On the swimming function of crinoid cirri

Tomasz K. Baumiller · G. Alex Janevski

Abstract Crinoid cirri are generally considered primarily as structures that anchor the animal to the substrate; however, a swimming function for cirri has also been suggested. Most notably, it has been claimed that an extant comatulid, *Dorometra nana*, was observed swimming with its cirri. Because no muscles have ever been found in the cirri of crinoids, cirrus movement must involve another mechanism, and recent reports of contractile properties of crinoid ligament suggest that it might be the connective tissue that is responsible. Given the reported mechanical properties of cirral ligament, and the morphology and weight in water of *D. nana*, we tested the claim of cirrus swimming using a biomechanical model. Our results indicate that the thrust generated by cirri can account only for a very small fraction of what would be needed to overcome the weight of the animal in water, suggesting that *D. nana* cannot swim with its cirri. A similar approach applied to the Jurassic isocrinid, *Pentacrinus briareus* (=*P. dichotomus*), with unusually numerous, long and flattened cirri, also fails to support previously hypothesized cirrus swimming in this taxon.

Keywords Echinoderms · Biomechanics · Paleobiology

Introduction

The *Treatise on Invertebrate Paleontology* (1978) defines cirri as generally undivided, jointed appendages of the

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crinoid stem or the centrodorsal (Breimer 1978). These appendages characterize most extant crinoids, including isocrinids and comatulids, but are missing from many Paleozoic groups as well as some post-Paleozoic taxa such as the millericrinids and cyrtocrinids. It is generally accepted that one function of cirri is to anchor the animal to the substrate (Clark 1915). Anchoring by cirri is done actively, i.e., each cirrus bends slowly aborally allowing it to grasp the substrate. Release from the substrate is accomplished by unbending orally.

Exactly how crinoid cirri can generate movement has been a major puzzle. Whereas the presence of a transverse ridge on the cirral facets in certain crinoids, such as isocrinids and comatulids, clearly serves as a fulcrum around which oral–aboral movement can occur, no muscles have been found in the cirri of extant crinoids (Fig. 1). The cirrals are connected to each other by ligaments that insert into the skeleton on the oral and aboral sides, on opposite sides of the transverse ridge. In addition, a central canal pierces each cirrus and contains extensions of the coelom and the nervous system. Finally, thin layers of dermis and epidermis form the outermost layers of each cirrus.

The absence of muscles in cirri necessitates that some other mechanism was responsible for their motility. Over the years a variety of mechanisms have been proposed. Teuscher (1876) suggested that motility could be accomplished by varying hydraulic pressure in the cirral coelom and that the hydraulic pressure would act antagonistically with the elastic ligaments. Holland and Grimmer (1981) found bundles of 5 nm filaments associated with the cytoplasm epithelial cells lining the cirral coelom and suggested that because coelom lies orally to the transverse ridge, their active contraction could bend the cirrus in an aboral direction, while elasticity of the oral ligaments could
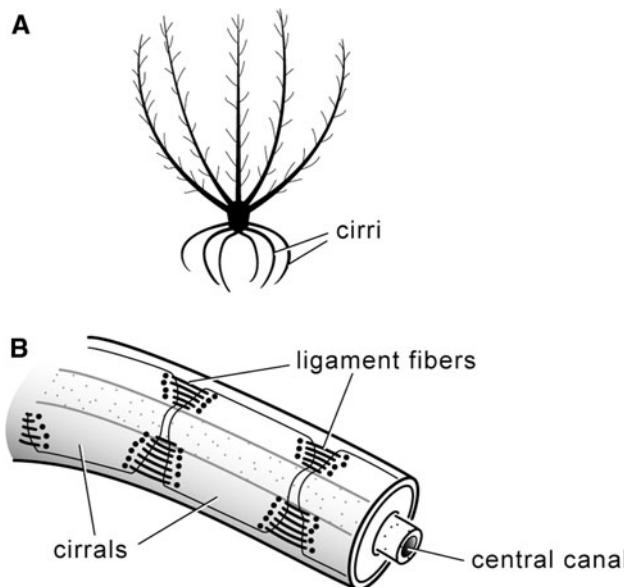
Fig. 1 A schematic drawing of **a** comatulid crinoid with its cirri and **b** the structure of an individual cirrus. Modified from Holland and Grimmer (1981)

straighten it. They also proposed that active control over the mechanical properties of ligament could be involved in the functioning of cirri, as it has been known for some time that certain echinoderm connective tissue is characterized by rapid changes in viscosity, stiffness, and strength, and that the animal has active neural control of these properties (Takahashi 1967; Wilkie 1983; Heinzeller and Welsch 1994; Lange et al. 1994; Wilkie et al. 2004; Wilkie 2005). Holland and Grimmer (1981) suggested that actively reducing the stiffness of the ligaments could allow the crinoid to easily reposition its cirri, and once in position, increasing ligament stiffness could lock the cirrus into a given posture making for an effective anchoring device.

In a series of mechanical experiments with cirri of the stalked crinoid *Metacrinus rotundus* Birenheide et al. (2000) demonstrated that in spite of lacking muscles, an amputated cirrus could produce a force. Because the amputated cirrus had an open coelomic canal, the force could not be produced by Teuscher's coelomic pressure mechanism (1876). The contractile filaments in the walls of the coelomic canals also could not have produced the force as suggested by Holland and Grimmer (1981), because in *M. rotundus* the coelomic canal passes through the center of the articular ridge and thus contraction of canal tissue would not bend the cirri but only bring the cirrals closer to each other. Based on this and other mechanical experiments with crinoid arms and cirri, Birenheide et al. (2000) concluded that the force must be produced by the ligaments, and provided some data on their contractile properties (Birenheide and Motokawa 1996, 1998; Motokawa et al. 2004). If this claim is proved to be true, it will

represent the first and only example of contractility of ligament in all animal phyla.

Although the molecular mechanism of crinoid ligament contractility remains unknown and this property has yet to be reproduced in other labs, the work of Motokawa and Birenheide does provide a basis for exploring the functional implications of this property: e.g., whether cirri could fulfill functional roles other than anchoring the animal to the substrate. Using arguments from functional morphology, it has been suggested that some extinct crinoids' cirri were used in swimming (Hauff 1984) and in active filtration (Seilacher and Hauff 2004). Perhaps the most compelling evidence for cirrus swimming was offered by A. H. Clark who stated that a juvenile comatulid, *Dorometra nana*, was observed "to have been swimming entirely by means of its cirri" (p. 607, Clark 1921). Could these or other claims of crinoid cirrus swimming be true? Do the contractile properties of crinoid ligament reported by Motokawa and Birenheide allow cirri to generate sufficient thrust to overcome the animal's weight in water? The purpose of this paper is to test this by using morphological data from *D. nana*, published data on ligament contractility, and a biomechanical model of crinoid swimming.

Materials and methods

A specimen of *D. nana* collected by C. G. Messing near the Christensen Research Institute, Madang, Papua New Guinea was used to obtain morphological data. The specimen weighed 0.2×10^{-3} N in air and 5×10^{-4} N in water, has 10 arms of 3.3 cm length and 40 cirri (Fig. 2). The length of the cirri averages 0.63 cm, and their diameter at mid-cirrus is 0.2 cm (Fig. 3).

If *D. nana* were to swim using its cirri rather than its arms, the thrust generated by cirri would have to be at least equivalent to weight in water (WIW) of *D. nana*, i.e., sufficient to overcome the gravitational force. To generate such upward thrust, we assume that each cirrus completes a power stroke (Fig. 4). The power stroke begins with the cirrus oriented with its distal tip pointing upwards, 45° above the horizontal. It then pivots aborally around its base subtending a 90° angle, such that at the end of the stroke the distal tip points downward, 45° below horizontal. The cirrus remains straight throughout the power stroke, pivoting only around its base. The 90° power stroke and the orientation of the cirrus are conservative assumptions that would result in the production of maximal thrust.

To calculate the thrust generated by a cirrus during the power stroke, we developed an analytical model based on biomechanical principles. The model is described in detail
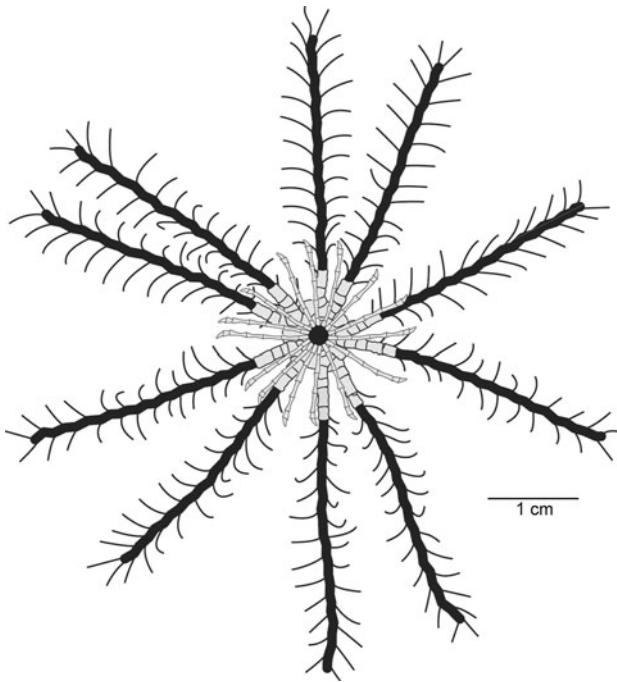
Fig. 2 A schematic drawing of *D. nana*
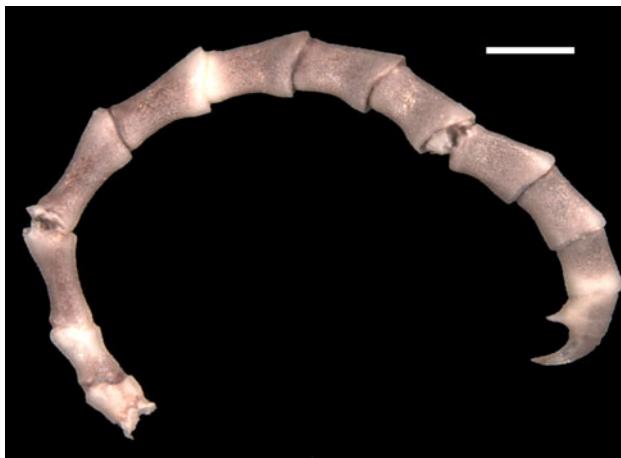
Fig. 3 Cirrus of *D. nana*. *Scale bar* = 1 mm

in Janevski and Baumiller (2010), and here we provide a brief summary. During the power stroke, the cirrus moves through the water at some average velocity, U. It thus experiences a force of drag that can be estimated using the following formula

$$D = \frac{1}{2}C_d\rho SU^2 \tag{1}$$

where C_d is the drag coefficient, p is the fluid density, U is as above, and S is the surface area of the object perpendicular to the direction of motion (Vogel 1994).

To estimate the drag coefficient (C_d) of cirrus, we assumed that because it resembles a circular rod it has an
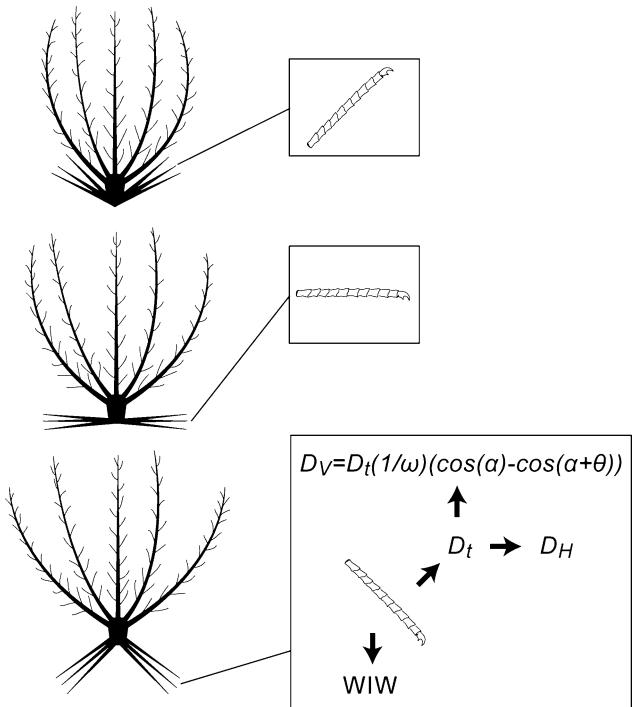
Fig. 4 A schematic diagram illustrating the hypothesized power stroke of *D. nana*. Labels as in text: D_t total drag, D_H horizontal component of drag, D_V vertical component of drag, *WIW* weight in water

equivalent coefficient of drag, which for a circular rod is 0.5 (Hoerner 1965). The value of ρ employed was that of seawater, 1.024 g cm^{-3}. The value of S was calculated as the product of the average length of each cirrus and its average diameter.

Estimating the velocity of the cirrus is more complicated. In addition to the detailed knowledge of its skeletal morphology, one needs to know the length of ligament between cirrals and its placement relative to the central ridge. Moreover, the ligament's mechanical properties, such as its speed of contraction, must be known. Morphological data were obtained directly for the specimen of *D. nana*, while the length and position of the ligament were estimated using published scanning electromicrographs of the cirri of the isocrinid *Metacrinus rotundus* (Fig. 2 in Birenheide et al. 2000). There are few data on mechanical properties of crinoid ligament; however, the speed of contraction has been reported by Motokawa et al. (2004). In experiments with a six-element (6 mm) arm piece of the isocrinid, *Metacrinus rotundus*, they found a maximum bending speed of 43.5 μm s^{-1}. According to their calculations, this corresponds to ligament shortening speed of $0.05L_0$ s^{-1}, where L_0 is the initial length of the ligament. Assuming these values, the tip of a 12-element long cirrus of *D. nana* would have a maximum bending velocity of 100 μm s^{-1}.

The above data can now be used to calculate the drag experienced by a cirrus in a power stroke using Eq. 1. It must be noted, however, that the calculation is made more complicated by the fact that the cirrus pivots around its base such that the linear velocity is not constant at all points—it is 0 at the cirrus base and maximum at the tip. Also, in calculating drag we are interested only in its vertical component as that is what works against the downward force of gravity. Given the above, we use a slightly modified expression for drag perpendicular (D_t) to the cirrus developed by Janevski and Baumiller (2010):

$$D_t = C_d \rho U^2 S/6 \tag{2}$$

To calculate the vertical component of drag (D_V), the following expression was used (see Janevski and Baumiller 2010 for details):

$$D_V = D_t(1/\omega)(\cos(\alpha) - \cos(\alpha + \theta)) \tag{3}$$

where D_t is the total drag calculated from Eq. 2, ω is the angular velocity, α is the starting position of the cirrus with respect to vertical, and θ is the angle through which the cirrus rotates.

To calculate the total thrust that could be produced by cirri, we assumed that at any given moment half of the 40 cirri are in the power stroke while half are in a recovery stroke, thus the vertical component of drag calculated in Eq. 3 for each cirrus must be multiplied by 20. We also assume conservatively that cirri do not produce thrust in the opposite direction during the recovery stroke, and thus ignored this negative contribution in our calculations.

Results

The amount of thrust produced by 20 cirri of *D. nana* in a drag-based power stroke is sufficient to overcome a mass of 8.5×10^{-10} N. Given that *D. nana* has a WIW of 5×10^{-4} N, the thrust produced is five orders of magnitude less than that would be required, making it inconceivable that *D. nana* could swim by using its cirri. Even if the cirri had muscles, which in echinoderms have an order of magnitude higher contractile speed than ligament (Tsuchiya 1985), the cirri would still produce a maximum thrust that is several orders of magnitude less than necessary to overcome the force of gravity on *D. nana*. Thus, in *D. nana* it is not only contractile speed of ligament that prevents cirri from functioning as swimming paddles, but also their small surface area. Clark's claim about cirrus swimming by *D. nana* must, therefore, be dismissed as erroneous. Given the small size of *D. nana*, it is plausible that even a small amount of upward current or convection could have made the animal appear as if moving through the water while its arms remained still, and perhaps some

of the cirri were moving at that time. But clearly, cirrus movement though perhaps coincidental with the animal's movement, was not its cause.

Discussion

While we restricted the above analysis to test the claims of cirrus swimming in an extant crinoid, it is possible to extend the approach to extinct forms. The Early Jurassic crinoid, *Pentacrinites briareus* (=*P. dichotomus*), has a relatively large crown (diameter $\sim$ 30 cm) and short stalk ($\sim$ 20 cm), but its most striking feature is its cirri. Not only are the cirri nearly as long as the arms ($\sim$ 15 cm long), but also because the stalk consists only of nodals, lacking internodals, the cirri cover the entire stalk. Furthermore, the cirri are circular or elliptical in cross section only at the distal tips; for most of their length, they are flattened with width 2–3 times their breadth (Hauff 1984; Seilacher and Hauff 2004). The unusual morphology of cirri and stalk in *P. briareus* (=*P. dichotomus*) has led to some interesting interpretations of cirrus function. For example, Hauff (1984) suggested that they were used for swimming, whereas Seilacher and Hauff (2004) proposed that the cirri generated current toward the crown, making *P. briareus* (=*P. dichotomus*) an active filter feeder.

The swimming function can be evaluated using the approach described above for the extant *D. nana*. However, instead of estimating the WIW of an entire *P. briareus* (=*P. dichotomus*), which is difficult for fossil specimens, we can simply ask whether the thrust generated by a single cirrus is equivalent to or greater than the WIW of the cirrus itself. Using data from Hauff (1984), we estimated the WIW of a cirrus which is 15 cm long, 0.5 cm in width at its widest dimension and 0.2 cm in its narrowest dimension, with a density of 1.44 gm cm^{-3}, which represents the median density of extant isocrinid stalks (Janevski and Baumiller 2010). The WIW of such a cirrus is 6.4×10^{-3} N and the maximum velocity of the cirrus tip is 10 cm s^{-1}. Given the tip velocity and applying Eqs. 1, 2, and 3 above, the thrust generated is 1.36×10^{-3} N, approximately 1/4 of the thrust needed to overcome the force of gravity on the cirrus. Clearly, because the WIW of an individual cirrus is greater than the thrust it can produce, adding the WIW of stalk nodals and the crown only makes the situation worse. Thus, it appears that even the most extreme cirrus morphologies would not have allowed for crinoids to swim solely through the use of cirri.

If muscle-less cirri could not have been the sole mechanism for thrust generation, perhaps they could have contributed to the thrust generated by the arms. This scenario makes little sense if we consider, first, how trivial the contribution of thrust is to *D. nana* and, second, that the

addition of each long-flattened cirrus to *P. briareus* (=*P. dichotomus*) actually decreases its swimming ability as each new cirrus adds extra WIW that thrust generated by the arms would have to overcome. In other words, from the standpoint of functional morphology, the large number of flattened, long cirri argues against them being a swimming adaptation.

Finally, we have only considered cirrus swimming from the perspective of constraints imposed by ligament shortening speed on thrust generation, but other biomechanical approaches could be applied to the problem. For example, one may consider the problem from the perspective of maximal force that crinoid ligament can generate or from an energy-budget perspective. In this instance, however, such approaches are unnecessary as contractile speed alone demonstrates that cirrus swimming is virtually impossible.

Conclusions

Although it is generally accepted that the primary function of crinoid cirri is to anchor the animal to the substrate and that in comatulids and isocrinids cirri are especially well-designed for active anchoring, a purported swimming function of the cirri has also been mentioned in the literature. We evaluated Clark's (1921) report of cirrus swimming in the extant comatulid, *D. nana*, by examining in detail the relevant morphology of *D. nana*, together with published mechanical properties of crinoid ligament (Motokawa et al. 2004), in a biomechanical swimming model. Our results indicate that the thrust generated by cirri is several orders of magnitude smaller than needed to overcome the downward force of gravity of *D. nana*. Furthermore, even assuming that cirri of *D. nana* possessed muscles, which they do not, they could not produce the necessary thrust. We thus conclude that the reported cirrus swimming by *D. nana* was in error.

Extending the biomechanical swimming model to an extinct Jurassic isocrinid, *P. briareus* (=*P. dichotomus*), which has been hypothesized as a cirrus swimmer (Hauff 1984), shows that its very many, long, flattened cirri are not an adaptation for swimming—in fact, each additional cirrus adds more WIW than thrust.

Finally, while the reported contractility of crinoid ligament (Birenheide and Motokawa 1996, 1998; Birenheide et al. 2000; Motokawa et al. 2004) is an astounding property with profound implications for crinoid functional morphology, its mechanical behavior imposes explicit limits on what it can and cannot do.

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