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Form, Function, Food and Feeding in Stellate Echinoderms*

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Abstract

The stellate echinoderms (crinoids, ophiuroids, asteroids) have arms that are involved in feeding. Arms are extensions from the central body and affect the form of the organism. The arms of crinoids, ophiuroids and asteroids differ in structure and have different characteristics. Crinoids are pentaradiate and primitively pentabrachiate, with an internal skeletal support that permits up and down movements. Although branching of the arms occurs, the basic structure remains unchanged. This, along with the mouth on the upper surface, *i.e.* directed away from the substrate, means that the food of crinoids has always been microplankton. The mouth of ophiuroids is directed towards the substrate. The internal skeletal support of their arms permits both up and down and lateral movements. Like crinoids, most ophiuroids are pentaradiate and pentabrachiate, with supernumerary arms being limited in number. Branching of ophiuroid arms occurs only in some euryalids. Ophiuroid arms also have spines, which do not occur in the arms of crinoids. With these characteristics, food of ophiuroids includes not only microplankton but also nekton, benthic particles and small prey. The major distinction of asteroids from crinoids and ophiuroids is that skeletal support of asteroid arms is external. Like ophiuroids, the mouth is directed toward the substrate. Unlike crinoids and ophiuroids, digestion in asteroids involves direct contact between the stomach and the prey and is extraoral in most asteroid taxa. Expansion of the oral surface increases the area over which the stomach can be extended and increases the capacity for feeding. This has occurred in two ways in stellate echinoderms: extension of the interradii in five-armed species and connection of the proximal parts of the rays in multiarmed species. Asteroid arms are not branched. Modified spines (pedicellariae) are used for feeding. The array of food is more extensive in asteroids because of these features including surface prey, particles, multiple small prey, macroprey and nekton. The form of the arm of each stellate group has constraints and potentials that determine food and feeding.

Key words: Crinoidea, Ophiuroidea, Asteroidea, functional morphology

Introduction

Crinoids, ophiuroids and asteroids are considered stellate echinoderms, with extensions from their central body (Strathmann 1975; Lawrence 2010). Despite this common feature, the arms of each class are distinct in their form and function. The consequences of the differences in the form and function of arms on food and feeding are considered here.

Crinoids

All crinoids share the same basic organization and are composed of highly similar elements that are arranged in the same manner and have the same functions (Ubaghs 1978a). A basic feature of

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crinoids is their posture, with the mouth oriented upwards, which condemns them to feeding in the water column. Another is the internal skeletal support of the arms by the brachials and the lack of a direct connection between the radial water canal and the skeleton. *Apektocrinus ubaghsi* Guensburg & Sprinkle, 2009 (Early Ordovician) seems to be an exception because it has floor plates above the brachials that are associated with the bases of the tube feet (Guensburg & Sprinkle 2009). A third is that the tube feet are the sole food capturing structure.

Meyer (1982) stated that there seems to be no reason for doubting that crinoids have been microphagous feeders throughout their evolutionary history. Brower (2005) also noted that the food grooves and covering plates of Ordovician crinoids are similar to those of modern forms indicating similar feeding habits in living and fossil crinoids. These conclusions indicate that crinoids have been conservative in their diet and feeding modes. Known food particle sizes range between 20 and 150 µm (Messing 1997) and include large eukaryotic protists (most phytoplankton), protozoans (foraminiferans and ciliates), rotifers, juvenile metazoans and copepod nauplii. Particles of this size have a low Reynolds number and viscosity of water dominates. These small particles are captured by the tube feet but not by larger arm structures.

If feeding is a function of the number of tube feet (Brower 2005), the question is, how is the number of tube feet increased? Modification and changes in body form associated with feeding has been limited to changing the number of arms and branching of arms and, therefore, the number of tube feet. Ubaghs (1978b) defined the crinoid arm as a jointed outgrowth of the central body mass. They are distinct from the appendages they bear, the ramules, armlets and pinnules (Webster & Maples 2008).

Production of multiple unbranched arms. The number of arms is primitively five (Ubaghs 1978a). Allagecrinids have multiple unbranched arms on one or more radials that extend from the central body (Moore *et al.* 1978). *Mitacatillocrinus* sp. had one unbranched arm associated with three radials and 22 unbranched arms associated with the other two (Moore 1962, in Ubaghs 1978a). Lane (1978) considered production of multiple unbranched arms an adaptive alternative to branched arms in effecting an increased ambulacral surface. Production of multiple arms by increasing the number of rays has not occurred. These crinoids retain the pentaradial condition on the tegmen. Crinoids are not multiradiate.

Production of branched arms. Production of branched arms in crinoids results from bifurcation of the brachials within the theca, near or just above its top (Ubaghs 1978a, Guensburg & Sprinkle 2003). Breimer (1978) also observed that, no matter the number of free arm ends, the arm bases are practically always laterally in contact because of their incorporation in the theca. When free of the theca, these initial branches can be considered arms. Webster & Maples (2008) recognized inconsistent usage of the terms referring to subsequent branches of the arms and gave definitions for ramules, armlets, and pinnules. Ramules are unbranched minor appendages either occurring irregularly along the arm or with regular occurrence at every fourth or greater number of brachials distally. Pinnules are unbranched minor appendages of the arm occurring in a regular pattern on the arms, typically on alternate sides of successive brachials. Armlets are minor secondary appendages occurring at irregular or regular spacing of every third or more brachials and which have small appendages.

Production of pinnules. Pinnules are the result of branching of brachials. Carpenter (1884) noted that the structure of the pinnule is the same as that of the arm. Increased density of the pinnules results from rearrangement of the brachials from uniserial to biserial (Ubaghs 1978a). The uniserial condition is retained in the comatulids (Messing 1997). The arrangement of the pinnules and variation in the length and spacing of tube feet (Meyer 1979) does not affect the form of the arm.

Production of ramules. Branching of arms has produced ramules in a variety of patterns (Bather 1900). It increases the filtering capacity of the arms. Ausich *et al.* (1999) considered dense filtration fans a highly specialized feeding system most successful in advanced cladids and modern articulates. Brower (1978) compared the filtration fan of *Glyptocrinus* (ten unbranched arms) and *Melocrinites* sp. (five branched arms). He concluded evolution in the Melocrinitidae involved hypertrophied ray trunks and an increase in complexity of the arm branching pattern. Cowen (1981) suggested that the reason for the rarity of the melocrinitid pattern was that the characteristics of the rigid skeleton of camerates were not found in other groups that were capable of supporting the system. He also noted the pattern was the most efficient for transport of food to the mouth.

Selective pressures for increasing or decreasing the number of arms. Little consideration has been given to the selective pressures that affect the number of arms and branching. Clark (1921) correlated multiple arms with distribution. He concluded highly multibrachiate comatulids with more than forty arms are characteristic of the littoral habitat of warm seas. The great majority of comatulid species with more than ten arms occur in tropical and subtropical seas at depths less than 200 m, and species with 25 to 30 arms tend to occupy intermediate depths with moderate temperatures. Hyman (1955) made the astute comment that this difference in arm number is in some way correlated with food conditions. There is an inverse relationship between the degree of arm development and the availability of food. Tropical and subtropical seas are usually oligotrophic. A low availability of food would be a selective pressure for increasing feeding capacity and efficiency.

Oji & Okamoto (1994) suggested the arm branching pattern in crinoids can be interpreted as a compromise between two selective factors, an efficient design factor for feeding and an anti-predatory factor. A proportional branching pattern that maintains a constant branching density distally is considered to be effective for planar organisms to gather resources. However, predation results in a high amount of arm loss. They proposed this pattern would be found if the potential for predation is low and said it fit a harvesting paradigm. In contrast, arm branching repeatedly in the proximal region results in a long free arm that is less effective in feeding. However, predation results in a low amount of arm loss if the sites of autotomy are spaced along the free arm. If the probability of attack is proportional to arm length, this arm branching pattern is most advantageous against predatory attacks. They said this fit an anti-predatory paradigm.

Ubaghs (1978b) noted a trend opposite to formation of multiple arms: elimination of arms. He gave the Codiacrinacea as an example. This group contains many generally small crinoids (microcrinoids) that have five, less than five or no arms. Ausich (2003) considered the reduction in number of arms as neotenic and suggested that feeding occurred with the tube feet projecting from the oral plates. The functional consequence of small body size that probably resulted in the failure to produce arms was not considered. Haude (2007) interpreted the occurrence of extremely bilaterally symmetrical crowns of two branched arms in the anomalous genus *Scoliocrinus* as indicating necessities based on geometry (enrolling and infolding of the arms) or from physics (exposure to prevailing unidirectional currents in special hydrodynamic regimes).

Constraints and potentials of crinoids. The constraints of crinoids appear to be their orientation, use of tube feet as the only active feeding structure, and their internal skeleton. Modification of their form is limited to production of multiple arms or branching of the arms.

Has this basic form been a constraint? Basic questions regarding the feeding of crinoids include why they have not evolved alternate modes of capturing food (*e.g.* spines or hooks) in addition to the tube feet and why they have not evolved multiple rays. Crinoids have evolved the functional equivalent by producing multiple appendages on the arms. Can constraints in the structure of the theca and the separation of the radial water canals from the internal skeleton have prevented crinoids from becoming multiradiate?

Ophiuroids

A major difference of ophiuroids from crinoids is their orientation, with the mouth facing the substrate. This means they feed not only in the water column but also on the substrate. Warner (1982) categorized them as microphagous feeders on particles suspended in the water or on the substrate captured with long articulated spines and tube feet and carnivorous feeders that capture prey by arm loops and modified short articulated spines.

Hyman (1955) and Spencer & Wright (1966) noted the uniformity in general body form of extinct and extant ophiuroids except in euryalids. It is a basic disc with distinct arms. Like crinoids, ophiuroids have an internal skeletal support of the arm. However it is not homologous to the brachials of crinoids because it is formed of ambulacrals that have become internal (Hyman 1955, Spencer & Wright 1966). This means that, in contrast to the crinoids, the radial water canal in ophiuroids is intimately associated with the axial arm skeleton. A second important difference from crinoids is that the lateral arm shields on the arms of some ophiuroid species have articulated spines that can be used to capture food. Forbes (1841) was so impressed with the spines of ophiuroids that he created the order Spinigrada, although he limited their function to motion. A third difference is that the arms are capable of both lateral and vertical movement (Hendler *et al.* 1995).

Ophiuroids without multiple arms. These species use their tube feet to capture food like crinoids but also use articulated spines and the arm itself to capture food (Warner 1982). They have the capacity to capture larger prey than crinoids. *Ophiocomina nigra* (Abildgaard, in O.F. Müller, 1785) uses tube feet to capture particles on the substrate and mucus-covered spines for suspension feeding, supplemented by capture of active invertebrate prey and large food particles by loops of the arm (Fontaine 1965).

Ophiocantha pentactis Mortensen, 1936 and *Ophiacantha vivipara* Llungman, 1870 have long arm spines and hold their arms across water currents to capture copepods (Dearborn 1977). *Pectinura maculata* (Verrill, 1869) and *Ophiomyxa brevirima* H. L. Clark, 1915 use loops of the arm to capture food (Pentreath 1970).

The euryalid *Astrobrachion constrictum* (Farquhar, 1900) wipes its arms across host coral colonies to obtain mucous and particles and extends its arms to capture nekton such as mysid shrimp with long spines at the end of its arms (Stewart 1988). None of the feeding methods in these species involve a change in arm form.

Ophiuroids with multiple arms produced without branching. Hyman (1955) stated that ophiuroids have five (rarely six or seven) arms that are not produced by branching. Several extinct stenurid ophiuroids such as *Kentrospondylu*s (Lower Devonian) had ten arms (Spencer & Wright 1966). Congeneric species can have either five or six or seven arms. *Ophiacantha vivipara* Ljungman, 1870 has six or seven arms and *Ophiacantha pentactis* Mortensen, 1936 has five arms (Smirnov 2010). There is no evidence that an increase in arm number from five to six increases feeding capacity. The failure to produce a large number of multiple arms without branching is unexplained. It might be attributed to the sharp distinction between arms and the disc but multiarmed brisingid asteroids have a sharp distinction between arms and the disc.

Production of multiple arms with branching. Branching of arms of ophiuroids to produce multiple arms is limited to the some members of the family Gorgonocephalidae. *Schizostella bifurcata* A. H. Clark, 1952 has arms that branch once beyond the disc while each of the arms of *Astrophyton muricatum* (Lamarck, 1816) produces two thick, stubby locomotory branches and two long, slender feeding branches (Hendler *et al.* 1995). *Gorgonocephalus caputmedusae* (Linnaeus, 1758) has ten arms that branch repeatedly beyond the disc. *Gorgonocephalus caputmedusae* produces small branches but, unlike crinoids, are not suspension feeders. They use hooks and spines at the end of the branches to capture nekton and possibly the tube feet to bind the prey after capture (Rosenberg *et al.* 2005). The difference in food and feeding of gorgonocephalids and other ophiuroids without branched arms suggests that the condition is related to the mode of feeding. Like crinoids, gorgonocephalids use the arms for prehensile movement and are slow moving. Branched arms might interfere with locomotion and burrowing in ophiuroids.

Constraints and potentials of ophiuroids. The orientation of the mouth to the substrate allows ophiuroids to feed on the substrate as well as in the water column. The primary difference from crinoids is that ophiuroids have used the potential of the arm skeleton to evolve articulated spines that produce mucus and that can be modified into hooks. This allows capture of larger prey by the entire arm with its appendages. Branching of the arms for feeding in ophiuroids other than gorgonocephalids seems constrained by their errant or burrowing nature. Gorgonocephalids, with branched arms, are limited in their locomotion and do not burrow.

Asteroids

An external support of the arm is the major difference between asteroids on one hand and crinoids and ophiuroids on the other. This has important effects on their diet and their feeding mechanisms. An additional consequence of an external body wall is a large coelom in which gonads and pyloric caeca occur. This may have been the selective pressure for the evolution of the external support of the arms. The tube feet of asteroids, however, are important in food capture and subsequent transport to the mouth (Jangoux 1982). A second major factor that distinguishes asteroids from crinoids and ophiuroids and affects their diet and their feeding mechanisms is the direct contact between the stomach and food, whether the food is ingested or not (Feder & Christensen 1966, Jangoux 1982).

Asteroids show a great variety in body form and feeding structures, including the arms, disc, spines, hooks and pedicellariae. Because of this, asteroids are able to feed on a much greater variety of food than crinoids and ophiuroids. Jangoux (1982) listed the food of asteroids as suspended or surface particles, surface or buried macroprey, surface films of microorganisms, colonial or encrusting invertebrates, and small swimming organisms.

Effect of area of the oral disc. Although the role of the oral disc in feeding has been recognized (Jangoux 1982), the effect of the size of the area of the disc has been little noticed. The stomach is never extended beyond the edge of the disc, probably because of the potential of damage from physical causes or predation. A consequence of an increase in the area of the disc is an increased area over which the stomach can extend. This results in an increased capacity to feed on surface films, small particles from the substrate, encrusting organisms such as sponges, bryozoans, colonial ascidians and corals, many small prey simultaneously, and larger prey.

One way the area of the oral disc can be increased is by extension of the interradii. Cuénot (1948) and Hyman (1955) described the different forms of asteroids from having arms attached to the cen-

TABLE 1. Area of oral surface of the disc of asteroids with different lengths of the major and minor radii (interradius). Calculated from data in Clark & Downey (1992).

	Radii (mm)	Interradii (mm)	Ratio	Area of oral surface (mm^2)
Ratio between 4 and 10				
Ophidiaster bayeri A.H. Clark, 1948a	15	3.8	4	50
Hydrasterias ophidium Sladen, 1889	28	4.0	7	50
Tamaria floridae Perrier, 1881	31	7.6	4.1	177
Linckia guildingi Gray, 1840	50	5.0	10	79
Echinaster modestus Perrier, 1881	78	15.6	5	804
Chaetaster nodosus Perrier, 1875	90	11.0	8.2	380
Asterias forbesi (Desor, 1848)	91	16.0	5.7	804
Narcissia trigonaria Sladen, 1889	123	20.2	6.1	1257
Doroaster constellatus Downey, 1970	220	31.9	6.9	3217
Ratio between 1.0 and 1.6				
Asterina phylactica Emson & Crump, 1978	7.5	4.7	1.6	1036
Podosphaeraster thalassae Cherbonnier, 1970	8.8	8.8	1	2125
Parvulastra exigua (Lamarck, 1816)*	12	9.2	1.3	529
Asterina fimbriata Perrier, 1875	16	11.4	1.4	517
Tosia parva (Perrier, 1881)	22	15.7	1.4	841
Poraniomorpha h. hispida (M. Sars in G.O. Sars, 1872)	40	28.6	1.4	3057
Poraniomorpha borealis (Süssbach & Breckner, 1911)	100	71.4	1.4	20867
Chondraster grandis (Verrill, 1878)	120	75.0	1.6	29451

* as *Pateriella exigua*

tral disc to stellate, pentagonal or round as the result of extension of the interradius. Hyman (1955) stated the arms shorten in these forms. They are actually shortened by the increase in the length of the interradius. The length of the ray does not decrease. Extension of the length of the interradius greatly increases the area of the oral disc (Table 1).

A second way the area of the disc can be increased is by connecting the proximal parts of adjacent rays of multirayed species as in the extinct *Lepidaster grayi* Forbes, 1850 and the extant *Acanthaster planci* (Linnaeus, 1758)*, Pycnopodia helianthoides* (Brandt, 1835) and *Heliaster helianthus* (Lamarck, 1816). The increase in mouth diameter in these species is much greater than in those in which the increase in area of disc is produced by an increase in the length of the interraddii.

Increase in the number of arms that are not joined proximally. Asteroids may be multiradiate without the rays joining proximally as found in species described in the previous section. The number of supernumerary rays that are not joined proximally in some species may be small, 6 or 7 as in *Leptasterias* or ten as in *Luidia heterozona.* There is no evidence that a small increase in number is adaptive but a large increase does affect feeding. *Labidiaster annulatus* has a large number of arms distinctly set off from the disc. It feeds on nekton (euphausid shrimp and amphipods) in the water column by grasping them with distal pedicellariae and on particles on the substrate (Dearborn *et al.* 1991). Brisingids also have a large number of arms set off from the disc, which have distal spines and hooks. This enables the brisingid *Novodinia antillensis* (A.H. Clark, 1934) to even capture nekton (Emson & Young 1994).

Branching of the arms. It is notable that asteroids do not have branched arms (Blake 1989). On rare occasions, specimens with branched arms apparently produced after distal arm loss have been found. As in ophiuroids, lack of branching may be due to the errant nature of asteroids.

Constraints and potentials of asteroids. Like crinoids and ophiuroids, constraints and potential of asteroids seem related to the skeletal arm support. The external skeleton of asteroids provides the potential for increasing the interradii and production of large numbers of rays. Both of these increase the area of the oral disc. A second major difference is contact digestion of prey in asteroids. The combination of these two characteristics increases the capacity to feed on a variety of prey, from surfaces, and small prey to macroprey. Only those asteroids that feed on nekton in the water column have used the potential of articulated spines (pedicellariae) to capture food. The absence of branching of the arm may be associated with the errant nature of asteroids.

Summary and conclusions

The structures involved in capture of food and characteristics of arms and food in stellate echinoderms are indicated in Table 2. Crinoids use only tube feet to capture food, and, therefore, solely feed on suspended microplankton. They vary in arm number but are always pentaradiate. This may be related to the requirements for support of the arms or constraints to branching of the ray on the tegmen.

Ophiuroids use their arms equipped with spines and/or hooks in addition to their tube feet to capture food. They feed on suspended microplankton and also on small prey and nekton. The limitation of producing only a few additional rays may be related to the requirements for support of the arms or

TABLE 2. Structures involved in capture of food and characteristics of arms and food in stellate echinoderms.

	Crinoids	Ophiuroids	Asteroids
Structures involved in capture of food			
Tube feet	x	x	x
Arms		x	x
Spines		x	x
Oral disc			x
Characteristics of arms and food			
Pentaradiate, no arms			Particles, surface feeders on films, encrusting or colonial organisms
Pentaradiate, unbranched arms	Plankton	Plankton, particles, small prey	Particles, small and large prey
Pentaradiate, branched arms	Plankton	Nekton	
Multiradiate, small radius:interradius			Particles, surface feeders on films, encrusting or colonial organisms
Multiradiate, large radius:interradius			Nekton

constraints from locomotion and burying. Euryalids with branched arms are pentaradiate and feed on nekton.

Asteroids use their oral disc in addition to their tube feet and modified spines to capture food. They feed on a greater variety of foods than crinoids and ophiuroids: particles, small prey, large prey, surface films, and encrusting or colonial organisms. This may be related to the variety of body forms, from pentaradiate forms with a small disc to pentaradiate or multiradiate forms with a large disc. The multiradiate condition may be related to the external support of the body wall.

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