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[SHORT COMMUNICATION]

The Behavior and the Morphology of Sea Lilies with Shortened Stalks: Implications on the Evolution of Feather Stars

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ABSTRACT—Extant crinoids can be divided into two groups, stalked sea lilies and stalkless feather stars. Feather stars are considered to have evolved from stalked ancestors by losing most of the stalk, but other differences are present between the two groups. The unsegmented centrodorsal, long and curved cirri near the crown, small calyx, and the ability to swim are all feather star features not found in the sea lilies. To figure out which of the above features evolved directly correlating with loss of the stalk in feather stars, we cut off the stalk from the sea lily *Metacrinus rotundus* and kept them alive in an aquarium. The specimens with shortened stalks were able to stand and crawl with their arms without the support of their stalks, but swimming was not observed for any of the animals. Morphologically, neither fusion of the remaining segments nor the reduction of the size of the calyx were observed, but the cirri became long and curved near the crown. Therefore, the extant sea lilies possess a potential to adapt to incidents of stalk loss. Specimens autotomizing most of their stalks were observed, suggesting that the potential is actually employed in nature. This mechanism linking the reduction of the stalk and the changes in the morphology of cirri may have played an important role in the evolution of the feather stars, if the stalked ancestors of feather stars also possessed this potential. Experimental zoological approaches as this study may provide new insights to the questions of evolution.

Key words: *Metacrinus rotundus*, crinoid, sea lily, feather star, evolution

INTRODUCTION

The present day crinoids consist of two groups, feather stars and sea lilies. Feather stars enjoy a more ecological success, with about 570 species occupying diverse habitats from the intertidal to the deep, and from the tropic to the polar sea. On the other hand, sea lilies, with some 80 species, live mostly at depths greater than several hundred meters. This difference is probably due to the stalkless condition in feather stars (Meyer and Macurda, 1977). Pentacrinoid larvae of feather stars do have stalks, but they abandon the stalks during development. This allows the adults to lead an eleutherozoic lifestyle, enabling them to flee from predators and occupy advantageous feeding sites much more efficiently. In contrast, sea lilies retain their stalk throughout their adulthood, resulting in a sessile lifestyle.

From fossil records and morphology of the larvae, it is considered that feather stars evolved from ancient sea lilies (Simms, 1988). But present day feather stars and sea lilies show several traits, other than the absence of the stalk, which differ between them (see Table 1). The stalks of sea lilies are segmented whereas the centrodorsals, a remnant of the stalk in feather stars, are not. The cirri growing from the proximal part of the stalk in sea lilies are short and straight, but those growing from the centrodorsal in feather stars are long and curved. The calyx is much smaller in feather stars than in the sea lilies. Feather stars possess more branchial articulations in the arms, and the arms are more muscular than those of sea lilies. There are also behavioral differences between the two groups as well.

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Table 1 Differences between sea lilies and feather stars.

	sea lilies	sea lilies with shortened stalks	feather stars
proximal stalk	segmented	segmented	unsegmented
proximal cirri	short	long*	long*
	straight	curved*	curved*
calyx	large	large	small*
muscular branchial articulations	some	some	increased*
swimming	no	no	yes*

*Features of feather stars.

Feather stars are known to have the ability to swim, but there have been no reports of swimming in sea lilies to date. It is considered that these changes occurred in feather stars so as to adapt to the stalkless condition. But it still remains to be seen when most of the traits were acquired in the evolution of feather stars. Although these traits could have evolved independent of stalk loss, there are possibilities that some of these traits evolved directly correlating with it. Fossil records have provided useful clues to this problem, but the quality of the data obtained depends on the condition of preservation. In this paper, we tried an experimental zoological approach, using the sea lily *Metacrinus rotundus*.

The stalk was cut off from some specimens of the sea lily, *Metacrinus rotundus*. Specimens with shortened stalks were able to stand and crawl with their arms, but could not swim. The shortened stalk remained segmented, but the cirri that grew from it was long and curved, similar to those growing from the centrodorsal of feather stars. Some sea lilies autotomized most of their stalk, suggesting sea lilies with shortened stalk may occur in the field. The information obtained here adds new insights to the evolution of the feather stars.

MATERIALS AND METHODS

Specimens of the modern stalked crinoid *Metacrinus rotundus* Carpenter were collected from depths of about 100–150 m at Suruga Bay, central Japan. They were carried to our laboratory and kept in a darkened, temperature-controlled aquarium (14±1°C) with circulating sea water.

The dissections were done with a scalpel while holding the sea lily underwater. The photographs of the specimens were taken using a digital camera, Coolpix950 (Nikon).

RESULTS AND DISCUSSION

The stalks were manually cut off from 11 specimens of the sea lily *Metacrinus rotundus*. The cut was done at various positions so that they had 2–5 mm of the stalk remaining (Fig. 1A). Sometimes, these animals lay on the bottom with their oral side facing upwards and calyx rested on the substrate (Fig. 1B). Other times, they lay sideways with their arms folded orally. But often, these animals were observed standing with their arms, raising their calyx and the remain-

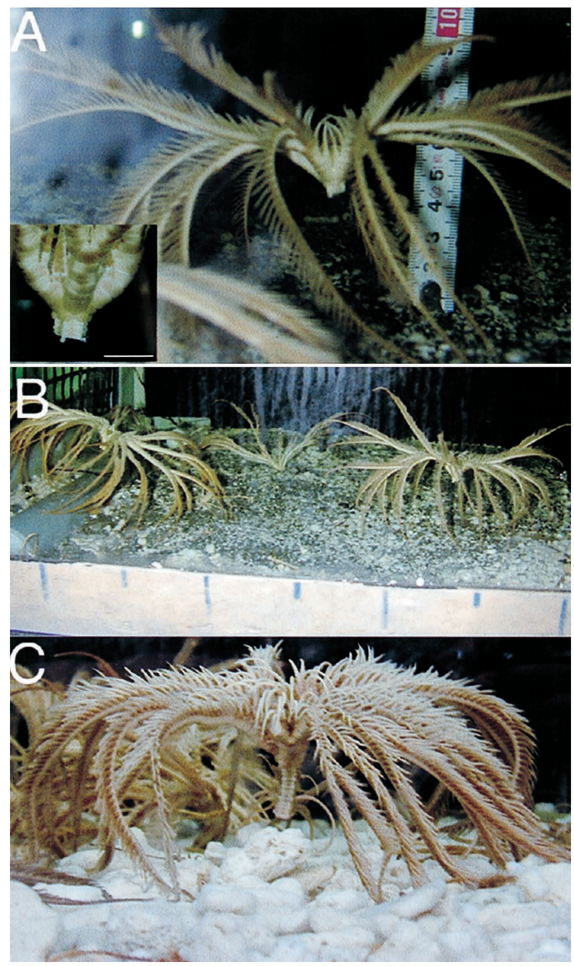

Fig. 1. Sea lilies with shortened stalks. (**A**) Specimen 36 days after the stalk was cut off with about 5 mm remaining. Some of the arms are raised from the substrate. A tape measure is seen in the background. Inset shows a close up view of the remaining stalk. No cirri are left. Bar: 1 cm. (**B**) Three animals 36 days after the stalks were cut off with about 5 mm remaining. Two of them are standing with their arms. The specimen in the middle has its calyx on the substrate while lifting its arms. (**C**) Specimen three weeks after it was transferred into the aquarium. It has autotomized most of its stalk, leaving about 3 cm. It is standing with its arms not using the remaining stalk as a support, just like the specimens with their stalks manually cut off.

ing stalk completely from the substrate (Fig. 1A, B). They were able to keep standing under a mild current, clinging to the bottom with the tip of the arms. Crawling was observed for some specimens, as they repositioned themselves inside the aquarium. During the motion, the calyx and the remaining stalk were kept lifted from the substrate. Swimming was not observed for any of the specimens, even when they were dropped and let to descend in an aquarium about 80 cm deep.

On another occasion, eight specimens of the sea lily *Metacrinus rotundus* were carried to our laboratory and transferred into an aquarium. Some specimens started autotomizing their stalks, and two weeks after transfer, four specimens had stalks less than 3 cm in length. These specimens were all capable of standing with their arms, lifting the calyx and the remaining stalks from the substrate (Fig. 1C). They were also able to crawl while keeping the calyx and the stalk lifted.

After two months, cirri grew from the remaining stalk (Fig. 2A, B). The cirri grew much longer while at the position close to the crown compared to normal stalked specimens (Fig. 2C). In some specimens, extremely long cirri grew from only the few most distal nodals (Fig. 2B). The long cirri curved outwards, in contrast with the straight cirri growing from the proximal part of the stalk in normal sea lilies (Fig. 2C). The long and curved cirri resemble those of feather stars growing from the centrodorsal.

Swimming was not observed for any of the specimens with the shortened stalk. Since stalkless specimens were able to stand and crawl, the arms of the extant sea lilies are muscular enough to support the calyx, without the help of the stalk. But the muscles were not enough to enable them to swim. The heavily calcified body may be too heavy for the arms to lift. Therefore, the ability to swim with their arms is a feather star innovation.

In the specimens with shortened stalks, nodals of the remaining stalk did not fuse, but long and curved cirri grew from them. Do the changes in the morphology of the cirri hold adaptational meanings? Although the sea lilies with shortened stalks were able to cling to the substrate with their arms, a strong current may carry them away, since they are missing cirri which has previously been suggested to work as ratchets (Baumiller *et al.*, 1991). Furthermore, they naturally feed with their arms recurved into the current (Macurda and Meyer, 1974; Fujita *et al.*, 1987), so they cannot feed efficiently facing upwards, as in Fig. 1. Clinging on the side of a rock facing the current can solve both problems. And it is the cirri, not the stalk, which is necessary for this. Furthermore, the cirri need to be curved outwards in order for the specimens to cling on to objects. Therefore, long and curved

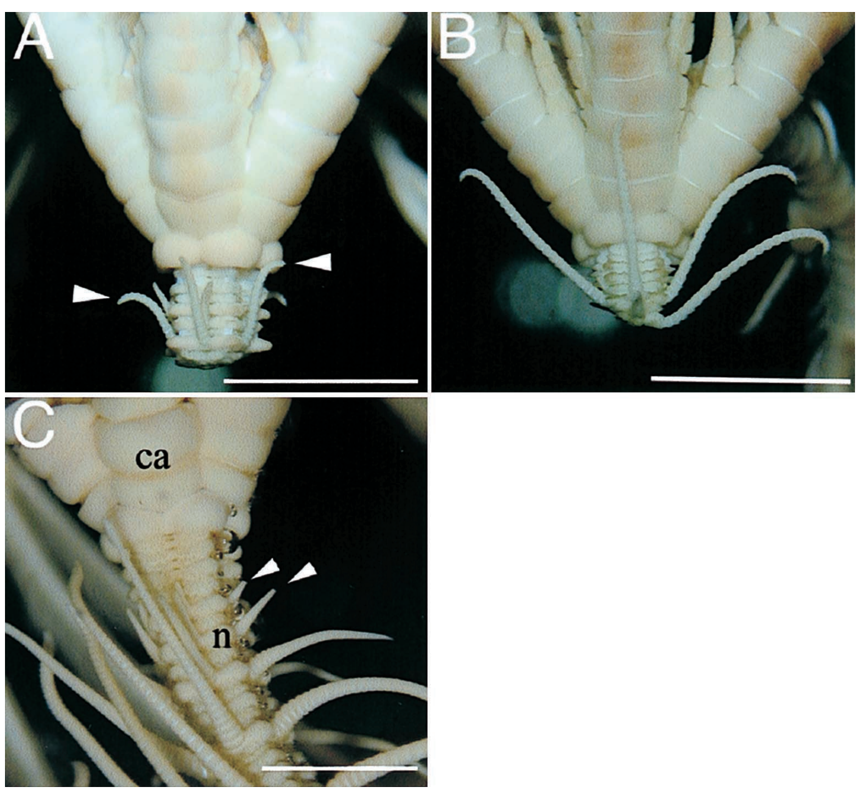

Fig. 2. Accelerated cirri growth at the proximal part of the shortened stalk. (**A**) Specimen 72 days after dissection. The stalk was cut off at a similar position as in Fig. 1A. The proximal cirri (arrowheads) are long compared to those in (C). The tips of all the cirri are curved outwards. (**B**) Specimen 136 days after dissection. The stalk was cut off at a similar position as in (A). Long cirri are growing from the two distal nodals only. The tips of the cirri are all curved outwards as in (A). (**C**) Normal stalk. Cirri growing from the proximal part of the stalk (arrowheads), close to the crown, are short. The tips of most cirri close to the crown are straight. ca: calyx, n: nodal. Bar: 1 cm

cirri are essential for the survival of crinoids with short stalks. Crinoids probably acquired the mechanism linking the short stalk and the morphological changes of the cirri under these ecological stresses.

Several specimens autotomized their stalks, resulting in stalks less than 3 cm in length. This suggests that specimens with short stalks occur in the field, and the potential to adapt to the environment after stalk loss is actually employed in nature.

In Table 1, we compared the features of the sea lilies with shortened stalks, with sea lilies and feather stars, and analyzed which of those features may have evolved directly correlating with the loss of the stalk in feather stars. The ability to swim is not directly correlated with stalk loss, for sea lilies with short stalks could not swim. The fusion of the nodals in the centrodorsal and the reduction of the calyx size are also not directly correlated with loss of the stalk. However, we were able to reproduce the long and curved cirri of feather stars in sea lilies with shortened stalks. As discussed above, this shows that present sea lilies have the potential to adapt to incidents of stalk loss. If the ancient sea lilies leading to the feather stars already possessed this potential, the long and curved cirri of feather stars may have evolved directly correlated with loss of the stalk using this mechanism. The fossils of the earliest known feather star *Paracomatula triadica* have long and thick cirri growing from the short segmented centrodorsal, but since they are broken midway, it can not be determined if they were curved (Hagdorn and Campbell, 1993). Closer inspections of other early feather star fossils shall be useful in finding out the morphology of the cirri. Additionally, fossils of a congenic species as this study, *Metacrinus fossilis* have short stalks, usually shorter than 5 mm, with long and thick cirri (Meyer and Oji, 1993). Further researches on the fossils of stalkless crinoids unrelated to feather stars shall be useful to determine whether the ancient sea lilies had the potential to adapt to stalk loss in general. Experimental zoological approaches such as this study shall be a powerful means of analyzing evolutionary problems, in collaboration with paleobiological studies.

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