SOME HYPOTHESES CONCERNING FOSSIL CRINIDS

N. GARY LANE
Department of Geology
Indiana University
Bloomington, IN 47405

PALEOECOLOGY

Were many Paleozoic crinoids facultative eleutherozoans?

Way back in 1911 Edwin Kirk, in his Ph.D. thesis, proposed that many Paleozoic pelmatozoans had an eleutherozoic habit. He thought that many were not rooted or fixed in one spot during their lifetime, but rather could break free and swim or crawl about. Recent observations from deep sea submersibles prove that some living stalked crinoids do, in fact, crawl and are not fixed to one spot (Messing et al., 1988).

Kirk thought that some Paleozoic crinoids broke loose from their stem upon reaching adulthood and that this explained why so many stems are found without heads attached. He also believed that other echinoderms, notably cystoids and blastoids, may have been eleutherozoic. Living stalked crinoids that move about typically perch on rocks or other objects that elevate them above the sea floor. This attitude may place them advantageously to intercept food-bearing currents. Living crinoids may have inherited this perching habit from their stemmed Paleozoic forebears who used other organisms—large sponges, coral heads, or other projections above a level bottom—as perches.

Careful morphologic studies may shed some light on whether or not specific Paleozoic crinoids could move about. Stemless Paleozoic forms like Agassizocrinus and Edriocrinus need to be looked at afresh, in light of these new observations. The style of root systems in Paleozoic forms may give some clues as to movement. Radicular cirri may have been spread over the sea floor as frictional stops to drifting, not buried in the sediment as fixed anchors. The living isocrinoids that move about have the runner-prop style of holdfast. Did Paleozoic crinoids with this type of anchor also have similar abilities? Who had this type of holdfast? The types of articulations in the arms may also give clues as to whether or not the arms could be used for crawling or swimming. Arms with muscular articulations, as in advanced poteriocrinoids, are the most likely candidates for such activity. The arms of flexible crinoids, whether muscular or not, may also have functioned in this fashion. Finally, assessment of arm damage and regeneration may give clues as to breakage due to crawling activities.

How did crinoids compete during their growth cycle?

Stemmed crinoids had to be successful animals at all stages of their life cycle in order to survive. This means that a crinoid that developed from a metamorphosed larva that had settled on the sea floor had to compete with a succession of other adult marine animals as it grew to adulthood. This
competition took the form of access to water currents for food and oxygen. When the crinoid was only two to three cm high it was in direct competition with brachiopods, bivalves and other animals that lived just above the sea floor. A few centimeters higher it was in direct competition with branching and fenestrate bryozoans. Still taller forms competed with glass sponges and short-stemmed peltmatozoans—cystoids, blastoids and short-stemmed crinoids.

Any change in adaptive strategies by any of these other groups could have adversely affected stalked crinoids. The ultimate decline in importance of crinoids in the world ocean may have been due to their inability to adapt to increasing competition at all levels of growth. Extinction of major groups may have been related to this successional nature of selective pressures exerted on crinoid populations.

The impetus for eleutherozoic freedom may have come from benefits derived from breaking away from this constant, repetitive competition with a succession of other animals. Interrupting the cycle by abrupt movement up onto perches, by both stemmed and stemless crinoids, may have been a successful evolutionary strategy that ultimately allowed living crinoids to persist, while other crinoids that could not facultatively break away from the succession of growth competition, failed to survive and became extinct.

Were there deep water stemmed crinoids in the Paleozoic?

Today all stalked crinoids are either bathyal or abyssal in their depth distribution. Virtually all Paleozoic crinoids that are known are thought to have lived in shallow water, neritic, environments. How and when did this transition take place? Were there both shallow water and deep water Paleozoic crinoids? If so, is there a fossil record for the latter forms? Did shallow water crinoids get shoved into deeper water in the Mesozoic or Cenozoic eras?, or did stalked crinoids become extirpated in shallow water while they continued to thrive in deeper water. If the latter case is true, when did this change occur?

The recent analysis by Jablonski and Bottjer (1988) involved post-Paleozoic crinoids. However, they lumped together middle shelf, outer shelf, and bathyal occurrences into a single "off-shore" category. While this may be the most refined classification that their data allowed, the fact remains that there are no shelf stalked crinoids alive today, they are all deeper water forms, and the relevance of their analysis is open to question.

CLASSIFICATION AND EVOLUTION

Is the present classification of the Class Crinoidea satisfactory at the family level and at higher levels?

There are numerous problems in the classification of crinoids that reflect uncertainties or misconceptions about the major aspects of evolution within this group of animals. The Class Crinoidea may not be a natural clade but rather
may be polyphyletic. In contrast, Ausich (1988) indicates that all crinoids share a common bauplan of the calyx.

The several subclasses may not be closely related to each other. For example, the Subclass Camerata has little apparent relationship to the other subclasses of crinoids. The symmetry, cup plate homologies, structure of the tegmen and nature of the arms in camerate crinoids bear little or no resemblance to these features in other Paleozoic forms. There is little indication of a common ancestor for camerates and other crinoids. Consideration might be given to elevating the Subclass Camerata to a separate class, and restricting the name Crinoidea to the other subclasses.

The other subclasses, however, are probably related to each other. The group termed "inadunates" should probably be abandoned or used only in an informal, lower case, way, similar to the way that regular and irregular echinoids are used today. If camerates were excluded from crinoids, then Inadunata would essentially be synonymous with Crinoidea. Perhaps several separate but equal subclasses should be recognized, as has been done in part by recent authors (Kelly, 1982, 1986; Ruzhov, 1985; Broadhead, 1988; Donovan, 1988). Such a classification might look like this:

Subclass Echmatocrinae
Subclass Hybocrinae
Subclass Disparida
Subclass Cladida
Subclass Flexibilia
Subclass Articulata

Groups not covered in such a scheme include the Coronoida (Brett, et al., 1983) and the uniserial, pinnulate Ordovician camerates. This arrangement places emphasis on the early, Ordovician, radiation of subclasses of crinoids that reflects in a minor way the more major radiation of echinoderm classes during that time interval.

The articulate crinoids certainly did evolve from the inadunates in Permian or Early Triassic time, although the details of this transition are poorly understood (Sims, 1988a; 1988b). The features that characterize articulates may have evolved by mosaic evolution from poteriocrinoids. There are Pennsylvanian-Permian families that include forms that have uniserial, pinnulate arms that branch on the second primibrachial and that lack an anal plate in the exterior of the cup. Sims selected the Erisocrinidae of the cladids as an outgroup for comparison with the articulates. While erisocrinoids share several features with the encrinoids of the Triassic, they are not nearly as similar to other Mesozoic crinoids as are other Late Paleozoic cladids like the aesioocrinoids, for instance. Sims placed emphasis on the presence of a nerve canal within the calyx plates of encrinoids and used this as basis for placement of this Triassic group in the articulates. However, there are advanced poteriocrinoids in the Pennsylvanian and Permian that have a similar condition of the axial nerves. The presence of biserial arms in the encrinoids is a strong basis for inclusion of these crinoids in the cladids. There is little
evidence available as to when the mouth and proximal ambulacral grooves became open to the exterior and were no longer submerged under tegminal plates. Sims (1988a) states that an open mouth and proximal food grooves are present in all Mesozoic crinoids and uses this character as a prime diagnostic feature, but these features have not been definitely identified on the tegmen of many Mesozoic crinoids. This must surely be one of the most important defining characters for the articulates. Careful study of European Triassic articulate tegmens may shed some light on this problem.

Are the cladids a single, coherent evolutionary unit?

The current distinction between dendrocrinoid and poteriocrinoid cladids is clearly in error and needs to be emended. The two principal differences between the two groups: presence or absence of true pinnules, and presence or absence of muscular articulations between radials and first pinnulibrachials, are either shared by families and genera now placed in separate suborders, in the case of pinnules, or have not been certainly differentiated, as in the case of articulations. A careful phenetic study of these crinoids, especially currently recognized genera and families of Devonian and Mississippian ages, needs to be undertaken. This should be followed by a cladistic interpretation of evolutionary lineages within these groups. Adequate character lists need to be developed for these groups as well as for other groups of crinoids.

Finally, the classification within the poteriocrinoids is almost certainly in a shambles. The very large number of Pennsylvanian and Permian genera of advanced poteriocrinoids are commonly differentiated on the basis of very slight morphological differences in the dorsal cups. These very carefully discriminated sets of species need to be tested for their validity. They may prove to be among the best studied fossil crinoids known, or they may include many synonyms. Again, careful phenetic studies of many characters need to be applied to these fossils in order to determine the taxonomic validity of genera and families as currently recognized. I predict that such studies would result in conspicuous revision of these important Late Paleozoic forms.

How did the comatulid crinoids evolve?

Sims (1988a) has recently addressed the origin of the comatulid crinoids, the dominant and most diverse group of living crinoids, that first appear in the Early Jurassic. What was the ancestral stock for these crinoids? There are two general possibilities. Sims (1988a) derived the comatulids from the stalked pentacrinooids by loss of the stem in the adult. Alternatively the comatulids may have evolved from a group that already had lost the adult stem, the Order Roveacrinida, which first appear in the Triassic and have a very patchy distributional history in the Mesozoic before they became extinct at the close of the Cretaceous. Sims dismisses the roveacrinooids as poorly understood. The morphologic features that are judged to
be useful for denoting genetic relationships need to be carefully considered. A cladistic analysis of Mesozoic stalked crinoids, the roveacrinoids and the comatulids should prove useful in helping to resolve this problem.

REFERENCES


