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Tomasz K. Baumiller

University of Michigan - Ann Arbor

Charles G. Messing

Nova Southeastern University, messingc@nova.edu

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STALKED CRINOID LOCOMOTION, AND ITS ECOLOGICAL AND EVOLUTIONARY IMPLICATIONS

Tomasz K. Baumiller and Charles G. Messing

ABSTRACT

In the past two decades, much direct evidence has been gathered on active crawling by stalked crinoids, a group generally thought to be sessile. Detailed descriptions of crawling mechanics of isocrinids in aquaria revealed only exceedingly slow movements ($\sim 0.1 \text{ mm sec}^{-1}$). Crawling at such speeds severely restricted the range of roles that this behavior could play in stalked crinoid biology and, consequently, in its potential impact on their ecology and evolutionary history. Here, we provide evidence collected *in situ* by submersible near Grand Bahama Island at a depth of 420 m for a different mode of crawling in stalked crinoids. Its most striking feature is a speed two orders of magnitude greater ($\sim 10\text{--}30 \text{ mm sec}^{-1}$) than previously observed. The biomechanical cause for the differences in speeds between the two crawling modes is related to the difference in the number of articulations, and thus length of the arm, involved in the power stroke. We suggest that the high speed mode may represent an escape strategy from benthic enemies such as cidaroid echinoids, which occur with stalked crinoids and have been shown to ingest them. A first-order tally of crinoid genera possessing morphological traits required for crawling is provided. Crawling may have characterized some Paleozoic taxa, such as some of the advanced cladids (a group very closely related to post-Paleozoic crinoids), but the Permo-Triassic extinction represents a major threshold between the largely sessile crinoid faunas of the Paleozoic and the increasingly dominant motile crinoids of the post-Paleozoic.

Tomasz K. Baumiller. Museum of Paleontology, University of Michigan, 1109 Geddes, Ann Arbor, Michigan 48109-1079, U.S.A. tomaszb@umich.edu

Charles G. Messing. Nova Southeastern University Oceanographic Center, 8000 North Ocean Drive, Dania Beach, Florida 33004, U.S.A. messingc@nova.edu

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INTRODUCTION

One of the better known traits of modern stalkless crinoids, the comatulids, is their ability to locomote. Not only can they use their arms to crawl

along the bottom, but some are capable of swimming for short distances (Clark 1915, 1921; Breimer and Lane 1978; Meyer and Macurda 1977, 1980; Macurda and Meyer 1983; Meyer et al. 1984; Shaw and Fontaine 1990). It has been argued that

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comatulid mobility is “an essential ingredient of the success of the group” (Meyer and Macurda 1977, p. 76). Not only are comatulids by far the most diverse crinoids today, with more than 500 species recognized compared to fewer than 100 stalked species (Roux et al. 2002), but they occupy a broader range of environments than stalked crinoids, which today are restricted to depths greater than 100m (Oji 1986). It has been claimed that locomotion in comatulids is associated with seeking a more advantageous habitat with, for example, more favorable flow and suspended food-particle regimes or less competitive overlap with suspension feeding neighbors. However, perhaps most importantly, comatulid locomotion has been associated with escaping from predators (Meyer and Macurda 1977; Shaw and Fontaine 1990). Not surprisingly, textbook treatments often compare diversity, abundance, and habitat between extant stalked and stalkless crinoids in the context of mobility and predation. For example, Prothero (2004, p. 230) contrasted “the rare stalked crinoids...found in low diversity (only 25 living genera) in habitats that have few predators” with the “more common (130 living genera) stalkless crinoids...which are highly mobile.”

The characterization of stalkless forms as highly mobile need not imply that all stalked crinoids are necessarily sessile, as there has been a long history of conjecture on the topic of stalked crinoid motility. For example, Buckland (1837, vol. 1, p. 436) considered fossil *Pentacrinus* “a locomotive animal” because of its mode of attachment and association with driftwood. Likewise, a free-living existence for extant isocrinids was proposed by Thomson (1873, p. 444), who thought their locomotory abilities were intermediate between comatulids, such as *Antedon*, and “permanently fixed crinoids.” Perhaps the most extreme view with regard to stalked crinoid “free mode of life” was espoused by Kirk (1911, p. 30) who argued that “[T]he number of stalked genera ... which were and are truly eleutherozoic ... is quite large.”

In these examples, the underlying argument used for inferring stalked crinoid locomotion was the mode of attachment—a crinoid lacking a stalk structure such as cementing holdfast that permanently fixed it to the substrate could be considered “free living.” Of course, although the free-living state is a necessary condition for locomotion, it is not sufficient. Some mechanism by which the animal moves is necessary and many ingenious hypotheses have been postulated with crinoids moving either actively or passively as part of the

plankton, pseudoplankton, nekton, or vagile benthos (Kirk 1911; Breimer and Lane 1978). These scenarios were supported by arguments from functional morphology and taphonomy. Nevertheless, because direct proof of active locomotion was lacking, the general opinion was that stalked crinoids were sessile, as evidenced by Lawrence’s (1987) statement that the isocrinids, the most likely candidates for locomotion among extant stalked crinoids, are “free-living *without the capacity to locomote*” (p. 187, italics added).

In the late 1980s, however, direct evidence of isocrinid crawling became available through *in situ* observations (Messing et al. 1988) and laboratory flow-tank studies (Baumiller et al. 1991). These studies revealed that isocrinids could relocate by crawling with their arms, dragging the stalk behind them. Subsequently, Birenheide and Motokawa (1994) provided a detailed account of crawling in laboratory specimens of the isocrinid *Metacrinus rotundus*. These observations indicated that crawling was exceedingly slow, roughly 0.1 mm sec⁻¹. Also, the biological role of crawling was not obvious, even though laboratory observations identified “current velocity and current regime” (Baumiller et al. 1991, p. 739) as potentially important factors.

These direct observations proved once and for all that at least some stalked crinoids, the isocrinids, could crawl. Nevertheless, the mechanism and speed of crawling *in situ* and its biological role remained unanswered. In this contribution, we address these questions relying on data collected by submersibles. These data reveal that isocrinids can crawl much faster than previously recognized, and that one biological role of crawling might be similar to that of comatulids, that is, an escape strategy from predators. Furthermore, crawling may be a plesiomorphic feature of the isocrinid-comatulid clade and might extend to the base of the advanced cladids/articulates in the late Paleozoic.

MATERIALS AND METHODS

Most of the materials used in this study were collected during a series of dives using the *Johnson Sea Link I & II* submersibles (Harbor Branch Oceanographic Institute, Fort Pierce, Florida) between February 1991 and October 1998. The data include tens of hours of video taken using an externally-mounted video camera, hundreds of still photographs taken using externally-mounted as well as handheld reflex cameras, and time-lapse photographs taken with a Photosea (now Hydrovision) 1000A 35-mm underwater camera

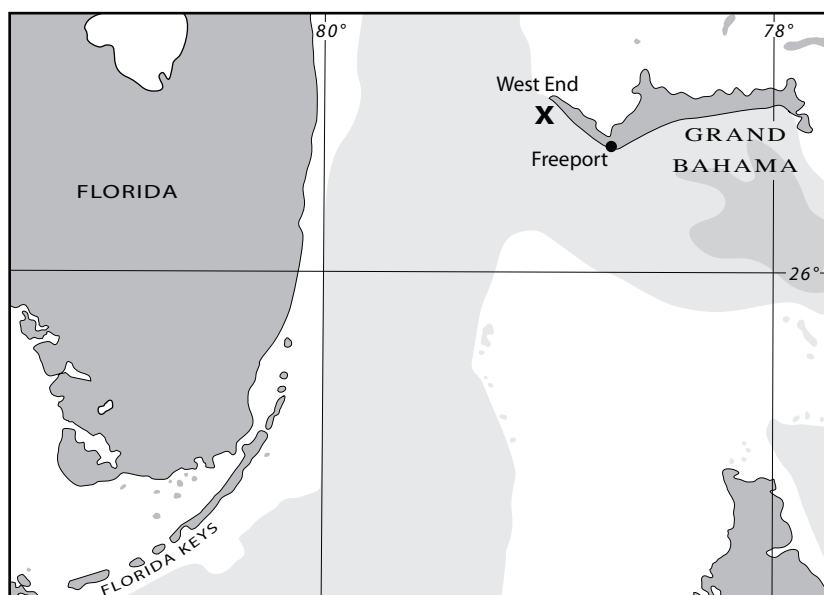


Figure 1. A map of the locality, marked by “x”, near the west end of Grand Bahama Island where the submersible work on isocrinids was conducted.

connected to a Photosea 1500S 150 watt-sec Strobe and mounted on a tripod deployed on the seafloor via submersible.

Linear measurements were obtained from video images by using a pair of laser-generated dots visible on videotape and spaced 100 or 200 mm apart (depending upon the system used); the dots were produced by a pair of parallel lasers flanking the submersible's external video camera. Measurements were made post-dive by pausing the videotape; a millimeter rule was placed on the video screen over the scale bar and then over the image. All measurements were rounded to the nearest centimeter. A digital clock appearing on the videotape was used to measure time to the nearest second. Crawling speed was calculated as the ratio of the linear distance covered by the crawling crinoid to elapsed time. Because the orientation of the submersible and the camera changed during videotaping, and because magnification did not remain constant, crawling speeds were calculated incrementally.

The study area, on the southwestern margin of Little Bahama Bank south of Settlement Point (west end of Grand Bahama Island) in 391-434 m, covered an area approximately 460 m (east-west) by 360 m (north-south) and was centered on 26°37.6'N lat., 78°58.9'W long. (Figure 1). The bottom consisted of flat or sloping, submarine-cemented, carbonate pavements (hardgrounds) veneered with sediment. This substrate interspersed with areas of deeper, often bioturbated,

chiefly pelagic foraminiferan/thecosome sediment. Comprehensive descriptions of regional bank-margin geology of the northern Bahamas are in Neumann et al. (1977), Mullins and Neumann (1979), and Hine and Mullins (1983).

Measured current velocities ranged from 0 to 400 mm sec⁻¹, although flow sometimes clearly exceeded this. Temperatures recorded *in situ* range from 12° C (February 1991) to 17° C (October 1991). Detailed analyses of the flow environment in the northern Straits of Florida are in Düing (1975), Schott and Zantopp (1985) and Leaman et al. (1987).

ISOCRINID CRAWLING

Finger-Tip Pull

While indirect evidence of isocrinid motility had been gathered through submersible observations since at least the mid 1980s (Messing 1985; Messing et al. 1988; Baumiller et al. 1991), direct evidence of crawling has until now consisted of one *in situ* report (Messing et al. 1988) and two sets of laboratory observations (Baumiller et al. 1991; Birenheide and Motokawa 1994). These direct observations revealed that during crawling the crinoid is prone on the substrate with most of the stalk horizontal. Only the proximal portion bent sharply away from the substrate, such that the oral-aboral axis of the calyx orients sub-vertically with the oral surface pointing up (Figure 2.1). The arms, arranged radially around the calyx, have their long

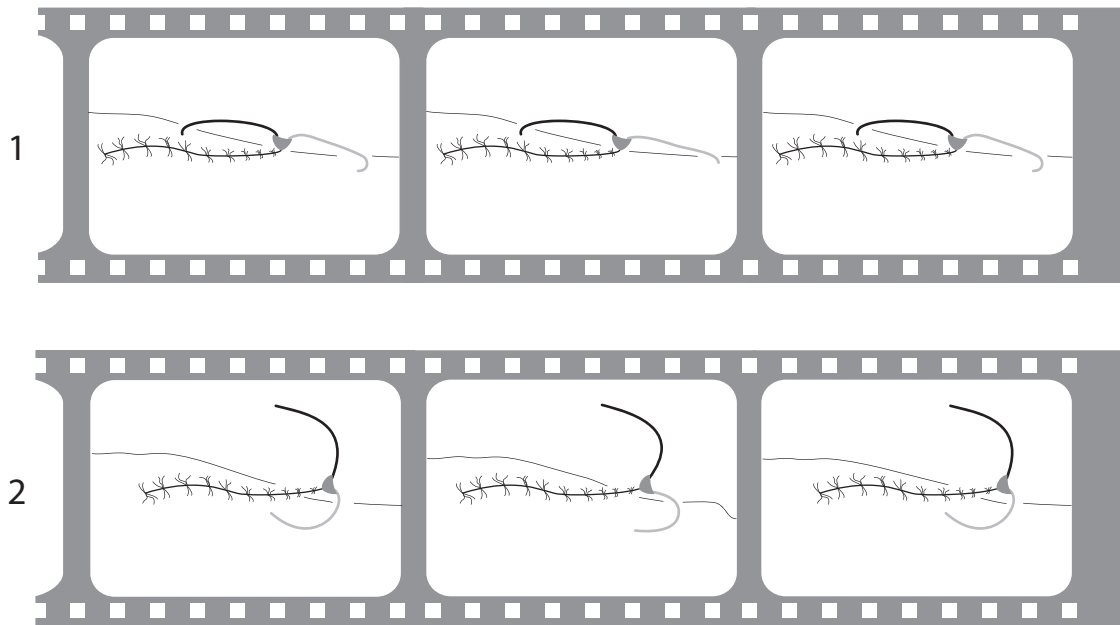


Figure 2. A schematic diagram of the two types of isocrinid locomotion. The top panel (2.1) shows the finger-tip pull and the bottom panel (2.2) shows the elbow-crawl.

axes sub-parallel to the substrate with ambulacra facing up. Crawling involves a repeating sequence of movements by the leading arms, that is, those directed away from the stalk, consisting of a power and a recovery stroke by each of the leading arms: 1) with the distal tip strongly flexed and pressing against the substrate, the rest of the arm curls slightly aborally, pulling the animal forward (power phase); 2) the arm tip lifts off the substrate and the arm straightens by extending orally (recovery phase); and 3) the tip lowers against the substrate and the sequence is repeated. This sequence is somewhat analogous to crawling using one's fingertips, and we refer to it as the "finger-tip pull" mode of crawling. The movement of the leading arms is out of phase; while some arms flex and pull, others straighten. The non-leading arms, that is, those on the side and closer to the stalk, are slightly flexed aborally and, together with the stalk and cirri, are pulled passively by the leading arms. In some instances, these arms have been observed to push the individual forward by anchoring the tip in the substrate, and extending orally (Birenheide and Motokawa 1994).

Elbow-Crawl

While finger-tip pull may characterize isocrinid locomotion under some circumstances, we recorded a very different crawling movement by a specimen of *Neocrinus decorus* on a ~5 minute video sequence during dive JSL 3479 (Figure 3).

This behavior may be described as "elbow-crawl" (Figure 2.2). With the crinoid prone, the entire stalk is nearly straight, such that the stalk and the oral-aboral axis of the calyx are nearly parallel to the substrate. Strong aboral flexure curves the radiating arms so that their tips point toward the stalk. Those arms adjacent to the substrate undergo a sequence of power and recovery strokes, while the rest of the arms, elevated above the substrate, remain strongly flexed aborally, but virtually static. As in finger-tip pull crawling, the power stroke consists of aboral flexure of the arm, while the recovery involves oral straightening. However, whereas in finger-tip pull, only the flexed tip of the nearly straight arm presses against the substrate, and the ambulacral pinnule-bearing surface of the arm orients upward, in elbow-crawl, the arms remain flexed aborally throughout the stroke cycle so that it is the pinnule-covered oral side of the middle third to distal half of the arm that creates traction with the substrate. In the recovery stroke, the middle of the arm uncurls slightly while the base of the arm flexes toward the mouth, bringing the entire curved middle and distal portions of the arm up and forward one or a few centimeters. In the power stroke, the arm base bends away from the mouth, pushing the more strongly flexed arm down and backward against the substrate. The pinnules may also aid crawling via a ratchet-like mechanism. During the recovery stroke, the pinnules are lifted off the substrate and spread out at an angle from



Figure 3. Recording of rapid crawling movement by a specimen of *Neocrinus decorus* on a ~5 minute video sequence. The two red laser dots are 20 cm apart.

the arm axis. In the power stroke, as they touch the substrate, they flex at an acute angle opposite the direction of motion, perhaps functioning like oars.

In both modes of crawling, there is no support for the claim that crinoids “‘walk about’ on [cirri]” (Clarkson 1998, p. 297). However, as has been previously noted (Baumiller et al. 1991), there is incontrovertible evidence for some motility of cirri during locomotion, which suggests that these appendages might be involved in locomotion, perhaps as ratchets or hooks.

Speeds

While isocrinids observed in the laboratory (Baumiller et al. 1991; Birenheide and Motokawa 1994) covered distances up to a meter using the finger-tip pull mode, their speeds were so slow that movement was nearly undetectable with the naked eye; for example, Birenheide and Motokawa (1994) reported speeds of 0.5 m h^{-1} ($\sim 0.1 \text{ mm sec}^{-1}$). In this context, the most striking feature of the elbow crawl mode recorded *in situ* is the much higher speed; *Neocrinus decorus* covered more than 3 m in just under 5 min, corresponding to an average

speed of 36 m h^{-1} ($\sim 10 \text{ mm sec}^{-1}$). In fact, the 5 min of recorded behavior consisted of spurts of even more rapid movement ($\sim 30 \text{ mm sec}^{-1}$) interspersed with intervals of slower crawling or no movement.

Traces

The arms and stalk of crawling crinoids interact with the substrate, and this activity ought to produce traces. Previously, Messing et al. (1988) recognized what they considered to be two types of traces left by a crawling isocrinid: “a drag mark over 1m long...” left by the stalk (p. 481); and “short radiating scratch marks” on the substrate around the crown and on the sediment surface behind an isocrinid made by the arms involved in crawling. Unfortunately, no photos of either trace are available. Our observations provide further proof for at least one such trace: in the video footage, grains of sediment are displaced as the stalk is pulled behind the crawling *N. decorus* producing a drag mark (Figure 4). While the low angle at which the video footage was shot makes it difficult to recognize any of the fine traces that would be

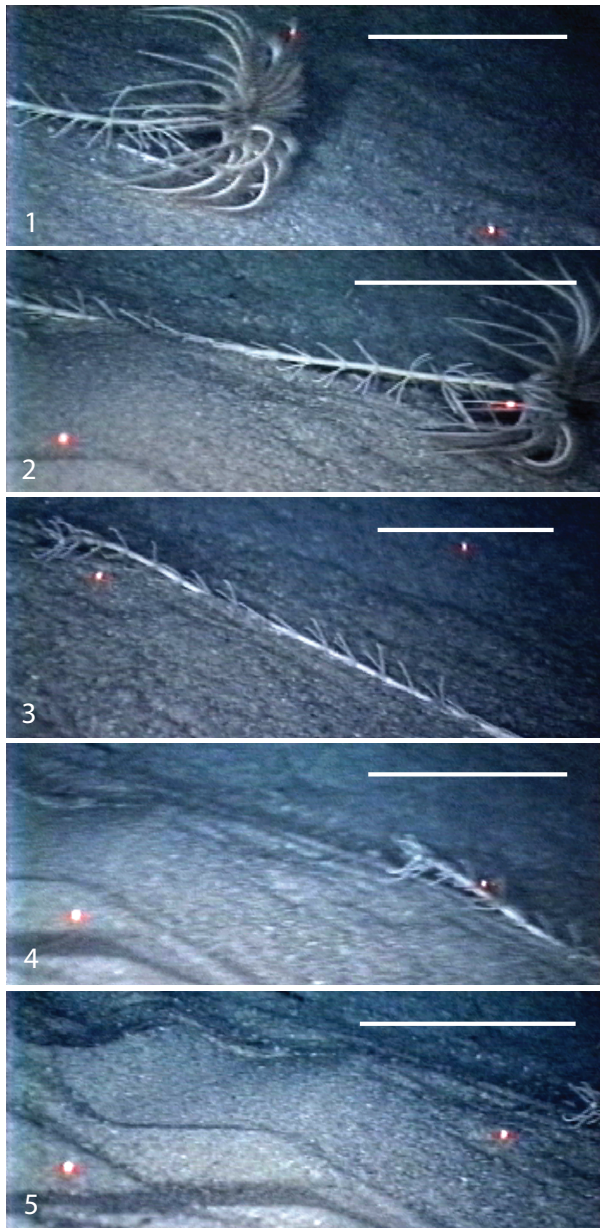


Figure 4. Still frames showing the drag mark left by the stalk of the isocrinid *Neocrinus decorus* just after it had crawled across the substrate (single arrow). Movement was from left to right, and the distal end of the stalk can be seen in the lower right corner (double arrow). Scale: 100 mm.

produced by the power strokes of the arms, experiments with comatulids crawling on fine-grained substrate reveal the types of traces that such behavior is likely to produce (Figure 5).

DISCUSSION

The crawling behavior of isocrinids, especially the fast mode of elbow-crawl reported for the first

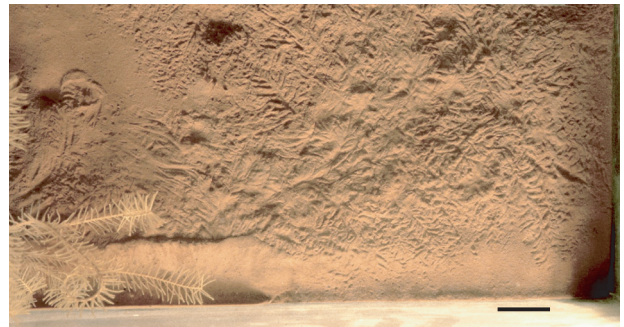


Figure 5. Traces left by a crawling comatulid, *Davidaster rubiginosa*, on mud covering the bottom of an aquarium (Discovery Bay Marine Lab, Jamaica). A few of the arms can be seen in the lower left corner. Scale: 20 mm.

time, has implications for several aspects of crinoid biology and paleobiology. First, we need to ask whether a biomechanical basis exists for the apparent differences in speed between finger-tip pull and elbow-crawl. Second, in light of the much more rapid speeds of crawling of isocrinids, we need to reconsider the biological role of crawling. Finally, from paleontological and evolutionary perspectives, crawling abilities of isocrinids lead us to ask how one might recognize crawling abilities among extinct crinoids and what is the history of this behavior?

Effect of Crawling Mode on Speed: Biomechanical Considerations

Although *N. decorus* observed *in situ* was moving down a slight slope and laboratory specimens used the finger-tip pull to crawl along a flat-bottomed aquarium, this alone is unlikely to account for the >100-fold difference in speed. More probably, the differences between the two modes of crawling account for the dramatically different speeds.

To illustrate how different modes of crawling may affect speeds, we will consider the horizontal component of displacement of the arm as it is flexed aborally for two scenarios (Figure 6). Figure 6.1 represents the finger-tip pull mode of crawling: starting with a nearly straight arm with its long axis horizontal, aboral flexure through an angle θ_1 on a distal articulation during its power stroke produces horizontal displacement, X_1 , of the distal tip which is in contact with the substrate. Figure 6.2 corresponds to elbow-crawl: starting with the arm partially curved, aboral flexure through an angle θ_2 on a proximal articulation during the power stroke produces horizontal displacement, X_2 , of the curved

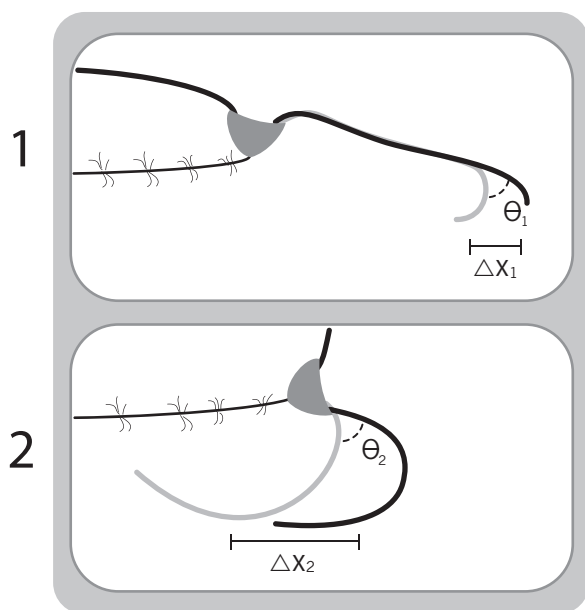


Figure 6. A schematic diagram of the two types of isocrinid crawling. In the top panel (6.1. finger-tip pull), movement of the arm tip is generated by aboral flexure through an angle θ_1 occurring on a distal articulation, producing a forward displacement, X_1 . In the bottom panel (6.2. elbow-crawl), movement of the arm tip is generated by aboral flexure through an angle θ_2 occurring on a proximal articulation, producing a forward displacement, X_2 . Assuming a constant rate of flexure, elbow-crawl results in a higher horizontal velocity.

part of the arm in contact with the substrate. In both scenarios, the amount of aboral flexure is of exactly the same magnitude ($\theta_1 = \theta_2$), but the horizontal displacement of the part of the arm in contact with the substrate in elbow-crawl is much greater than in the finger-tip pull ($X_2 > X_1$). Assuming that the speed of contraction on any arm articulation is independent of its position along the arm, elbow-crawl (Figure 6.2), because of the greater horizontal displacement, results in a higher speed of locomotion. In fact, it may well be that the contraction on a proximal arm articulation produces a greater force than on a distal arm articulation because of its larger size, and consequently larger cross sectional area of contractile tissues.

Of course, other differences between elbow-crawling and finger-tip pulling may contribute to the difference in speed. For example, the above-mentioned use of the pinnule “ratchet” in the former case may be an effective strategy of increasing traction with the substrate and preventing slippage of the arm during the power stroke. This could

have an impact on speed. A similar, but reversed, action occurs in swimming comatulids, in which the pinnules lie against the arm to provide much less resistance on the upward recovery stroke, and spread out at almost right angles to the arm axis on the downward power stroke, offering much greater surface area to act against the water.

Biological Role of Crawling

Regardless of how the differences in speeds between the elbow-crawl and the finger-pull modes of locomotion are achieved, speeds of 10-30 mm sec⁻¹ allow us to consider very different scenarios for its biological role than speeds of 0.1 mm sec⁻¹. For example, the suggestion that crawling may be stimulated by unfavorable micro-environmental conditions, such as inappropriate current velocities or microturbulence (Messing et al. 1988; Baumiller et al. 1991; Birenheide and Motokawa 1994), seems reasonable for both crawling speeds, as it would allow the animal to reach an environment with even a slightly different flow regime. Rapid crawling could also allow isocrinids to respond to disturbance by another organism. For example, Messing et al. (1988) reported an interaction between the isocrinid, *Cenocrinus asterius*, and a large, cidaroid echinoid, *Calocidaris micans*, in the vicinity of Georgetown, Grand Cayman. They inferred that disturbance of the crinoid’s filtration fan by the echinoid may have induced crawling. More recent observations (Baumiller et al. 2000) and analyses of gut contents of cidaroids lead us to conclude that the interaction may involve cidaroid feeding on live isocrinids. In this instance, an isocrinid crawling at 0.1 mm sec⁻¹ could not escape a cidaroid, whereas one crawling at 10-30 mm sec⁻¹ could. In fact, we have argued (Baumiller et al. 2000) that the active stalk shedding (autotomy) and crawling are part of a “lizard tail” strategy used by isocrinids to escape from benthic enemies, such as cidaroids.

Paleobiological Implications of Crawling

Since it is now established that some extant stalked crinoids, the isocrinids, can locomote under their own power and since its role in allowing the animal to respond to physical and biological cues by relocating is likely to be ecologically important, it is worth considering the history of crawling and its evolutionary implications. In reconstructing behavior of extinct organisms, one often relies on functional morphology (Plotnick and Baumiller 2000), and as a start, we have identified several features among stalked crinoids that are necessary,

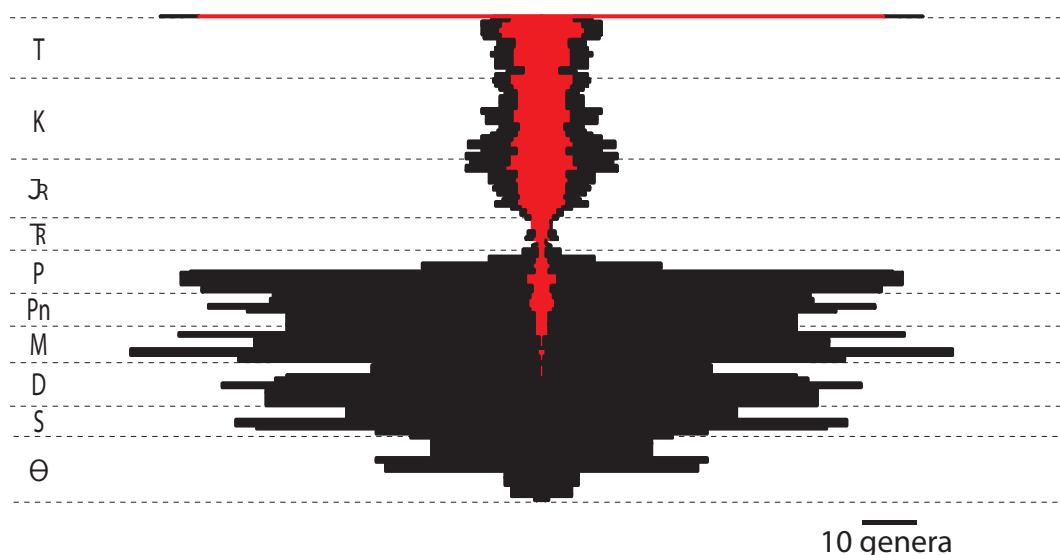


Figure 7. Generic diversity of crinoids through the Phanerozoic showing the relative proportions of taxa possessing locomotory traits (red) and those lacking such traits (black). Locomotory traits include muscular arm articulations with a well-developed fulcral ridge, fulcrum-bearing cirri distributed along the length of the stalk, absence of a cementing or root-like mode of attachment: for the Paleozoic, this includes only some cladid genera, while for the Mesozoic and Cenozoic, the comatulids, isocrinids, and holocrinids. Generic data from Sepkoski (2002) and Webster (2003).

although not sufficient, for crawling. Among these are ability of re-attaching the stalk to the substrate, and arms that are both flexible and strong enough to generate the power/recovery stroke to pull the animal along the bottom. Both features characterize the post-Paleozoic holocrinids and isocrinids (Simms 1999), and some of the taxa generally thought to be closely allied or ancestral to the post-Paleozoic articulates, that is, the Late Paleozoic advanced cladids (Simms and Sevastopulo 1993). Stalked crinoids belonging to these clades possess a stalk that bears cirri with a transverse ridge and a terminal claw-like cirral. With the transverse ridge acting as a fulcrum, such cirri are capable of rapid oral-aboral flexure and of acting as effective anchoring appendages for re-attachment; stalked crinoids lacking cirri or those bearing cirri with multiradiate articula lacked the ability to re-attach. It is also among these clades that one finds well-developed muscular arm articulations (Simms and Sevastopulo 1993). Such brachial articulations are characterized by a central fulcrum, which in extant isocrinids divides the facet into an oral (ambulacral) side bearing both muscles and ligaments and an entirely ligamentary aboral side. Thus oral-aboral flexure of the arms is a consequence of the antagonistic action across this fulcrum. While it is difficult to prove whether extinct crinoids with such arm articulations possessed similar soft tissues (Lane and Macurda 1975; Ausich 1977; Ausich and Baumiller 1993), the recently discovered con-

tractile properties of crinoid ligaments (Motokawa et al. 2004) suggest that such fulcrum-bearing facets, even if connected only by ligaments, could undergo active oral-aboral flexure to generate the power and recovery strokes during crawling, although undoubtedly at much lower speeds than if muscles were present. What is clear, however, is that a well-developed brachial fulcrum necessary for crawling characterized a number of Paleozoic lineages closely related to the post-Paleozoic articulates (Webster 2003).

Although trace fossil data, such as the drag marks or scratch marks discussed above, could provide more direct evidence of crinoid crawling, such trace fossils have yet to be recognized. Taphonomic information such as death posture may provide evidence of crawling, but to date it has only been employed to demonstrate crawling in Jurassic comatulids and stalked isocrinids (Baumiller et al. 2004, in press).

An exhaustive search of stalk, cirral, and arm morphologies necessary for crawling has yet to be completed, but a preliminary survey indicates that while some Paleozoic crinoids might have been capable of crawling, they were vastly outnumbered by taxa characterized by morphologies consistent with a fully sessile life habit (Figure 7). A dramatic change in proportions of these two functional types occurs after the Permo-Triassic extinction as taxa characterized by morphologies suggestive of crawling, namely holocrinids, isocrinids, and

comatulids, constitute at least half the total generic diversity throughout the Mesozoic and Cenozoic. This pattern is especially striking given that the record of the motile comatulids is probably grossly underestimated.

CONCLUSIONS

Stalked forms dominate the rich fossil record of crinoids and have been the subject of most paleontological studies. On the other hand, extant stalked crinoids occur only at depths inaccessible by scuba, so that the shallow-water, stalkless comatulids have received most attention. However, the increased use of research submersibles since the 1970s has revealed much about basic aspects of extant stalked crinoid biology, including the crawling behavior previously known among the comatulids. In fact, our study reveals that crawling ability may be well developed among isocrinids, allowing them to travel at speeds of approximately 10 mm sec^{-1} , or two orders of magnitude faster than previously reported. At such speeds, crawling may play a much broader range of roles in the biology of stalked crinoids than had been suspected, including escaping from benthic predators such as cidaroid urchins. In this way, locomotion may play a similar role in isocrinids as in comatulids (Meyer and Macurda 1977).

The crawling abilities of some stalked crinoids may also impact our understanding of the evolutionary history of the crinoids. Arguably the major feature of their evolutionary history is the Permo-Triassic extinction. Prior to this event, crinoids were a common faunal element in shallow marine environments, so much so that together with brachiopods, rugose and tabulate corals, stenolaemate bryozoans and a few other groups, they have come to symbolize the Paleozoic fauna (Sepkoski 1981). For crinoids, the Permo-Triassic represented a major evolutionary bottleneck and, although they rebounded impressively in the Mesozoic and Cenozoic, their diversity did not return to Paleozoic levels. This study suggests that, for crinoids, the Permo-Triassic also represented a major functional threshold, with the predominantly sessile faunas of the Paleozoic being replaced, especially in the later Mesozoic and Cenozoic, by motile forms. This pattern is consistent with Vermeij's (1987) suggestion that among echinoderms "locomotor deterrence" became a more common mode of resistance from predators in the Mesozoic and Cenozoic, while "better armor" characterized the Paleozoic.

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