FEEDING ACTIVITIES OF TWO SPECIES OF *CLYPEASTER* (ECHINOIDES, CLYPEASTEROIDA): FURTHER EVIDENCE OF CLYPEASTEROID RESOURCE PARTITIONING

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ABSTRACT

Clypeaster rosaceus and *C. subdepressus* have typical clypeasteroid feeding mechanisms and collect particulate material primarily by means of oral surface accessory podia with terminal suckers. They lack the specialized food collecting podia seen in sand dollars, and the poorly differentiated food grooves carry only part of the food material. Maps of surface ciliary currents are provided and it is shown that they are not part of the feeding mechanism. Feeding mechanisms are discussed with reference to clypeasteroid phylogenetics. *Clypeaster rosaceus* occurs in association with sea-grasses (*Thalassia testudinum*) and feeds extensively on dead leaves. *Clypeaster subdepressus* occurs on coarse biogenic sands and selects the upper size fractions (66% greater than 400 μm) for ingestion. Both are essentially epibenthic in habit and lack specialized spines to keep sand and debris from the body surface. Instead, they secrete an extensive sheet of mucus which prevents particles from falling between the spines. The suckered accessory podia of *C. rosaceus* have a mean tip diameter of about 180 μm, those of *C. subdepressus* about 130 μm. Although *Encope michelini* may occur in mixed flocks with *C. subdepressus* or *Leodia sexiesperforata,* they all feed on different fractions of the sediment. Probabilities of podial-particle encounters are insufficient to account for these differences and it is suggested that the basis of resource partitioning between sympatric species is due primarily to differences in size of food collecting podia.

INTRODUCTION

The Clypeasteroida is a large, diverse group of epibenthic and shallow burrowing echinoids ranging in size from the tiny fibulariids (<15 mm) to the huge plate-like clypeasterids (>180 mm). They are abundant in many tropical seas and extend into cold temperate regions (Mortensen, 1948). In a recent series of papers the morphology and feeding behavior of these urchins has been investigated. At the outset, Mooi and Telford (1982) accepted the prevailing hypothesis that sand dollars such as *Echinarachnius parma* (Lamarck), ingested fine particles sieved through the aboral spine canopy. However, particles substantially larger than could be accommodated by the sieve mechanism (100 μm) were found in the gut, and this suggested that some other mechanisms might be involved. In a study of *Echinocyamus pusillus* (O. F. Müller) Telford *et al.* (1983) developed a method for watching feeding from underneath, using a horizontally mounted microscope with an inclined mirror. By this means, direct observations of podial and lantern tooth activities were made of clypeasteroids in their natural orientation. Using similar methods in a re-examination of *Echinarach-*

nius parma intended to determine the possible contribution of the oral surface to feeding, Ellers and Telford (1984) concluded that most, and perhaps all, food gathering was accomplished by oral surface podia. This cast the first serious doubt on the sieve hypothesis. According to Telford *et al.* (1985), another major objection to the sieve mechanism is the physical impossibility of ciliary currents transporting material as proposed by Goodbody (1960), Seilacher (1979) and, indeed, as we ourselves thought at one time (Mooi and Telford, 1982). An entirely different mechanism has been proposed by Telford *et al.* (1985), based on the podial collection of particles which may subsequently be fractured by the lantern teeth. Although Kier (1974) had previously commented on the presence of "crushed" material in clypeasteroid guts, and Timko (1976) specifically described lantern activity in *Dendraster excentricus* (Eschscholtz), the lantern was thought to be inactive during feeding in *Mellita quinquiesperforata* (Leske) (Lane, 1977). More recently, Telford and Mooi (1986) have described the restriction of clypeasteroid species to specific substrate types and within limited particle size ranges. There is sufficient difference in the types and sizes of podia (Mooi, 1986a, b) to form the basis for the resource partitioning which appears to take place between sympatric species (Telford and Mooi, 1986).

The above studies have included the typical, little-specialized *Echinarachnius parma* (Echinarachniidae); three species, *Encope michelini* L. Agassiz, *Leodia sexiesperforata* (Leske), and *M. quinquiesperforata* (Mellitidae), specialized for hydrodynamically active environments (Telford, 1983); and one species, *Echinocyamus pusillus* of a family (Fibulariidae) specialized by miniaturization. The research has concentrated particularly on two areas: (a) Those structures and activities implicated in the supposed sieve hypothesis, notably spine morphology and spacing, ciliary currents and sites of mucus secretion; and (b) those involved in the proposed podial feeding mechanism, notably podial diversity, distribution, and dimensions. Our data have pointed to a widespread reliance on the podial mechanism.

In this paper we extend our observations to the family Clypeasteridae. This family is part of the sister group to all other clypeasteroid families (Smith, 1984). Therefore, members of the Clypeasteridae are very important because their feeding behavior might reflect the ancestral condition for the rest of the Clypeasteroida. In spite of their great abundance, size, diversity, and probable ecological significance, no previous studies of feeding in any species of *Clypeaster* have been reported. Our study deals with *C. rosaceus* (Linnaeus) and *C. subdepressus* (Gray), both abundant in the Gulf of Mexico, Caribbean, and adjacent waters. We show that their feeding mechanism is fundamentally the same as that of other clypeasteroids, and relies on podial collection and the crushing action of the lantern. Further evidence from species distributions and podial data are offered in support of our hypothesis of resource partitioning. Finally, an account of ciliary currents is given, which indicates their uniformity and ubiquity among the Clypeasteroida and confirms that, as in other species, they are not involved in food transport.

MATERIALS AND METHODS

Specimens of *C. rosaceus* were collected at several sites in the Florida Keys (Pigeon Key, Bahia Honda, Long Key) in the summers of 1982 and 1984, at depths of 2–5 m. Patches of *Thalassia testudinum* were found at all collection sites. At some sites, the turtle grass was so dense that only small, isolated areas of sand were visible. *Clypeaster subdepressus* was collected 2–3 miles off Pigeon Key, at depths of 10–15 m. The substrate consisted of coarse carbonate sand with conspicuous coral and shell debris and without significant plant cover. For live observation, specimens were maintained in the laboratory in running seawater on 10–15 cm of sediment from the

collection sites. Other specimens were fixed in the field by injection of 20% formalin in seawater and immediate immersion in 10% formalin in seawater. These specimens were used for examination of gut contents. For measurement of podial tip diameters, specimens were relaxed by slow addition of ethanol and fixed as described above. Forty-eight hours after fixing, specimens were transferred to 3% formalin in seawater for storage. The natural buffering capacity of seawater is sufficient to prevent etching of specimens in dilute formalin for periods of several weeks. Substrate samples were fixed by addition of concentrated formalin to give a final dilution by volume of 5% in seawater. Additional bathymetric and distributional data were obtained from the collection records of the Florida Department of Natural Resources (FDNR, Marine Laboratory, Tampa), from collections in the United States National Museum (USNM, Smithsonian Institution, Washington), and from those in the Museum of Comparative Zoology (MCZ, Harvard University, Cambridge, Massachusetts).

Representative samples of primary and miliary spines from the aboral surface, oral surface, ambitus, and infundibulum were drawn with the aid of a camera lucida. Podia were classified as accessory, food groove and large food groove types (Mooi, 1986a, b) and tip diameters of relaxed specimens were measured by eyepiece micrometer. Plastic thick sections (approximately 1 μm) of spines and podia were prepared using metachromatic staining methods (toluidine blue, cresyl violet) to determine the distribution of mucus secreting cells, as described by Mooi (1986a).

Surface ciliary currents were made visible by carmine particles or black ink and mapped as described by Telford *et al.* (1985). Observations of feeding activity on the oral surface were made using an inclined front-silvered mirror and stereomicroscope mounted horizontally on a swinging boom, as previously described (Telford *et al.*, 1983; 1985; Telford and Mooi, 1986). Analysis of particle size-frequency distributions of natural substrates and of material collected from the food grooves and infundibulum, was performed using a slight refinement of the method described by Telford and Mooi (1986). Small samples were strewn on a microscope slide and all particles within several fields of view were drawn using the camera lucida. The drawings were then spread on a "Summagraphics" M1103 digitizing tablet and their greatest orthogonal diameters were measured and recorded directly into a computer. A 1-mm stage micrometer was drawn with the camera lucida at the same enlargement for calibration. After determination of mean dimensions, the particles were sorted into size classes (<24.9, 25–49.9, 50–99.9, 100–199.9, 200–399.9, 400–799.9, >799.9 μm). Elongation (Leeder, 1982) was calculated as the ratio of lesser diameter to greater diameter. This particle size analysis cannot follow standard sedimentological procedures because the samples collected from individual animals are far too small for sieve analysis. Substrate and food particle size-frequency distributions were compared by Chi square. All statistical determinations followed the procedures of Sokal and Rohlf (1981).

RESULTS

The spines of these *Clypeaster* species are differentiated into two principal types, primaries and smaller miliaries interspersed between them. Both types vary in size, depending on their location on the test (Fig. 1). Histological examination showed that primary and miliary spines possess mucus secreting cells along their shafts and at their tips. In *C. rosaceus* the primary spines are alike in shape in all regions of the body. They range continuously in size from the small aboral spines (1.7 mm, length/width ratio 7.7) to the large infundibular spines (5.2 mm, l/w 12.6). Those of *C. subdepressus* are mostly shorter and more slender. The aboral primaries differ from the others in having slightly inflated tips. They are about 1 mm in length, with a
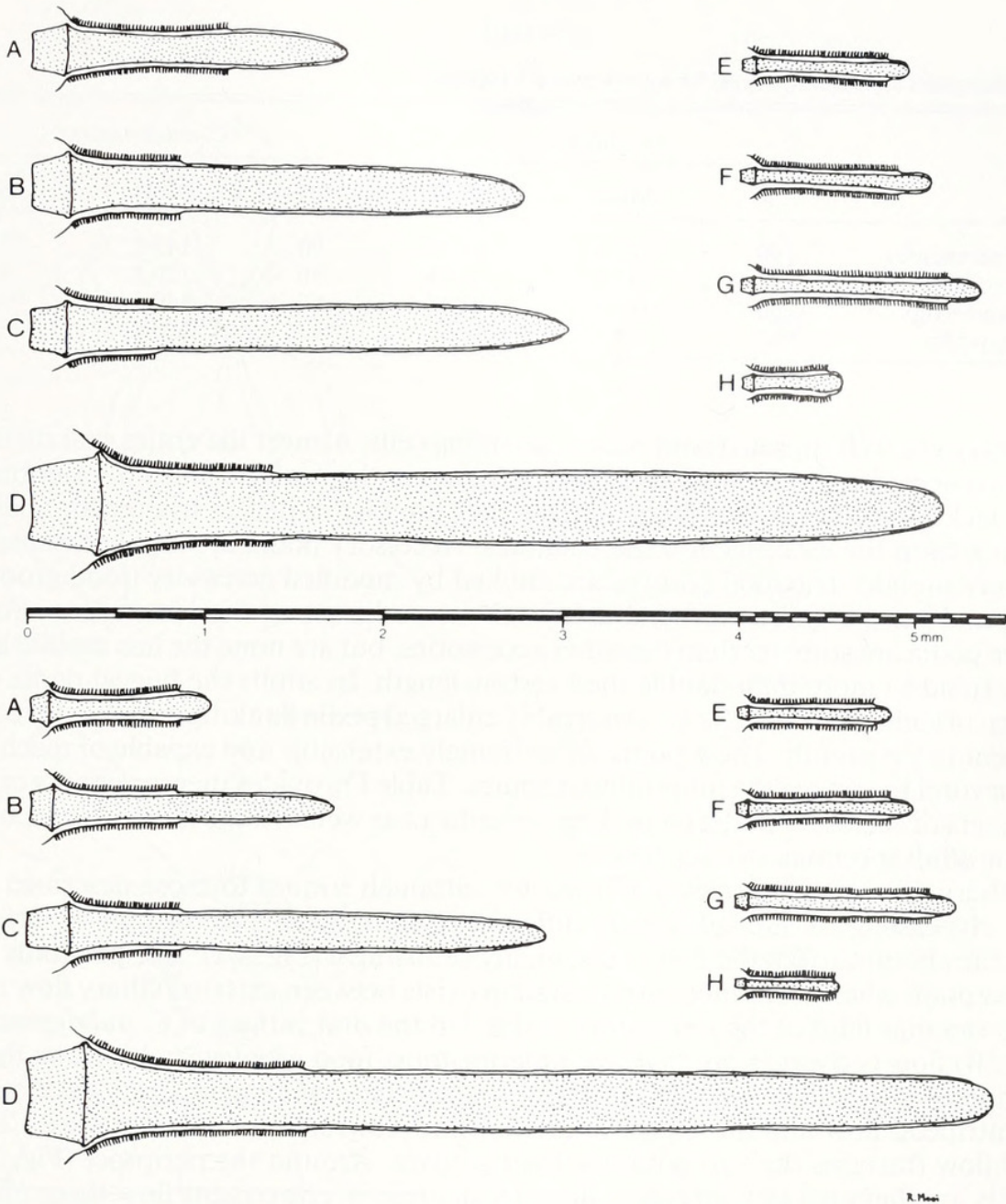
FIGURE 1. Spine types of *Clypeaster rosaceus* (above scale bar) and *C. subdepressus* (below scale bar). (A) aboral primary, (B) oral primary, (C) primary from around periproct (D) primary from inside infundibulum, near peristome, (E) aboral miliary, (F) oral miliary, (G) miliary from inside infundibulum, (H) miliary from food groove.

length/shaft-width ratio of 9.6 and a length/tip-width ratio of 6.6. In both species, the primary spines bear two well-defined rows of cilia which extend up to 1 mm from the base of the shaft. The miliary spines bear similar rows of cilia extending almost to the tip. The rows of cilia are easily discernible in living specimens as well as histological and SEM preparations. Unlike members of any other genus which we have examined, both species possess very small miliary spines, approximately 0.6 mm long, within the food grooves. Elsewhere, the miliaries range from 0.9 to 1.2 mm in length in *C. subdepressus* and are slightly longer in *C. rosaceus*.

Mooi (1986a, b) has described the histology and diversity of nonrespiratory podia in all clypeasteroid families. There are two principal types in *Clypeaster*, both of which bear terminal suckers. They are (1) accessory podia and (2) modified accessories or food groove podia. Examination of sectioned material showed these two types

Mean diameters of podial tips (μm) for two species of Clypeaster

	C. rosaceus			C. subdepressus		
	n	Mean	±S.D.	n	Mean	±S.D.
Aboral accessories	90	199.9	10.35	90	145.0	7.86
Oral accessories	90	181.5	8.58	90	129.8	8.78
Food groove (fg)	60	166.1	10.27	60	140.3	9.42
Large fg podia	12	234.2	24.39	12	196.2	23.45

of podia to be well supplied with mucus secreting cells. Almost the entire oral surface supports accessory podia, with only narrow zones in the center of each interambulacrum lacking them. On the aboral surface they are distributed in triangular patches tapering from the ambitus into the petaloids. Accessory podia are highly extensible and very mobile. The food grooves are flanked by modified accessory (food groove) podia and have a narrow central area without podia along the suture line. Food groove podia are stubbier than the other accessories, but are none the less mobile and may extend to more than double their resting length. In adults the buccal podia are the first of some 10–15 pairs of considerably enlarged podia flanking each food groove adjacent to the mouth. These podia are extremely extensible and capable of reaching well beyond the tips of the infundibular spines. Table I provides measurements of tip diameters of accessory podia from three ambulacra as well as large food groove podia for one adult specimen of each species.

Ciliary currents in species of *Clypeaster,* although similar to those described for other clypeasteroids, are sufficiently different in some details to warrant reporting. Over the aboral surface the flow is essentially centrifugal (Fig. 2A). The petaloids are an exception where a counter current system exists between external ciliary flow and water-vascular fluid of the respiratory podia. On the oral surface of *C. subdepressus* (Fig. 2B) flow converges on the three anterior-most food grooves and follows them centripetally towards the mouth. Posterior to the peristome there is a very small zone of centripetal flow and an extensive area of flow convergent on the midline. This latter flow traverses the two posterior food grooves. Around the periproct (Fig. 2C) there is another area of convergent flow. In all areas of convergent flow there must, of course, be a change of direction away from the test (shown by circled dots in Fig. 2) to satisfy the principle of continuity (Vogel, 1981). As centripetal currents flow towards the center they, too, are constantly converging and must, therefore, have some flow exiting the spine field and directed away from the test. Within the infundibulum the centripetal flow reaches almost to the peristome and passes along the shafts of the circum-oral spines. As a result of this convergence, there is a downward flow towards the substrate, in the center of the infundibulum. The decreased velocity of flow in these areas of directional change can lead to a build-up of ink or carmine particles. In naturally oriented *Clypeaster,* the bulk of these particles fall away from the test onto the substrate below the infundibulum. Along the posterior interambulacrum and at the posterior margin of the periproct, convergent flows are mutually deflected towards the substrate, with similar loss of particulate matter suspended in these flows. On the oral surface of *C. rosaceus* (Fig. 2D), the centripetal flow in the broad infundibulum is more pronounced, including all five food grooves. The genus *Clypeaster* is the only one in which ciliary flow along the food grooves has been observed, and, as already remarked, it is the only one with miliary spines within the food grooves. Irregularities in the sediment surface and activity of the spines ensure
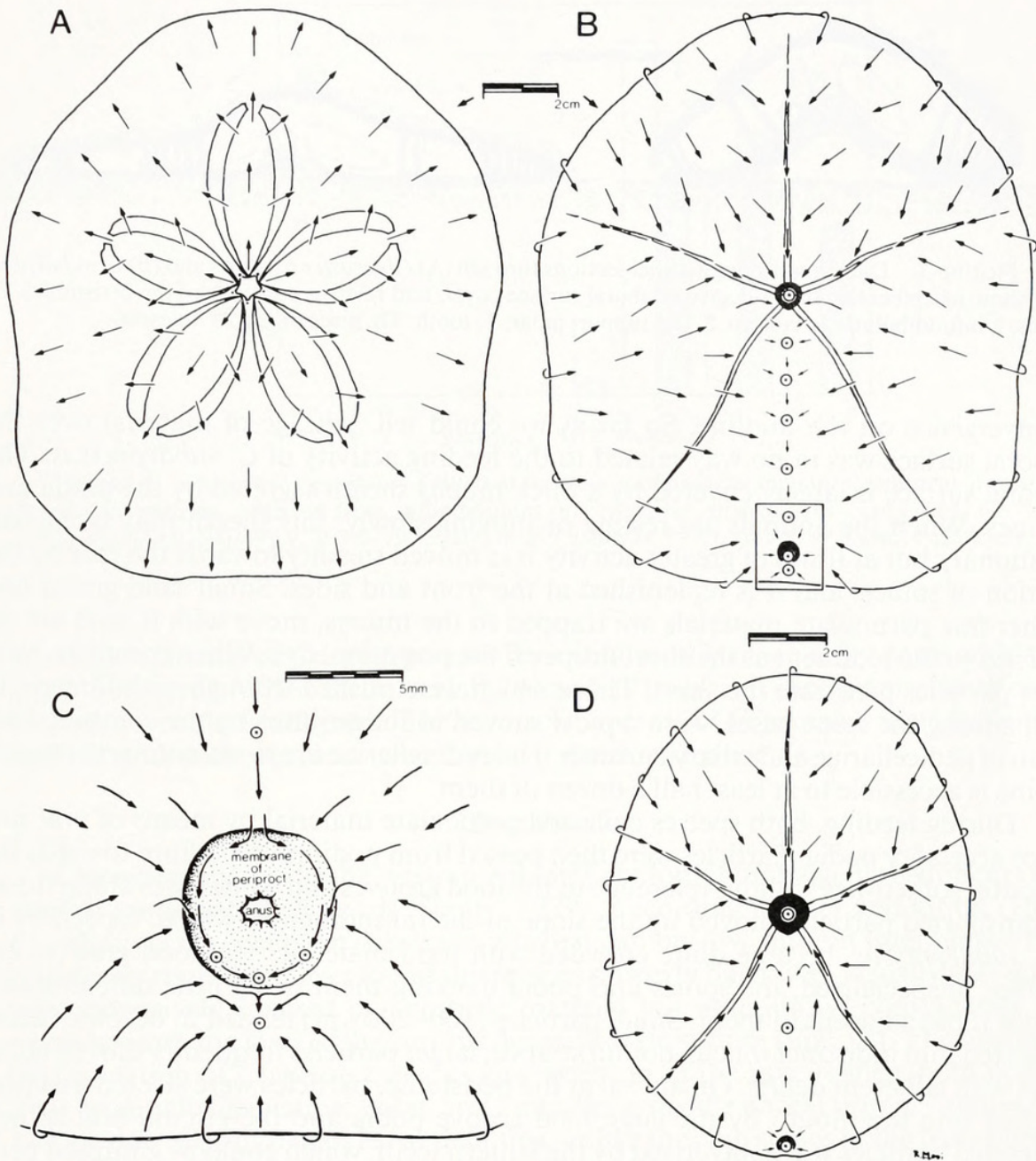
FIGURE 2.   Ciliary currents on *Clypeaster subdepressus* (A–C) and *C. rosaceus* (D). (A) aboral surface, (B) oral surface, (C) area around periproct (boxed in B), (D) oral surface. In A, B, and D, large arrows indicate strong ciliary flow, smaller arrows weaker flow. In B to D, circles with central dot indicate downward flow towards the substrate in living specimens (towards the viewer in these diagrams).

that neither species is ever likely to be so closely in contact with the substrate as to seriously impede escape flow around the margin.

The two species considered here are very different in shape and behavior. When resting on a more or less flat surface (Fig. 3), *C. rosaceus* contacts the substrate around the edge and the broad, deep infundibulum places the mouth high above the surface. The rounded ambitus is not obscured by sediment particles but the aboral surface may be partially covered by dead filaments of *Thalassia* or other material (Fig. 3A), held in place by accessory podia. *Clypeaster subdepressus* is much flatter on the oral surface (Fig. 3B). Numerous particles picked up by podia around the ambitus are passed upward to the aboral surface by the combined action of spines and podia. On the aboral surface, particles move principally towards the posterior with a slight
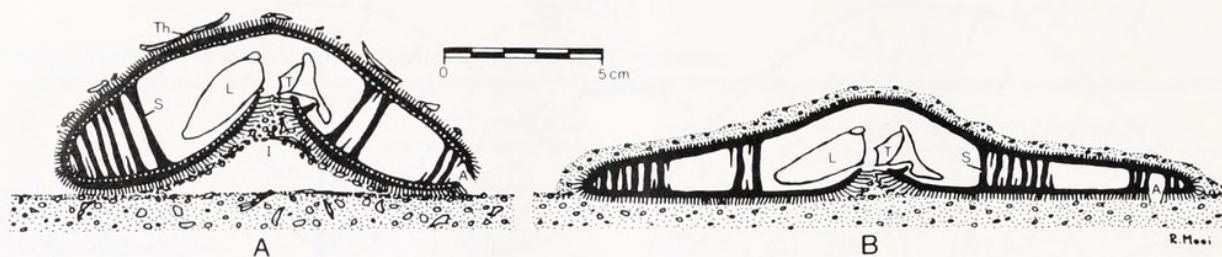
FIGURE 3.   Diagramatic longitudinal sections through (A) *Clypeaster rosaceus* and (B) *C. subdepressus* showing epibenthic habit, degree of aboral surface cover, and relative positions of the peristomes. A, anus; I, infundibulum; L, lantern; S, test support pillar; T, tooth; Th, piece of dead *Thalassia*.

convergence on the midline. So far as we could tell, passage of material over the aboral surface was in no way related to the feeding activity of *C. subdepressus.* The aboral surface is largely covered by a thick mucus sheath secreted by the podia and spines. When the animals are resting or moving slowly, this sheath may be almost stationary but at times of greater activity it is moved steadily towards the rear by the action of spines, and it is replenished at the front and sides. Small sand grains and other fine particulate materials are trapped in the mucus, move with it, and are returned to the sediment as the sheet drops off the posterior edge. When complete, very few particles penetrate the sheet. Those which were pushed through with forceps, to fall among the spine bases, were rapidly moved to the ambitus by the combined action of pedicellariae and ciliary currents. The pedicellariae are so numerous that every spine is accessible to at least half a dozen of them.

During feeding, both species collected particulate material by means of oral surface accessory podia. Particles were then passed from podium to podium towards the mouth, sometimes without reference to the food grooves and sometimes along them. Transported particles moved up the slope of the infundibulum which, especially in *C. subdepressus,* became quite crowded with food material. The food grooves are rather unspecialized, the spines and podia flanking them being little differentiated from those adjacent to them. Small particles (100–200 μm) tended to become incorporated into indistinct mucus-bound strands; larger particles frequently moved alone but with adherent debris. On arrival at the peristome, particles were steered and propelled into the mouth by the large food groove podia and the circum-oral spines. Ingested particles were pulverized by the lantern teeth, which could be glimpsed periodically during observations of feeding. However, some particles, particularly large ones such as mollusc shells, were occasionally rejected. This was achieved by simply releasing the particle, or sometimes it was swiftly and methodically passed back to the ambitus against the prevailing centripetal particle movement.

Food material ingested by *C. rosaceus* included fragments of corals, coralline algae and large amounts of dead *Thalassia.* No attempt was made to determine the particle size-frequency distributions of substrate and ingestate of *C. rosaceus* because the presence of so much *Thalassia* vitiates the method. The material collected by *C. subdepressus* was analyzed and compared to the natural substrate (Fig. 4). The surrounding sediment was devoid of particles below 50 μm, had over 64% between 100 and 400 μm, and 35% larger than that. The mean grain size was 337.4 ± 200.9 μm with a mean elongation value of 0.69. This represents a poorly sorted sediment from which the very fine material has been removed by current activity. Within the food grooves and infundibulum, only 33% were in the 100–400 μm fraction and 26% were greater than 800 μm, compared to only 5% in the substrate. The mean grain size was much larger, 582.2 ± 417.6 μm. These differences are statistically highly significant ($P \ll 0.001$), but the elongation value (0.71) was not significantly different. The
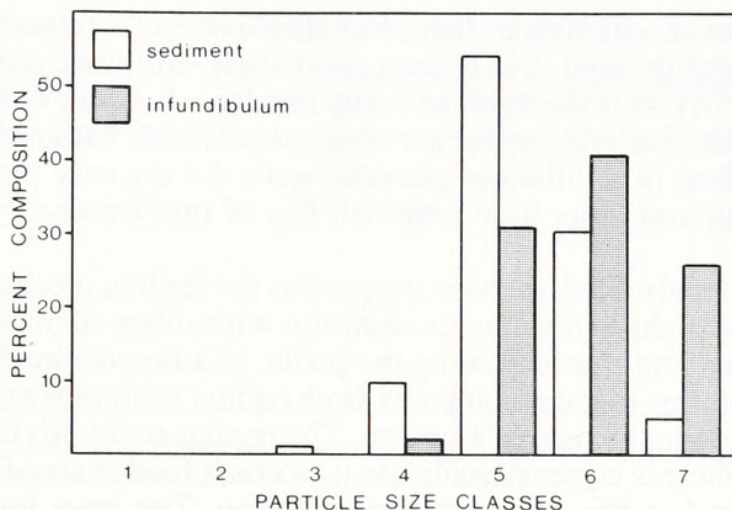
FIGURE 4. Percent composition of different size classes of particles in natural sediment at collection sites and of material collected from infundibulum of *Clypeaster subdepressus.* Size classes (1–7) were <25.0, 25.0–49.9, 50.0–99.9, 100.0–199.9, 200.0–399.9, 400.0–799.9, and >799.9 μm, respectively.

intestinal contents of *C. subdepressus* consisted mostly of a chalky paste with a few larger fragments. When the material is passed as feces, it is loose, not mucus bound and not particularly adherent. The stomach contents of *C. rosaceus* included pulverized material and conspicuous amounts of shredded leaves.

DISCUSSION

Clypeaster species of the western Atlantic are found on biogenic sediments such as algal sands and shell debris (Serafy, 1979). According to Kier and Grant (1965), *C. subdepressus* occurs on substrates where it can burrow without interference from turtle grass roots. We never found this species properly burrowed. Usually individuals were extensively covered by substrate material but were always conspicuous, and never beneath the level of the surrounding substrate surface (Fig. 3B). The unspecialized spination of *Clypeaster* species and secretion of the mucus sheet both point to their essentially epibenthic habit. In *C. subdepressus* the aboral primary spines (Fig. 1A) are only slightly expanded at their tips, unlike the club spines of the truly burrowing mellitids (Telford *et al.,* 1985; Telford and Mooi, 1986). The miliary spines (Fig. 1E) have simple rounded tips and lack any crown-like expansions or terminal sacs (Mooi, 1986c). Both *C. rosaceus* and *C. subdepressus* produce copious amounts of mucus from spines and aboral podia. Mucus secretion by podia is a common occurrence among clypeasteroids (Mooi, 1986a, b). Goodbody (1960) suggested that the miliary spines of *Leodia* were sites of mucus secretion, but Mooi (1986c) has shown that only *Clypeaster* has mucus secreting cells in its miliary spines. The presence of mucus secretory cells in the primary spines further distinguishes the genus. In *C. subdepressus* the mucus covers much of the animal and forms a sheet or tent which traps fine and large particles. The mucus sheet prevents material from entering the spine field and is analogous in function to the canopy of club spines and miliary sacs found in the mellitids (Telford *et al.,* 1985; Telford and Mooi, 1986; Mooi, 1986c) and the mucus envelope of spatangoids (Smith, 1984). Beneath this protective covering, ciliary currents sweep away any stray particles that might chance to penetrate it. Observing an undisturbed animal from underneath, with its aboral mucus sheet in place, there are very few particles to be seen in the ciliary currents. The interspine spaces are kept scrupulously free of debris. Although extensive, the mucus cover on

C. rosaceus was not as complete as that of *C. subdepressus. Clypeaster rosaceus* was never found covered by sand, but it does cover itself with large pieces of shell and plant debris (Fig. 3A), as is the habit of many regular echinoids. Presumably its elevated shape and concave oral surface are adaptations to life within the beds of turtle grass. The wide, deep infundibulum provides space for the easy movement of long pieces of *Thalassia* and other food material, free of interference from living turtle grass and spines.

In the papers already cited, we have shown that the feeding mechanisms of several clypeasteroid species share features in common with other echinoid groups. Food material is collected and transported by the podia, in a manner analogous to that of spatangoids. In contrast to the spatangoids, both regular echinoids and clypeasteroids possess a fully functional Aristotle's lantern. The regular echinoids use the lantern to bite and scrape, whereas clypeasteroids use it to crush food material. The species of *Clypeaster* described in this paper are no exception. The great bulk of their food consists of particles collected and transported by oral surface accessory podia and it is thoroughly crushed by their large and powerful lanterns. We obtained no evidence that either species made use of fine material trapped in mucus. When carmine particles or black ink were being used to trace ciliary currents, it was apparent that some of the material reached the mouth area although it was often caught in mucus long before that. Some of it also became adherent to sand grains and was subsequently ingested. The mucus sheet covering most of the aboral surface traps fine material, all of which is returned to the substrate as the sheet trails off the posterior edge. As we have shown elsewhere (Telford *et al.,* 1985; Telford and Mooi, 1986) use of carmine and, to a lesser extent ink, can be misleading. A load of fine particles sufficient to be clearly visible vastly exceeds the amount normally encountered among the spines. It is possible that this stimulates mucus secretion. Furthermore, carmine particles are known to stick to almost any surface, including sand grains. We suspect that adhesion to the podia and some of the material in the food grooves is just such a passive effect, as we found with *Mellita* (Telford *et al.,* 1985), *Leodia* and *Encope* (Telford and Mooi, 1986). We cannot say categorically that ciliary borne material is not ingested, in fact some probably is. We can unequivocally state, however, that there is absolutely no evidence of its systematic collection; that remarkably little fine material is apparent in the sediment or in the ciliary currents and, finally, that the overwhelming bulk of the material ingested is collected by the podia. Field observations on these species by Kier and Grant (1965) are fully compatible with our findings.

Comparison of the size-frequency distributions of particles in the sediment and those from the infundibulum of *C. subdepressus* (Fig. 4) shows that large particles are collected with greater frequency than their occurrence in the sand. The oral surface accessory podia, responsible for collection of food, have suckered tips with a mean diameter of 130 μm (Table I). There appears to be a complex relationship between podia and particles which determines the composition of the material collected. Several factors are involved, including podial-particle encounters, handling efficiency, particle desirability, and the requirements for subsequent processing. The probability of a single podium encountering a grain of one particular size class can be estimated as the contribution of that size class to total sediment area. Thus, in a sample of natural sediment we would expect 54% of them to be in size class 5 (Fig. 4), for which the mean dimension is 300 μm. The product of grain proportion (0.54) and grain area (300^2) divided by the total area of all the grains is 0.2208. If particles were picked up in simple proportion to the frequency with which a podium encounters that grain size, then 22.1% should be in class 5, 40.8% in class 6 and 26.0% in class 7. Large particles are indeed favored, but simple encounter frequency alone cannot explain the observed size distribution of particles in the infundibulum. The relationship be-

TABLE II

Percent by number of particles in natural sediment for habitat of Clypeaster subdepressus *and estimated percentage by mass*

Particle size	Observed % by number	Estimated % by mass
Class 3	1.0	0.0
Class 4	10.0	0.2
Class 5	54.0	9.1
Class 6	31.0	44.6
Class 7	4.0	46.0

Each size class represents twice the linear dimensions of the preceeding one. Mass is proportional to length^3, or eight times the mass of the next lower particle size class.

tween podial and grain dimensions is probably critical in particle handling. Thomas and Hermans (1985) have described the elegant duo-gland adhesive system responsible for attachment and release of the podia of a starfish. Mooi (1986a, b) has described the structure and action of the terminal suckers of clypeasteroid tube feet. Both processes, adhesion-release and suction, appear to operate in the collection and transport of particles. Our data suggest that particles of about five times the podium diameter might be optimal, and that below this size, effectiveness of the pick-up and transportation mechanisms diminishes. Larger particles could be handled cooperatively by several podia at once but above about twelve times the sucker diameter, effectiveness again falls off. No doubt particles are not equally attractive for reasons other than their size. Ellers and Telford (1984) observed that the presence of diatoms dramatically stimulated feeding in *E. parma,* and Telford *et al.* (1985) recorded a disproportionate accumulation of diatoms and foraminiferans in the food grooves of *M. quinquiesperforata.* It appears that sensory structures in the tube feet (Mooi, 1986a, b) enable clypeasteroids to discriminate between particles. Finally, the preferred size of particles collected might also be related to the dimensions and mechanics of the lantern apparatus where subsequent processing must take place.

It should be stressed that the data presented here consist of actual linear measurements of two dimensions and are therefore not directly comparable to sieve data. We have avoided using the standard sieve particle size classes, usually expressed in ϕ units, because that would invite spurious comparisons. It is apparent in Table II that when our data are transformed to approximate mass data (proportional to length^3), an entirely different impression of sediment composition is obtained. Grains are picked up individually during feeding and in our opinion frequency of particle size occurrence is more important in their selection than the accumulated mass passing through a screen, which is the form of data normally reported in sieve analyses.

Bathymetric range, geographical distribution, and the factors discussed above could provide the basis for resource partitioning by clypeasteroid species (Telford and Mooi, 1986). *Clypeaster subdepressus* has a bathymetric range of 5–210 m (Serafy, 1979) but most commonly occurs well below 50 m (Table III). Kier and Grant (1965) found it as shallow as 5 m, but mostly around 12 m, as we did ourselves. It inhabits coarse biogenic sand and we have been unable to find a reference to any *Clypeaster* species occurring on siliceous, terriginous sediments. This does not mean that some deep water species, such as *C. lamprus* H. L. Clark, could not occur on non-biogenic sediments. Although we found *C. subdepressus* co-occurring with *Encope michelini* at several localities, we never found it in association with *Leodia sexiesperforata.* However, the latter two species were often found in mixed flocks from 3–10 m on

TABLE III

Bathymetric ranges, substrate preferences, and podial diameters of clypeasteroid species

| Species | Common depth (m) | Natural substrate | | | Mean sizes (μm) | |
		Type	Sorted	Size (μm)	Food	Podia
C. subdepressus	10–20	c	p	200–800	580	130
E. parma	0–50[1]	s	m	100–400	—[2]	90
M. quinquiesperforata	0–4	s	w	100–400	170	70
E. michelini	3–10	e	m	100–400	180	100
L. sexiesperforata	2–5	c	w	100–400	140	70
E. pusillus	10–20	s	p	>1000	350	60

[1] Stanley and James (1971).
[2] Method for collecting these data not developed at time of observation.
Unless otherwise indicated, original data can be found in reports of Telford and co-workers: See literature citations.
Substrate types were categorized as biogenic carbonates (c), terrigenic siliceous sediments (s), or either (e). Degree of sorting was ranked as poor (p), moderate (m) or well (w). The particle size range listed includes 70–90% of the total number of particles in the sample. Mean food size refers to material collected by the podia and transported towards the mouth directly or via the food grooves.

rather finer carbonate sands. As shown in Table III, *Leodia* generally occurs shallower than 5 m, *Encope* deeper. These bathymetric data from our field experience are very similar to those reported in the literature (Mortensen, 1948; Serafy, 1979; *inter alia*). For example, Kier and Grant (1965) found *Leodia* in 3–8 m depths, and they specifically commented on the preference of *C. subdepressus* for greater depths. It is quite apparent from these data and other collection records (USNM, MCZ, and FDNR) that *L. sexiesperforata* and *C. subdepressus* have almost completely separate bathymetric and substrate size ranges. *Encope michelini* occupies an intermediate range. It overlaps with *L. sexiesperforata* when that species is approaching its preferred depth limit and on relatively coarse sand, as we found at Torch and Long Keys, Florida. When *E. michelini* is itself near its preferred habitat limits, it overlaps with *C. subdepressus,* as at Pigeon Key, Florida. Detailed field data for all of these species are scarce, especially substrate analyses, and further evidence regarding their spatial separation is urgently needed. None the less, the data presented here and in Telford and Mooi (1986) indicate that within their broad geographical ranges, habitat preferences tend to keep the species separate (by bathymetric range, substrate type, and size, *etc.*). Where species do co-occur (*L. sexiesperforata* with *E. michelini* and *E. michelini* with *C. subdepressus*), differences in podial sizes affecting particle collection and transport, as well as lantern sizes affecting ingestion and crushing, cause them to feed preferentially on different particle fractions. This is of considerable ecological and biogeographical interest and has previously received very little attention. We have summarized all of the available data on common depth of occurrence, as well as particle and podial dimensions, in Table III. Generally, the mean food particle size is around two to five times the podial diameter and drawn from the most abundant particle size classes in the surrounding substrate. The exception is the minuscule *Echinocyamus pusillus* which has the smallest podia but lives in the coarsest substrate from which it selects relatively scarce small particles during feeding. This species does not actually swallow many of its food particles, it scrapes them with the lantern teeth and then releases them (Telford *et al.,* 1983). Unlike other clypeasteroid species, *Echinocyamus pusillus* lives in frequently disturbed environments, where it nestles between pebbles.

Populations of clypeasteroids are often dense and must play a significant role in reworking the sediment and recycling nutrients. The absence of very fine particles in many of the substrates examined suggests that clypeasteroid fecal material, released on or close to the surface, must be swept away by water currents or more rapidly dissolved as a result of increased surface area/volume ratios. *Clypeaster rosaceus* is specialized for existence among *Thalassia* plants and for a diet mostly of dead leaves. It is sometimes found adjacent to turtle grass patches in open sandy areas with *Encope,* where its diet is augmented by relatively large fragments of *Halimeda* and other coralline algal debris, pieces of coral and even bits of mollusc shell. Thus *C. rosaceus* also appears to feed mostly on resources not specially sought after by scutelline species with small podia. According to Kier and Grant (1965) it may also co-occur with *C. subdepressus.* Whether or not the two species then select essentially the same particle fractions is not known.

This study of feeding in *Clypeaster* species is also important because of its phylogenetic implications. The Clypeasteridae is part of the sister group (Clypeasterina) to the remaining members of the order Clypeasteroida (Smith, 1984). The feeding mechanism in *Clypeaster* is simpler and less refined than that of scutelline sand dollars such as *E. parma* (Ellers and Telford, 1984) or the mellitids (Telford *et al.,* 1985; Telford and Mooi, 1986). In *Clypeaster* the food grooves are simple, straight furrows and carry only a fraction of the food. In addition, they are unique in having small miliary spines along their length. In *Echinarachnius* and, more particularly, the Mellitidae, they are precisely defined, extensively branched, and convey all of the food to the mouth. Associated with the food grooves is the greater specialization of the podia. In *Clypeaster* there is little differentiation of the podia flanking the food grooves and those in adjacent areas. In the scutellines specialized podia actually occupy the food grooves and are solely responsible for moving food towards the mouth. Oral surface accessory podia in *Clypeaster* are not morphologically distinguishable from those of the ambitus or the aboral surface. In scutellines the oral surface bears barrel-tipped podia specialized for collection and transport of food material (Mooi, 1986a, b; Telford *et al.,* 1985; Telford and Mooi, 1986). In the most highly derived scutellines (the mellitids) these barrel-tipped podia are further divided into those specialized for gathering particles from the sediment and those for transporting them to the food grooves. Feeding by podial collection of sand also occurs in cassiduloids such as *Cassidulus caribbearum* (Lamarck) (Gladfelter, 1974) and *Apatopygus recens* (Milne-Edwards) (Higgins, 1974), which do so without the aid of food grooves. Since the cassiduloids represent an outgroup for the clypeasteroids (Smith, 1984), this feeding mechanism is plesiomorphic for the Clypeasteridae and culminates in the apomorphic, highly specialized podia and food grooves of the Mellitidae. The absence of such specialized structures in *Echinocyamus* (Fibulariidae) (Telford *et al.,* 1983) is an apomorphy associated with miniaturization and is not indicative of the ancestral condition.

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