, p. 519–540.
- HAGADORN, J.W., and BOTTJER, D.J., 1997, Wrinkle structures: Microbially mediated sedimentary structures common in subtidal siliciclastic settings at the Proterozoic-Phanerozoic transition: *Geology*, v. 25, p. 1047–1050.
- HAGADORN, J.W., and BOTTJER, D.J., 1999, Restriction of a late Neoproterozoic biotope: Suspect-microbial structures and trace fossils at the Vendian-Cambrian Transition: *PALAIOS*, v. 14, p. 73–85.
- KIDWELL, S.M., and BAUMILLER, T., 1990, Experimental disintegration of regular echinoids: Roles of temperature, oxygen, and decay thresholds: *Paleobiology*, v. 16, p. 247–271.
- LEWIS, R., 1986, Relative rates of skeletal disarticulation in modern ophiuroids and Paleozoic crinoids: *Geological Society of America Abstracts with Programs*, v. 18, p. 672.
- LI, X., and DROSER, M.L., 1997, Nature and distribution of Cambrian shell concentrations: Evidence from the Basin and Range Province of the western United States (California, Nevada, and Utah): *PALAIOS*, v. 12, p. 111–126.
- LIDDELL, W.D., 1975, Recent crinoid biostratigraphy: *Geological Society of America Abstracts with Programs*, v. 7, p. 1169.
- MEYER, D.L., 1971, Post-mortem disintegration of Recent crinoids and ophiuroids under natural conditions: *Geological Society of America Abstracts with Programs*, v. 3, p. 645–646.
- MOORE, J.N., 1976a, Depositional environments of the Lower Cambrian Poleta Formation and its stratigraphic equivalents: *Brigham Young University Geology Studies*, v. 23, p. 23–28.
- MOORE, J.N., 1976b, Depositional environments of Lower Paleozoic rocks in the White-Inyo Range, Inyo County, California: A field trip road log: *in* MOORE, J.N., and FRITSCH, A.E., eds., *Depositional environments of lower Paleozoic rocks in the White-Inyo Mountains, Inyo County, California*, Pacific Coast Paleogeography Field Guide 1: Society of Economic Paleontologists and Mineralogists Pacific Section, p. 1–12.
- NELSON, C.A., 1966, Geologic map of the Blanco Mountain quadrangle, Inyo and Mono Counties, California: United States Geological Survey Quadrangle Map GQ-529, scale 1:62500.
- NELSON, C.A., 1971, Geologic map of the Waucoba Spring quadrangle, Inyo County, California: United States Geological Survey Quadrangle Map GQ-921, scale 1:62500.
- NELSON, C.A., 1976, Late Precambrian-Early Cambrian stratigraphy and faunal succession of eastern California and the Precambrian-Cambrian boundary: *in* MOORE, J.N., and FRITSCH, A.E., eds., *Depositional environments of lower Paleozoic rocks in the White-Inyo Mountains, Inyo County, California*, Pacific coast paleogeography field guide 1: Society of Economic Paleontologists and Mineralogists Pacific Section, p. 31–42.
- PAUL, C.R.C., and SMITH, A.B., 1984, The early radiation and phylogeny of echinoderms: *Biological Reviews of the Cambridge Philosophical Society*, v. 59, p. 443–481.
- SEILACHER, A., 1982, Posidonia Shale (Toarcian, s. Germany)—stagnant basin revalidated: *in* MONTANARO-GALLITELLI, E., ed., *Paleontology: Essentials of historical geology: S.T.E.M. Mucchi, Modena, Italy*, p. 25–55.
- SEILACHER, A., REIF, W.E., and WESTPHAL, F., 1985, Sedimentological, ecological, and temporal patterns of fossil lagerstätten: *Philosophical Transactions of the Royal Society of London B*, v. 311, p. 5–23.
- SPRINKLE, J., and GUENSBURG, T.E., 1995, Origin of echinoderms in the Paleozoic evolutionary fauna: The role of substrates: *PALAIOS*, v. 10, p. 437–453.
- STEWART, J.H., 1970, Upper Precambrian and Lower Cambrian strata in the southern Great Basin, California and Nevada: United States Geological Survey Professional Paper 620, 206 p.
- SUNDBERG, F.A., and MCCOLLUM, L.B., 1997, Oryctocephalids (Corynexochida: Trilobita) of the Lower-Middle Cambrian boundary interval from California and Nevada: *Journal of Paleontology*, v. 71, p. 1065–1090.
- THAYER, C.W., 1975, Morphologic adaptations of benthic invertebrates to soft substrata: *Journal of Marine Research*, v. 33, p. 177–189.

ACCEPTED DECEMBER 22, 2000

