

## Feeding mechanism of the brisingid starfish *Novodinia antillensis*

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**Abstract.** This paper describes the food and feeding mechanisms of the bathyal brisingid sea-star *Novodinia antillensis* (A. H. Clark, 1934). *N. antillensis* is shown to be an opportunistic suspension feeder capable of capturing living planktonic crustaceans of a wide range of sizes. The sea-star extends its 10 to 14 arms into water currents to form a feeding fan with a large surface area, and uses highly retentive pedicellaria on the lateral arm spines to grasp and retain prey. The flexible arms form arm loops to complete the capture. The pedicellaria have a structure very similar to that used by other species known to capture macroscopic prey and, although they are an order of magnitude smaller, they probably function in a similar manner.

### Introduction

Although members of the sea-star order Brisingida are relatively common animals in the deep sea, they have been little studied because of their inaccessibility and fragility. With the exception of taxonomic studies (Downey 1986, Clark and Downey 1992), biological information on brisingids is fragmentary and mostly anecdotal. There are two families within the Brisingida. The limited information available (Jangoux 1982, Downey 1986) suggests that members of the family Brisingidae may have several methods of feeding. The characteristic posture with the arms extended upwards into the water column described for various North Atlantic brisingids (Pawson 1976, Downey 1986, Tyler and Zibrowius 1992) suggests that Brisingidae may be suspension-feeders.

Of the information available in the literature, however, only the observations that the gut of *Odinella nutrix* contained mysids and cumaceans (Fisher 1940) appear to support this suggestion. The other publications which mention gut contents describe items of benthic origin. Sars (1875) examined the gut contents of *Brisingella coronata*; he found bottom living crustaceans and annelids, and suggested that *B. coronata* was a detritivore.

Mortensen (1927) also examined this species and noted that the gut contents included foraminiferans and a variety of small animals. Although any of these food items could be obtained from the water column as a result of re-suspension, it seems more likely that this species obtains food from the sediment surface. It is possible that other species in the family do likewise.

Downey (1986) suggests that members of the family Freyellidae, which are found on soft bottoms and cannot raise the arms above the disc, are not suspension-feeders. This idea is supported by Ruff (1991) who, on the basis of gut contents, suggested that *Astrocles actinodetus* and *Astrolirus panamensis* sweep carcasses of calanoid copepods and gammaridean amphipods from the sea floor. Freyellids have, however, been seen with the arms extended into currents by Pawson (1976), Tyler and Zibrowius (1992), and by the present authors off Hawaii, and may be suspension-feeding. These data suggest that the Brisingida as a group may use a variety of methods to obtain food, and it is possible that some species may use more than one method.

While there are many observations of posture, virtually nothing is known of the details of the food-capture mechanism in any brisingid. In reporting that "mysids were held fast by the pedicellaria" of *Odinella nutrix*, Fisher (1940) implied that the pedicellariae might be involved, but he thought that the mysids "might have become attached in the trawl".

In order to obtain a better insight into the feeding mechanisms of this unusual group of starfish we have undertaken in situ studies of feeding behaviour of *Novodinia antillensis* (A. H. Clark, 1934), a member of the family Brisingidae, found commonly at bathyal depths in the Bahamas area. The behavioural observations are supported by detailed studies of its arm morphology.

### Materials and methods

Observation of *Novodinia antillensis* (A. H. Clark, 1934) in situ and collection of specimens were carried out from the submersibles "Johnson Sea Link I and II" on the sea bottom near to the Bahamas

Islands. Still photographs were taken by means of a laser-focussed Benthos 35 mm camera with an 80 mm lens. Detailed close-up observation was achieved by use of a Photosca T.V. 300 video camera mounted on a pan-and-tilt head external to the submersible and having remote zoom and focus capability. Selected parts of specimens were fixed on board ship in neutral-buffered formalin, prepared for conventional histology, sectioned at 8 to 10  $\mu\text{m}$ , and stained in Milligan's trichrome or Alcian blue-PAS (Humason 1979).

Material for transmission electron microscopy (TEM) was fixed in 2.5% glutaraldehyde buffered in 0.2 M phosphate buffer (pH 7.6). This material was decalcified in a mixture of 2% ascorbic acid and 0.3 M NaCl (Dietrich and Fontaine 1975) and post-fixed in a mixture of equal parts of 2% osmic acid and 2.5%  $\text{NaHCO}_3$  (pH 7.2) (Wood and Luft 1965). The specimens were rinsed in buffer, dehydrated through a graded ethanol series, and embedded in Epon. Ultrathin sections were cut with a Reichert ultramicrotome, conventionally stained with uranyl acetate and lead citrate, and mounted on naked copper grids. TEM was carried out using a JEOL 100C electron microscope. Material for examination by scanning electron microscopy (SEM) was prepared in a variety of ways. Some material was fixed in buffered glutaraldehyde as described for TEM, while some was simply air-dried. To allow study of skeletal elements, tissues were digested using a commercial bleach (sodium hypochlorite) solution, and the remaining ossicles were washed and dehydrated. All preparations were mounted on stubs, critical-point dried in Freon 113, and sputter-coated with gold. Specimens were examined with a Hitachi S510 scanning electron microscope.

## Results

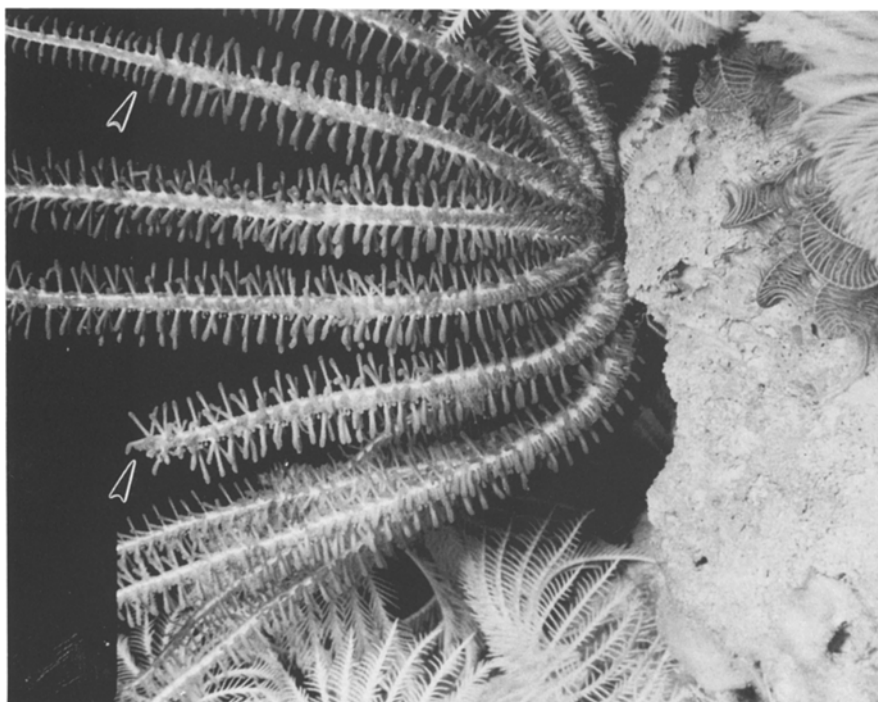
### Size, arm number and regeneration

The individuals of *Novodinia antillensis* observed and/or collected had from 10 to 17 arms, with arm lengths ranging from 250 to 400 mm. Some smaller sea-stars were clearly still in the process of arm addition. As many as four arms, complete but smaller in both length and basal width, were seen inserted between larger arms. Most

specimens showed evidence of arm damage, with arms showing clear evidence of arm-tip regeneration (Fig. 1). Comparison with adjacent arms indicated that up to 30% of an arm had been removed.

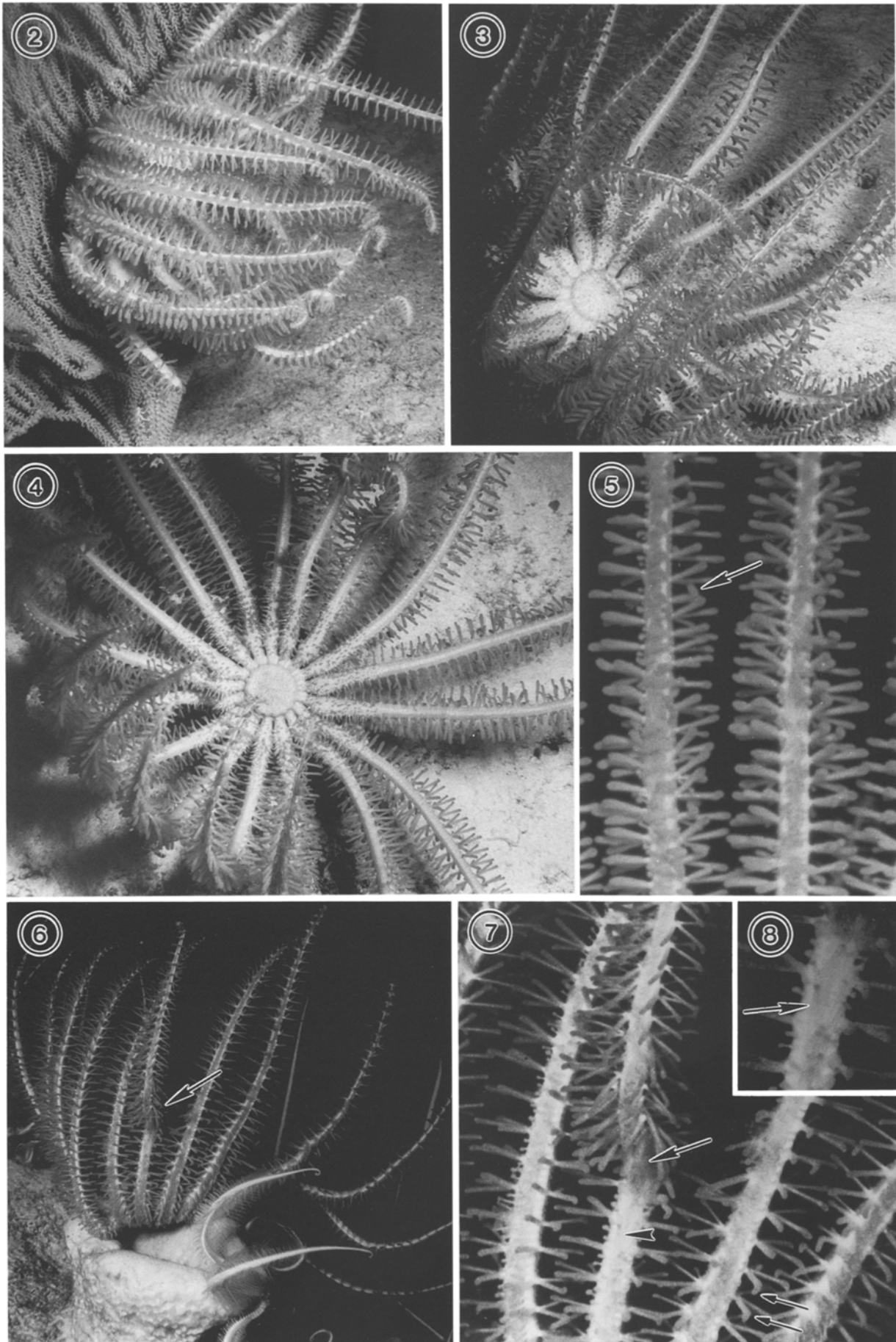
### Habitat and distribution

The sea bottom adjacent to the Bahamas Islands is topographically heterogeneous. In most areas the principal substratum is irregular, steeply sloping, sediment-covered rocky surfaces, often interspersed with areas of vertical cliff. There are, however, also other areas which are flat or gently sloping. This variability in bottom topography means that although current speeds at bathyal depths are generally low, in some places where the underwater contours cause funnelling and similar effects they are accelerated. All specimens of *Novodinia antillensis* observed during this study were attached to some form of hard substratum in areas where the currents were stronger. They were found at depths from 610 to 748 m (the maximum depth surveyed). Many were seen attached to



**Fig. 1.** *Novodinia antillensis* on summit of rocky pinnacle surrounded by stalked and comatulid crinoids. Note arm posture (parabolic fan arrangement), with lateral spines forming a sieve structure and open mouth in centre of disc. Local current is towards the observer. Also note presence of arms in early and late stages of regeneration (arrowed)

**Fig. 2.** *Novodinia antillensis*. 2: Attached to a large gorgonian. 3: showing regular basket-type posture characteristic of individuals in low currents; 4: from above, showing dishd parabolic arm arrangement; 5: parts of 2 arms, showing lateral arm spines forming a complex sieve; tips of spines are unsupported and some (arrow) are bent back by current; 6: attached to a large sponge, showing parabolic arm arrangement; captured food item held by the lateral spine pedicellariae and tube feet is arrowed; 7: part of Fig. 6, showing an arm loop with a contained food item (top arrow); note tube foot posture near a captured food item (arrowhead); spine tips bent back by current flow are indicated by small arrows on bottom right; 8: enlarged section of Fig. 7, showing tube feet extended and oriented towards prey item held in arm loop



rocky outcrops on the steep underwater slopes (Fig. 1) or clinging to vertical cliffs. Some, however, were found attached to large sponges, sea fans and stony corals (Fig. 2: 2, 6). Frequently, *N. antillensis* formed part of an association of large sedentary or semi-sedentary filter-feeding animals characteristically including sponges, gorgonians, hydrozoans, stalked crinoids, comatulid crinoids, ophiacanthid and euryaline brittle-stars (Fig. 1).

### Feeding posture

*Novodinia antillensis* characteristically holds its arms above the substratum in postures that resemble those of other confirmed suspension-feeding echinoderms (Warner 1977, Hendler 1982, Emson et al. 1991). Several clearly distinct patterns of arm posture have been observed and photographed during our surveys. In the most frequently observed natural posture, the arms combine to produce a regular basket-like appearance with the arms bent upwards into the water column and the arm tips curled inwards over the disc (Fig. 2: 3). This posture is achieved by the upward bending of the arms from the base and, since virtually the entire arm is lifted off the substratum, provides the sea-star with the maximum exposure to currents. Each arm segment bears three elongate lateral spines on each side, extended at right angles to the main axis of the arm. Together, these form a regular, evenly spaced, and complex sieve structure (Figs. 1, 2: 2–7). The disc remains anchored to the bottom through the grip exerted by the proximal tube feet of the arms. This posture is characteristic of areas with gentle currents.

Individuals on level bottoms where the current is discernably stronger often lay a few of their upstream arms against the substratum and extend the remainder into and towards the current in a parabolic fan arrangement (Pattern 2, Fig. 2: 4). In strong currents, some starfish perched upon sponges or stony corals show a similar pattern, except that all their arms are bent forward into the current to form a dished shape (Pattern 3, Figs. 1, 2: 6). No individuals were ever seen with all of their arms in contact with the substratum.

### Food capture

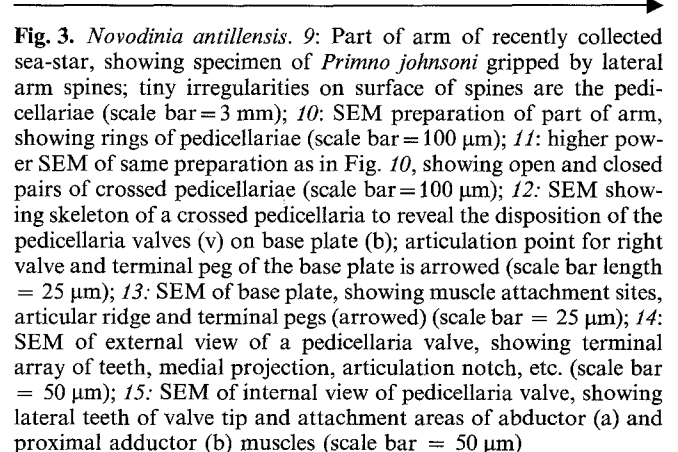
We have watched several *Novodinia antillensis* for periods of up to 10 min and much of this observation was recorded on video tape. Unless food items impinge on the arms, little activity is seen. Thus, in most sea-stars, the only movement of the arms was an occasional very slow bending of individual arms towards or away from the general arm array. Neither long exposure to the lights of the submarine nor even violent stimulation during collection resulted in rapid or extensive arm-bending. However, several individuals observed had one or more arm tips coiled when they were found (Fig. 2: 4), or an arm bent orally into a loop. In a few cases it was possible to see a trapped food item in such a loop (Fig. 2: 6, 7).

No active movement of the lateral arm spines was observed, although it was noted that the spine tips ap-

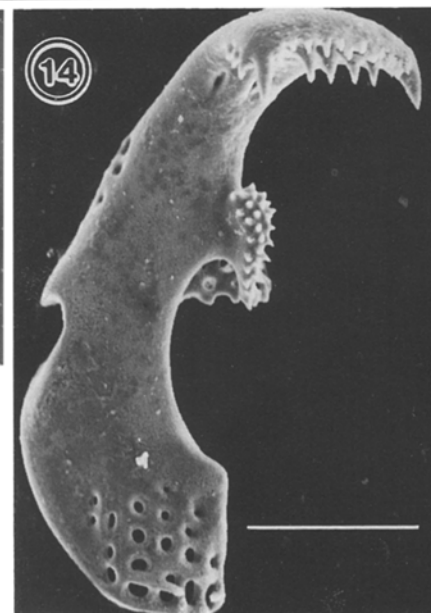
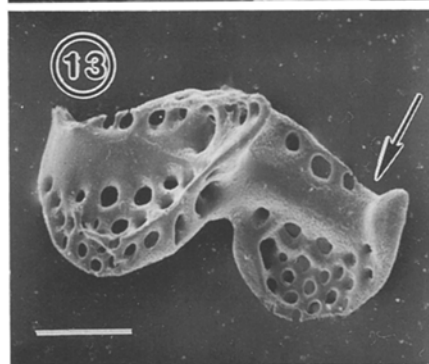
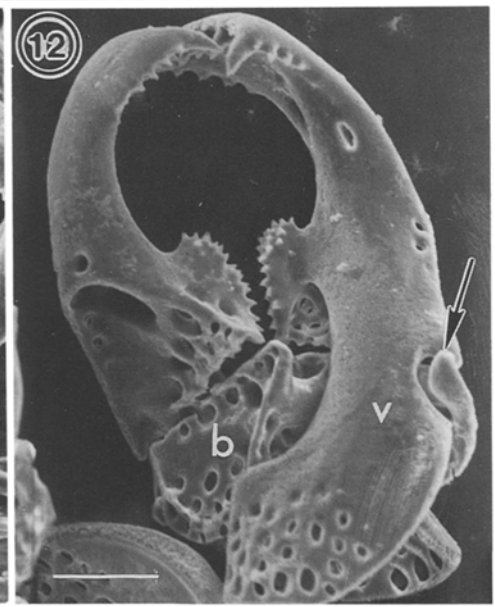
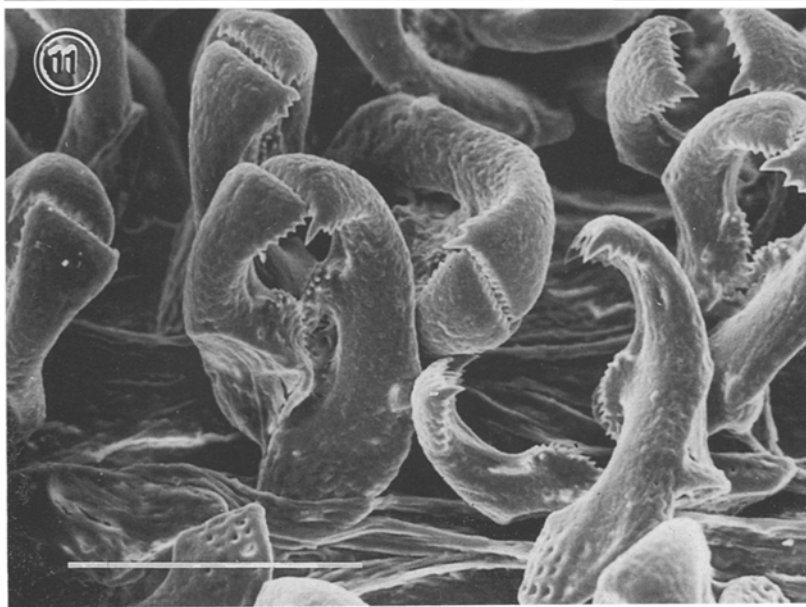
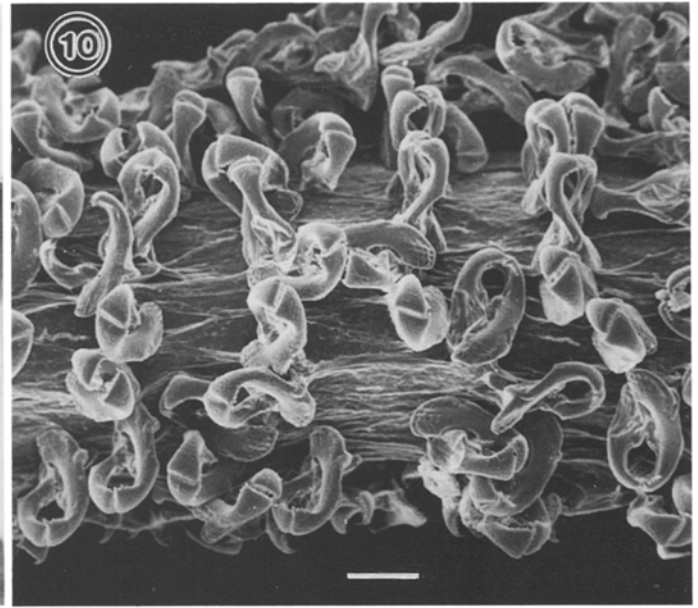
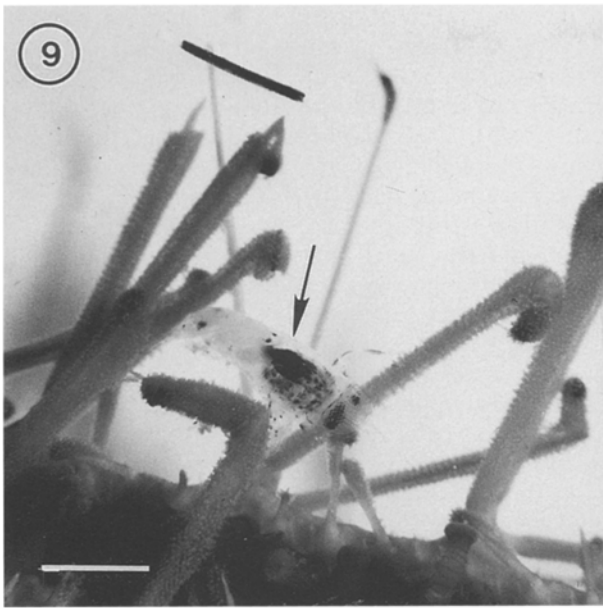
peared to be flexible and were sometimes bent back by currents, giving a clear indication of the direction of flow (Fig. 2: 5, 7). The tube feet were clearly visible on video and in photographs of starfish with the arms extended in a feeding posture. They were not extended along the whole length of the arm (Fig. 2: 2, 5, 7). In fact, on most individuals the only obviously extended tube feet were near the arm base, with the numbers extended decreasing rapidly with distance from the disc. Some individual tube feet could be seen to extend out beyond the tips of the spines.

We observed and recorded the capture of large and small crustaceans on only two occasions. Crustaceans which came into contact with the arm spines at any point along the arm or the general arm surface appeared to be restrained. Some broke free, but others became firmly attached to the spines. This initial phase of capture was followed by strong local bending of the arms which, after periods of 1 to 2 min, resulted in the formation of enveloping arm loops at the site of capture (Fig. 2: 6). A still photograph taken of such an arm loop showed a number of spines adhering to the prey item, with the flexible spine tips apparently wrapped round it (Fig. 2: 7). The photograph also showed that the tube feet to either side of the arm loop were extended and orientated towards the arm loop (Fig. 2: 7, 8). In the individual photographed, the area over which the tube feet were activated into extension was rather small, thus involving only a few pairs of tube feet. Although we could not see this, we presume that the tube feet inside the arm loop were gripping the food.

On one occasion, after observing an individual capture numerous crustaceans stimulated into swimming activity by the lights of the submersible, we were able to collect the sea-star. After carefully transferring it to the surface in a closed container, it was examined in the laboratory. Several crustaceans of differing sizes were adhering to its arms, each gripped by a number of arm spines. These crustaceans were of various sizes and included a copepod, a mysid, and two specimens of a hyperiid amphipod (*Primno johnsoni*) (Fig. 3: 9). The mysid and the amphipods were >1 cm in length.



**Fig. 3.** *Novodinia antillensis*. 9: Part of arm of recently collected sea-star, showing specimen of *Primno johnsoni* gripped by lateral arm spines; tiny irregularities on surface of spines are the pedicellariae (scale bar = 3 mm); 10: SEM preparation of part of arm, showing rings of pedicellariae (scale bar = 100 µm); 11: higher power SEM of same preparation as in Fig. 10, showing open and closed pairs of crossed pedicellariae (scale bar = 100 µm); 12: SEM showing skeleton of a crossed pedicellaria to reveal the disposition of the pedicellaria valves (v) on base plate (b); articulation point for right valve and terminal peg of the base plate is arrowed (scale bar length = 25 µm); 13: SEM of base plate, showing muscle attachment sites, articular ridge and terminal pegs (arrowed) (scale bar = 25 µm); 14: SEM of external view of a pedicellaria valve, showing terminal array of teeth, medial projection, articulation notch, etc. (scale bar = 50 µm); 15: SEM of internal view of pedicellaria valve, showing lateral teeth of valve tip and attachment areas of abductor (a) and proximal adductor (b) muscles (scale bar = 50 µm)



## Gut contents

The stomachs of nine sea-stars were closely examined for gut contents; four yielded gut contents. The recognizable elements comprised whole specimens or parts of calanoid copepods, mysids, leptostracans and euphausiids. Several items were identifiable. The same sea-star which was collected with crustaceans attached to its spines also contained gut contents. These included fragments of more than 50 copepodid larvae and adult calanoid copepods of the genus *Pleuromamma*. The euphausiids were between 1.5 and 2.0 cm in length and were identified as *Euphausia americana* Hansen, 1911; the copepods were identified as the planktonic forms *Phyllopus bidentatus* Brady, 1883, *Scottocalanus securifrons* Scott, 1894 and *Rhincalanus cornutus* Dana, 1849. The condition of both the euphausiids and the copepods was such as to indicate that they had been captured live.

No detritus or other fine material was found in any of the guts of the sea-stars examined. All available photographs of individuals of this species in situ (7 individuals) and the arms of individuals brought into the laboratory were also examined for evidence of other possible food material. No detrital material was seen adhering to the arms of the starfish observed in situ, and although some detritus was found adhering to the arms of individuals examined in the laboratory, this could have become attached after collection.

## Anatomy and function of the food-catching and manipulating structures

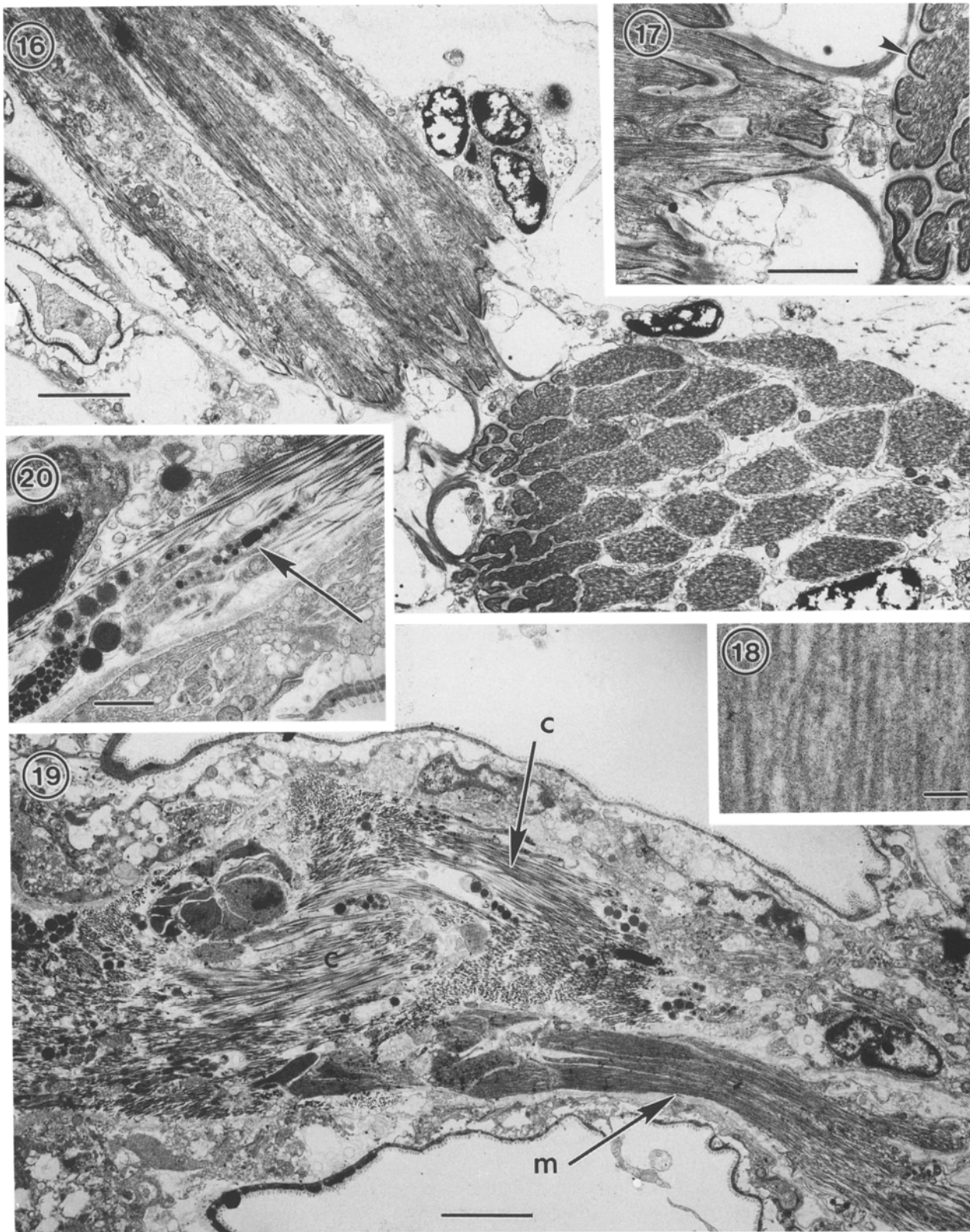
Inspection of the arm spines showed that they are soft to the touch and are widest near their tips. The skeletal ossicle does not reach to the tip, leaving approximately the last quarter unsupported and flexible. Examination of histological sections revealed a thick layer of diffuse connective tissue between the epidermis and the ossicle and also filling the whole of the interior near the tip. Individuals of *Novodinia antillensis* examined in the laboratory soon after collection had many of the arm spines stuck together. Experimentation revealed that the spines adhere securely to almost any pliable surface. This adhesive ability became reduced after the starfish had been in the laboratory for some time. Examination of the lateral spines with SEM revealed the surface to be packed with close-set arrays of crossed pedicellariae (Fig. 3: 10, 11). Each consists of two elongate jaws mounted on a small base piece (Fig. 3: 12, 13) and attached to the spine by a narrow stalk (Fig. 4: 19). The skeleton of each jaw or valve is  $\cong 150 \mu\text{m}$  in length and divided into two parts by the notch, indicating the position of articulation with the basal piece (Fig. 3: 12, 14, 15). The outer part of the valves of these pedicellariae are inwardly curved, armed with sharply pointed spines, and broadly forcipate. The spines are confined to two areas, the valve tip and an inner medial projection (Fig. 3: 12, 14, 15). The largest spines are at the corners (Fig. 3: 14) (corresponding to the canine teeth of Chia and Amerongon 1975), and are 12 to 15  $\mu\text{m}$  in length. Between them are two rows of smaller

teeth, the outer set 2 to 3  $\mu\text{m}$ , and the inner 7 to 8  $\mu\text{m}$  in length (Fig. 3: 14). These teeth interlock closely in closed pedicellariae (Fig. 3: 10, 11, 12). A series of 4 to 5 teeth of decreasing size runs down the lateral face of each valve (Fig. 3: 12, 15). The prominent medial projection bears three rows of small (2 to 3  $\mu\text{m}$ ) spinelets. Because of these spines and teeth, the pedicellariae appear to be strongly adapted for piercing and gripping objects.

The basal part of each valve is spatulate in shape and perforated proximally by a series of holes, while the inner surface is excavated to accommodate the attachments of a large muscle (Fig. 3: 15). The basal piece itself (Fig. 3: 13) has an upper ridge on which the valves rest, and articulate and terminal pegs which interlock closely with the pedicellariae (Fig. 3: 12). Attachment points for three sets of muscles are present on each side of the basal piece. The basal piece is linked to the stalk by strong collagenous connections.

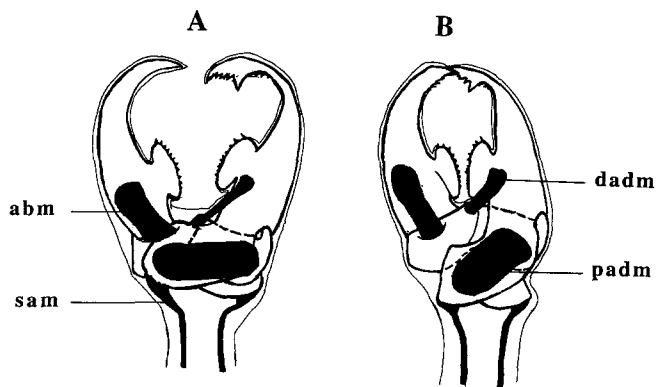
The opening and closure of the pedicellaria is carried out by the complex of abductor and adductor muscles located in the basal part of the pedicellaria and running from the pedicellaria to the basal piece. Examination of sections of pedicellaria has allowed interpretation of the role of the muscles and ligaments in the functioning of a pedicellaria. Because the pedicellariae are so small, some elements were only identifiable using electron microscopy. Three sets of muscles can be distinguished within the body of the pedicellaria. Of these, by far the largest are those linking the outer part of the proximal end of the jaws with the basal ossicle (padm, Fig. 5). These are composed of multiple bundles of smooth muscle (Fig. 4: 16, 18) and are attached by dense non-fibrillar material to the stereom of the basal ossicle (Fig. 4: 17). The structure of the ossicle/muscle junctions is such that the muscles derive part of their support from the outer limiting layer of the muscle on the other side of the basal piece (Fig. 4: 16, 17). The insertions of these large muscles indicate that they have an adductor function (padm, Fig. 5). Discrete, but less massive muscles composed of smooth muscle bundles run up and out from the outer end of the basal ossicle to insert on the outside of the jaw above the fulcrum. Their insertions are clearly compatible with an abductor function (abm, Fig. 5). Finally it is possible to detect fine strands of muscle linking the basal ossicles with the inner surface of the opposing valves (dadm, Fig. 5).

Each pedicellaria is attached to the spine proper by a stalk. This is principally composed of collagenous fibre bundles (Fig. 4: 19). These pass proximally from the stalk into the spine proper and attach to the meshwork of collagenous fibrils forming part of the central structure of the spine. They also pass into the pedicellaria to form a central ligament. Nerve cells containing inclusions similar to those found associated with mutable collagenous tissues in brittle-stars and other echinoderms by Wilkie, Motokawa and other investigators (reviewed by Wilkie and Emson 1988) are prominent adjacent to the collagen of the stalk (Fig. 4: 20). Two small but discrete smooth-muscle strands run peripherally through the stalk (m, Fig. 4: 19: sam, Fig. 5). These strands penetrate into the spine surface tissues, spread out, and link with the colla-



**Fig. 4.** *Novodinia antillensis*. 16: TEM micrograph showing parts of main adductor muscles of both valves of a pedicellaria; because of angle of sectioning, one muscle is cut longitudinally, the other transversely (scale bar = 5  $\mu$ m); 17: TEM showing muscle attachments (arrowed) to basal ossicle (scale bar = 2  $\mu$ m); 18: TEM showing smooth-muscle fibres in longitudinal section (scale bar = 0.1  $\mu$ m);

19: TEM of pedicellarial stalk; most of material is collagen (c), but one of the pair of muscle strands running through stalk is visible (m) (scale bar = 5  $\mu$ m); 20: TEM showing putative neurosecretory vesicles in nervous tissue running through pedicellarial stalk (scale bar = 1  $\mu$ m).



**Fig. 5.** *Novodinia antillensis*. Drawings based on SEM preparation in Fig. 3: 12, showing arrangement and relative sizes of pedicellarial muscles. Muscles are shown in black, and dimensions are based on examination of histological sections. (A) Valves closing; distal and proximal adductor muscles semi-contracted, abductor muscle part relaxed. (B) Valves closed (as in Fig. 3: 12); distal and proximal adductor muscles contracted, abductor muscle relaxed. abm: abductor muscle; dadm: distal adductor muscle; padm: proximal adductor muscle; sam: stalk adductor muscle

gen of the spine matrix. In the pedicellaria these muscle bands run out laterally from the junction of the stalk with the pedicellaria to insert on the outer ends of the pedicellarial valves. (sam, Fig. 5). Their insertions are such that they must have an adductor function.

## Discussion

The results strongly suggest that *Novodinia antillensis* is an opportunistic macroscopic suspension-feeder which uses the lateral arm spines to create a complex filter structure and the closely set arrays of pedicellariae on the arm spines to grip organisms which pass between the arms. The tube feet do not appear to be involved in the initial capture, but are employed in retention of the prey and, presumably, in its transfer to the mouth. The only activity of the tube feet observed in this study was the extension of tube feet towards captured food items. They are clearly used to grip captured prey immediately after capture and are probably used during transfer to the mouth. It seems very likely that small items such as the copepods found in the gut are passed to the mouth by the tube feet in a way similar to that described for brittle stars (Warner and Woodley 1975, Emson and Mladenov 1992). The very limited evidence available suggests that large food is transferred to the mouth in an arm loop, in which it is gripped by the tube feet, rather than being passed to the base of the arm by the tube feet. This would certainly seem to be a more secure method of transfer of struggling active prey items. The suggestion of Pawson (1976) that food caught by brisingids would be passed to the mouth by ciliary currents seems unlikely, but Pawson was envisaging that brisingids would feed on microscopic particles.

The gut contents confirm that *Novodinia antillensis* can capture living pelagic animals, and show that both

small and large animals are arrested by a sieve of this kind. On the other hand, neither the gut contents nor the postures observed support the contention that this species sweeps material from the bottom, as has been suggested for some other brisingids (e.g. Ruff 1991). Equally there is no evidence from the gut contents to suggest that *N. antillensis* intercepts suspended detrital material. We suspect that *N. antillensis* is principally dependent for its nutrition on intercepting living and dead planktonic and benthopelagic crustaceans. Such material appears, from our observations, to be relatively abundant at these depths. Food collection appears to be passive in this species, there being no evidence to support the suggestion of Lawrence (1987) that the slender distal portions of the arms are more actively involved in food capture than other parts.

The pedicellariae are clearly the means by which initial capture of the prey is achieved. In structure they closely resemble the prey-catching pedicellariae described for *Stylasterias forreri* (Chia and Amerongen 1975) and *Labidiaster annulatus* (Dearborn et al. 1991). The high degree of gross anatomical similarity to those prey-catching pedicellariae suggests that they function in a similar fashion. Those of *Novodinia antillensis* are, however, an order of magnitude smaller (*L. annulatus*, 1.3 mm; *S. forreri*, 1.26 mm; *N. antillensis* 125  $\mu$ m) and much less robust, which probably affects the size of prey items they can capture. The ability of the spine tips of *N. antillensis* to bend in response to increased currents appears to be an elegant adaptation allowing the filter structure to operate efficiently in different current strengths. The swollen nature of the spines due to the elaboration of low-density sub-epidermal material in the arm spines is of interest. This material increases the diameter of the spines, with the dual effects of increasing the surface area available for pedicellariae and decreasing the gap between adjacent elements of the sieve.

Dearborn et al. (1991) observed the pedicellariae of *Labidiaster annulatus* being used to capture active crustaceans in laboratory conditions and state that "prolonged contact with pedicellariae causes them to open and (subsequently) grasp the prey". It appeared that the closed pedicellariae gripped appendages such as the antennae of crustaceans and could maintain a grip for long periods. Nevertheless, despite the size and number of these pedicellariae and the active bending of the arms to support the entanglement of the prey, the capture mechanism was inefficient in *L. annulatus* and prey frequently escaped. Dearborn et al. comment that capture of moribund prey is more certain.

The pedicellariae of *Novodinia antillensis* are very small in comparison with those of *Labidiaster annulatus*, and yet restrain live crustaceans rapidly and capture prey proportionately much larger than those caught by *L. annulatus*. It is clear that the pedicellariae of *N. antillensis* are very efficient. This suggests that many small pedicellariae are more efficient than a few large ones at restraining prey. It is possible that the soft swollen nature of the spines is important here. It could be speculated that prey impinging on the yielding surface of a spine come instantly into contact with a very large number of small gripping



organs which act somewhat like "velcro" and form a very effective trap. Certainly the spines are extremely adhesive.

The interpretation of the function of some of the muscles of crossed pedicellariae is difficult, and there have been different views expressed. Much depends upon exactly where muscles insert with respect to the fulcrum of the pedicellaria. Thus, what appears to be the same muscle is interpreted in different species as the proximal abductor by Chia and Amerongon (1975) and Roberts and Campbell (1988), but as the proximal adductor by Smith (1937), Hyman (1955) and Dearborn et al. (1991). If the muscles insert differently in different species, both interpretations may be correct.

The situation for *Novodinia antillensis* appears to be that three of the four sets of muscles apparent have adductor capability. Of these, by far the largest are those interpreted by Chia and Amerongon (1975) and Roberts and Campbell (1988) as the proximal abductors. Their insertions and size are such as to make an abductor role unlikely in *N. antillensis*, and we consider that these are adductor in function as suggested by Smith (1937), Hyman (1955) and Dearborn et al. (1991). In view of their size relative to the adductor muscles running from the stalk to the outer end of the pedicellarial valves, we further suggest that they provide the main adductor effort. We follow Dearborn et al. in referring to them as the proximal adductor muscles. The muscles connecting the outer ends of the valves with the spine proper via the stalk can, in view of their insertions, only have an adductor function. These are termed the proximal adductor muscles by Chia and Amerongon and by Roberts and Campbell, but do not appear to have been seen by Dearborn et al. We refer to them as the pedicellarial stalk adductor muscles. All authors are agreed that an adductor function can be ascribed to the small muscles running up onto the inside of the valves (the distal adductor muscles). The size of these muscles suggests that they play only a minor part in adduction. It is possible that they have a role in controlling orientation of the pedicellarial valves during adduction. In this species, therefore, the only muscles with a clear abductor function are those termed the distal abductor muscles by Roberts and Campbell.

The similarity in feeding methodology of the sea-stars to co-existing gorgonocephalid brittle-stars such as *Astracme mucronata* is remarkable. Both have an extensive sieve structure in which the elements of the sieve are relatively widely spaced. In both, the collecting structures can form a concave, dished structure bent towards the current in a posture Warner (1977) described as being optimally for certain efficient types of passive filter-feeders. Moreover, the capture technique of both groups involves adherence of large prey to microscopic hook structures and the bending and coiling of the arms for the retention of prey (Emson et al. 1991).

The similarity of the gross anatomy of other brisingids to that described for *Novodinia antillensis* and the remarkable similarity in structure of the pedicellariae of the lateral arm spines (see e.g. Fig. 69 of Clark and Downey 1992) suggest that many members of the family Brisingidae may use similar techniques to capture food. That

many are macroscopic filter-feeders is suggested by the postures described for other brisingids.

The postures shown by *Freyella elegans* (Porcupine Sea Bight, 4000 m; Gage and Tyler 1992), by the unidentified species illustrated by Pawson (1976) (from 1°50'N, 80°39'W; 2934 m), by *Brisingines multicostata* and *F. spinosa* (Porcupine Bank, 2500 to 2900 m; observed by Tyler and Zibrowius 1992) and by the species illustrated by Downey (1986), are all similar to the kinds of posture seen in *N. antillensis*. While the actual food captured may be different, it seems certain that the capture technique is likely to be very similar. The abundance of brisingids in the deep sea clearly demonstrates its effectiveness and indicates the presence of a reliable food source. Recent work by Roe and other investigators (e.g. Roe 1988), has shown that the abundance of both carcasses of planktonic copepods and of living planktonic and benthopelagic members of these and other crustacean groups (e.g. mysids and euphausiids), is much higher just above the bottom in many deep-water areas. The brisingids have evolved a highly efficient means of exploiting this source of nutrition.

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## References

- Chia, F.-S., Amerongon, F. (1975). On the prey-catching pedicellaria of a starfish *Stylasterias forreri* (de Loriol). *Can. J. Zool.* 53: 48–75
- Clark, A. M., Downey, M. E. (1992). *Starfishes of the Atlantic*. Chapman & Hall, London
- Dearborn, J. H., Edwards, K. C., Fratt, D. B. (1991). Diet, feeding behaviour and surface morphology of the multi-armed Antarctic seastar *Labidiaster annulatus* (Echinodermata: Asteroidea). *Mar. Ecol. Prog. Ser.* 77: 65–84
- Dietrich, H. F., Fontaine A. R. (1975). A decalcification method for ultrastructure of echinoderm tissues. *Stain Technol.* 50: 351–354
- Downey, M. E. (1986). Revision of the Atlantic Brisingida (Echinodermata: Asteroidea), with a description of a new genus and family. *Smithson. Contr. Zool.* 4. 35: 1–57
- Emson, R. H., Mladenov, P. V. (1992). Field and laboratory observations of the feeding of *Macrophiothrix variabilis* (Lamarck) with notes on the feeding of *Ophiactis savignyi* (Müller and Troschel). In: Morton, B., (ed.) *The marine fauna and flora of Hong Kong. Proceedings of the Fourth International Marine Biological Workshop*. Hong Kong University Press, Hong Kong, p. 769–778
- Emson, R. H., Mladenov, P. V., Barrow, K. (1991). The feeding mechanism of the basket star *Gorgonocephalus arcticus*. *Can. J. Zool.* 69: 449–455
- Fisher, W. K. (1940). *Asteroidea*. 'Discovery' Rep. 20: 69–306
- Gage, J. D., Tyler, P. A. (1992). *Deep sea biology*. Cambridge University Press, Cambridge
- Hendler, G. (1982) Slow flicks show star tricks; elapsed time analysis of basket-star (*Astrophyton muricatum*) feeding behaviour. *Bull. mar. Sci.* 32: 909–918

- Humason, G. L. (1979). Animal tissue technique. 4th ed. W. H. Freeman & Co., San Francisco
- Hyman, L. H. (1955). The invertebrates. Vol. 4. Echinodermata. McGraw Hill. New York.
- Jangoux, M. (1982). Food and feeding mechanisms: Asteroidea. In: Jangoux, M., Lawrence, J. M. (eds.) Echinoderm nutrition. Balkema, Rotterdam, p. 117–160
- Lawrence, J. M. (1987) A functional biology of echinoderms. Croom Helm, London
- Mortensen, T. (1927). Handbook of the echinoderms of the British Isles, Oxford University Press, Oxford
- Pawson, D. L. (1976). Some aspects of the biology of deep sea echinoderms. *Thalassia jugosl.* 12: 287–293
- Roberts, M. P., Campbell, A. C. (1988). Functional anatomy of pedicellaria from *Asterias rubens* L. In: R. D. Burke et al. (eds.) Echinoderm biology. Balkema, Rotterdam, p. 725–733
- Roe, H. S. J., (1988). Midwater biomass profiles over the Madeira Abyssal Plain and the contribution of copepods. *Hydrobiologia* 167/8: 168–181
- Ruff, R. R. (1991). A new species of *Bathynoe* (Polychaeta: Polynoidae) from the Northeast Pacific Ocean commensal with two species of deep-water asteroids. *Ophelia* (Suppl.) 5: 219–230
- Sars, G. O. (1875). I. On some remarkable forms of animal life from the great deeps off the Norwegian coast. II: Researches on the structure and affinities of the genus *Brisinga*, based on the study of a new species *B. coronata*. Christiania University, Christiania
- Smith, J. E. (1937). On the nervous system of *Marthasterias glacialis* (L). *Phil. Trans. R. Soc. (Ser. B)* 227: 111–173
- Tyler, P. A., Zibrowius, H. (1992). Submersible observations of the invertebrate fauna of the continental slope south west of Ireland (NE Atlantic Ocean). *Oceanol. Acta* 15: 211–226
- Warner, G. F. (1977). On the shapes of passive suspension feeders. In: Keegan, B. F., O'Ceidigh, P., Boaden, P. J. S. (eds.) *Biology of benthic organisms*. Pergamon, Oxford, p. 567–576
- Warner, G. F., Woodley, J. D. (1975). Suspension feeding in the brittle-star *Ophiothrix fragilis*. *J. mar. biol. Ass. U.K.* 55: 199–210
- Wilkie, I. C., Emson, R. H. (1988). Mutable collagenous tissues and their significance for echinoderm palaeontology and phylogeny. In: C. R. C. Paul, Smith, A. B. (eds.) *Echinoderm phylogeny and evolutionary biology*. Oxford Scientific Publications, Oxford, p. 311–330
- Wood, R. L., Luft, J. H. (1965) The influence of buffer systems on fixation with osmium tetroxide. *J. Ultrastruct. Res.* 12: 22–45

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