

COLLECTION OF FOOD BY ORAL SURFACE PODIA IN THE SAND
DOLLAR, *ECHINARACHNIUS PARMA* (LAMARCK)

OLAF ELLERS¹ AND MALCOLM TELFORD

Department of Zoology, University of Toronto, Toronto, Ontario, Canada M5S 1A1

ABSTRACT

In *Echinarachnius parma* all spine types have cilia arranged in two bands along the shaft. Ciliary currents flow perpendicular to these bands and reversals were not observed. On the aboral surface the bands of cilia were oriented perpendicular to lines radiating from the apex. Flow visualization using dyes and particles showed that aboral currents flow radially towards the ambitus. In contrast, on the oral surface, currents flow from anterior to posterior and the bands of cilia are arranged at right angles to this axis. Oral surface ciliary currents do not carry particles to the mouth nor to the food grooves. At least 80% of the particles carried over the aboral surface are lost at the ambitus. Only particles < 20 μm , if any, pass around the ambitus and these were not seen to enter the food grooves.

Light microscope observations showed that oral surface and ambital podia continuously probe the substrate and draw particles towards the test. Particles are passed from podium to podium, to the food grooves, and thence to the mouth. The rate of particle collection and passage along the food grooves is much higher when concentrated diatoms are offered than with normal sand substrate. This oral surface activity has not been reported before in any sand dollar.

Echinarachnius parma discriminates against substrate particles larger than 230 μm in diameter, but does not especially select those less than 100 μm . Statistical analysis showed significantly fewer particles > 230 μm in the gut, when compared to natural sediment ($P < 0.05$). However, there was no significant difference in proportions of smaller particles. Thus there is no evidence that these sand dollars used an aboral sieving mechanism which would have concentrated particles < 100 μm from the substrate.

INTRODUCTION

Sand dollars (Clypeasteroidea) are flat, irregular echinoids with a lantern apparatus. They live on soft substrates, mostly in shallow water. *Echinarachnius parma* (Lamarck) occurs in the north Atlantic and Pacific on mixed sandy substrates (Harold and Telford, 1982), where it extends from the intertidal zone to depths of about 1600 m (Mortensen, 1948). All sand dollars are adapted to collect particulate food from the substrate material and also to maintain their position on or in the bed of mobile sediment in moving water. In the recent literature a dichotomy of opinion has emerged between those who interpret sand dollar morphology primarily in terms of feeding (Ghiold, 1979; Seilacher, 1979; Alexander and Ghiold, 1980; Smith and Ghiold, 1982; *inter alia*) and those who give primacy to hydrodynamic forces (O'Neill, 1978; Telford, 1981, 1983; Telford and Harold, 1982).

Goodbody (1960) was the first investigator to provide a detailed description of feeding in any sand dollar [*Leodia sexiesperforata* (Leske)]. According to his observations, substrate material was passed over the aboral surface, supported on the club-

Received 6 February 1984; accepted 23 March 1984.

¹ Present address: Department of Zoology, Duke University, Durham, North Carolina 27706.

shaped spines. Small organic and inorganic particles which fell between the spines were swept to the ambitus in ciliary currents, transferred to the oral surface, and then swept into the food grooves for transport to the mouth. This explanation of feeding has been very widely accepted and has provided the basis for later descriptions of feeding in *Mellita quinquiesperforata* (Leske) (Ghiold, 1979; Alexander and Ghiold, 1980; Lane and Lawrence, 1982) and in *E. parma* (Mooi and Telford, 1982; Ghiold, 1983). Seilacher (1979) coined the descriptive term "rocking sieve" for this mechanism and treats sand dollars as little mobile sieves. In his opinion sand dollars had deep-burrowing ancestors and their modern flattened form is an adaptation to sifting surface sediments while burrowing to shallow depths.

In contrast to this conventional view, Telford (1981, 1983) has argued that sand dollars are specially adapted for life in moving water on unstable substrates and, by implication, they might well have had a non-burrowing ancestry. The flattened form is seen as an adaptation reducing the drag profile; the lunulate sand dollars (Mellitidae, Atricypeidae, and Rotulidae) are further modified to reduce lift; shallow burrowing is a behavioral adaptation which effectively places the organism low in the boundary layer or entirely beneath it. These ideas do not contradict the notion of feeding by sieving the sediment. However, that mechanism is not essential in the hydrodynamic interpretation of form, whereas it is the very basis of interpretation for adherents to the rocking sieve hypothesis.

Feeding mechanisms need to be critically re-evaluated in light of these different explanations of sand dollar morphology. The first suggestion of the ciliary-mucus model [for *Dendraster excentricus* (Eschscholtz)] was given by McGinitie and McGinitie (1949), with minimal supporting data. Chia (1969) accepted this view but Timko (1976) re-examined feeding in *D. excentricus* and rigorously demonstrated that it collects particles by use of spine-cone traps, pedicellariae, and podia. Later, O'Neill (1978) proposed a mechanism for the exploitation of hydrodynamic forces in group facilitation of feeding in this species. To date, Timko's (1976) work has contained the only suggestion of food collection by oral surface podia in a sand dollar. All investigators have remarked on substrate probing by podia and on the activity of ambital and aboral podia in drawing particles onto the spine canopy, which has been reaffirmed by Ghiold (1983). In spite of this, Ghiold (1979, 1983) and Lane and Lawrence (1982) rejected any involvement of podia on the oral surface during food collection. Seilacher (1979) mentioned the activity of oral surface spines in stirring the sediment and allowed the possibility of podial collection of particles. More recently, Telford *et al.* (1983) have shown that *Echinocyamus pusillus* (O. F. Muller) (Fibulariidae) relies entirely on the podia for collection and transportation of food particles. In several investigations, analysis of sand dollar gut contents has demonstrated the ingestion of particles considerably larger than could be accommodated by the sieving mechanism (Chia, 1969; Ghiold, 1979, 1983; Mooi and Telford, 1982; Lane and Lawrence, 1982). These results have remained unexplained or have been dismissed as accidental.

The present study was undertaken to examine and quantify the possible contribution of the oral surface to feeding in *Echinarachnius parma*. This eventually included a complete re-examination of the rocking sieve mechanism, the ciliary transport of particles, and their passage around the ambitus.

MATERIALS AND METHODS

Echinarachnius parma was collected from the intertidal zone of Bar Road, a natural causeway near St. Andrews, New Brunswick, in August 1982.

The aboral surface of live sand dollars was observed from above using a conventional dissecting microscope; the oral surface from below using a single-plane mirror; and the ambitus from the side using a boom-mounted dissecting microscope (Mooi and Telford, 1982). Ciliary currents were made visible by several means, including carmine particles, yeast, milk, diatoms, or small sand grains pipetted onto the sand dollar. The direction of flow was mapped on oral and aboral surfaces as well as around the ambitus. Observations of podial activity were made using natural substrate from the sand dollar bed, concentrated planktonic diatoms, filamentous and adherent pennate diatoms, hydrated *Artemia* eggs and nauplii, and carmine particles. These experimental materials, alone or in various combinations, were pipetted onto the aboral surface, around the ambitus, or introduced beneath the animals for oral surface observations.

Specimens were relaxed with ethanol (Mooi, 1983) and fixed for SEM in 2% glutaraldehyde for 24 hours, then transferred to 2% buffered formalin for storage. Small pieces of test with attached spines were critical point dried and sputter coated with gold before examination with a Cambridge 180 SEM. Additional observations of spines and podia were made by light microscope.

Inorganic particle size-frequency distribution in gut contents was compared to that of natural substrate. Sand dollars rapidly empty the digestive system during live dissection (Hyman, 1958; *inter alia*). Bell and Frey (1969) found that guts remained full if specimens were fixed immediately after collection. Accordingly, for this purpose, 15 sand dollars were collected from Bar Road and immediately preserved in 10% formalin. They were all collected from a small area of the beach, less than 4 m apart. Directly adjacent to each sand dollar a 1 cm deep substrate sample was taken, using a glass jar 5.5 cm in diameter, and preserved in 10% formalin. From the intestine of each animal small samples of well mixed material were pipetted onto microscope slides. The sand grains were classified into groups by maximum dimension and counted. Particles less than 7 μm , which represent a minute fraction by volume (<1%), were not counted. Substrate samples were treated similarly and the sand grain size-frequency distributions were compared using a Mann-Whitney U-test (Sokal and Rohlf, 1981).

RESULTS

On the aboral surface, ciliary currents flow radially, centrifugally from the apex (Fig. 1). At the ambitus the direction of flow is downward, but with a continued centrifugal component. On the oral surface ciliary currents flow from anterior to posterior over the entire surface.

Cilia were found in two bands on opposite sides of all spines (Fig. 2, 3). The distance to which the bands extend up the spine is characteristic of each type. Fringe spines have an additional semi-circular band of cilia around the base, aborally (as noted previously by Mooi and Telford, 1982). Intercilium distances are approximately 1 μm . Although SEM micrographs (Fig. 3) indicate that cilia are 15–20 μm in length, light microscope measurements indicate that they are longer, up to 25 μm . This difference is possibly due to shrinkage during preparation. Echinoderm epidermal tissue is difficult to prepare for SEM, and even with critical point drying from acetone it shrinks. Because of the rigid underlying skeleton of calcite, the epidermis frequently tears with shrinkage, as the micrographs (Fig. 3) show.

Aboral club-shaped spines are oval in cross section at their distal ends. The orientation of the oval is not constant with respect to the longitudinal axis of the sand dollar (Fig. 1). Anteriorly, the major axis of the oval is perpendicular to an imaginary line passing through the apex and the spine. Posteriorly, the major axis is parallel to

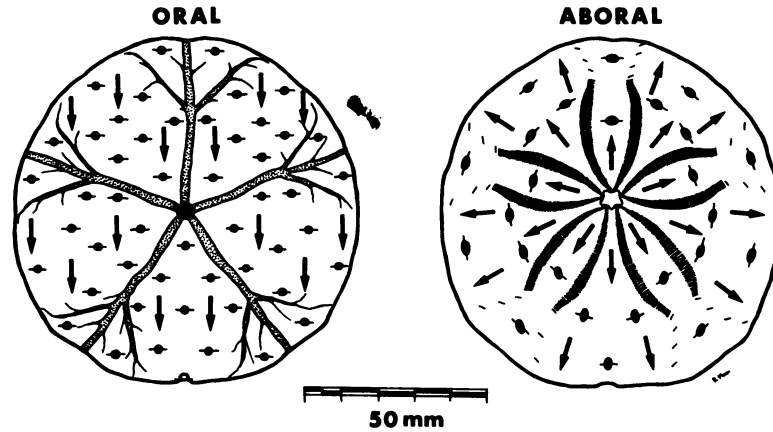


FIGURE 1. Ciliary currents and spine orientation on A) aboral and B) oral surface of *Echinarachnius parma*. Spines are shown as diagrammatic cross sections, circles (locomotory), and ovals (club shaped), with cilia at right angles to shaft. Orientation of the expanded tips of club-shaped spines is not constant but cilia on them are always arranged at right angles to lines radiating from the apex. Oral surface ciliary currents flow from anterior to posterior.

such a line. The orientation of the cilia on the aboral spines is independent of that of the spines themselves. On both club-shaped and miliary spines, it is always perpendicular to a line passing through the apex and the spine. Thus, these bands of cilia are arranged at right angles to the test radii. On the oral surface, cilia are oriented at right angles to the longitudinal axis of the test. In all observed instances currents

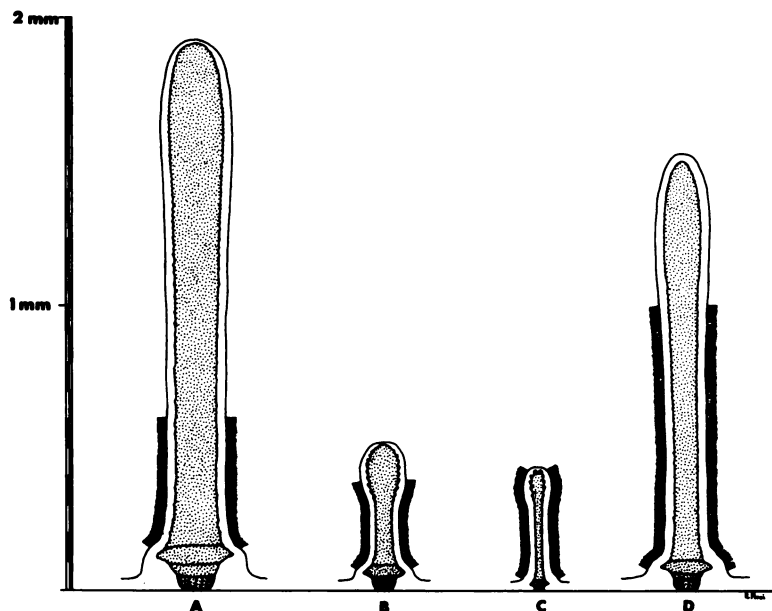


FIGURE 2. Distribution of cilia on major spine types: A) fringe, B) club-shaped, C) miliary, and D) locomotory. Fringe spines have an additional semi-circling of cilia aborally around the base (not shown).



FIGURE 3. SEM micrographs of aboral miliary and club-shaped spines. Ciliary bands on some spines are clearly visible, arrows indicate those that are less conspicuous. Scale bar: 100 μm . A) Two diametrically opposed bands on club-shaped spine; B) more oblique view of another club-shaped spine and bands of cilia on a miliary spine.

flowed perpendicularly to the orientation of the ciliary bands, they were unidirectional and we never saw reversals of flow.

Between spines on the aboral surface, particles were carried to the ambitus by ciliary currents. The maximum size of particle (about 100 μm) that could be carried in this way is determined by the mean inter-spine distance (Mooi and Telford, 1982). In fact, even particles which were small enough to be transported between spines often bumped into them. This slowed their progress through the spine field and there was a negative correlation (-0.63 ; $P < 0.01$, $n = 32$) between particle size and net rate of transportation. For a 60 μm particle the rate was 0.08 mm s^{-1} and for a 10 μm particle 0.78 mm s^{-1} . The rate for small particles was probably maximal because they followed streamlines around spines while particles greater than 20 μm collided with them. At the ambitus small particles (10–20 μm) were swept downward around the edge of the test. Larger particles ($>20 \mu\text{m}$) were carried out of the aboral current, coming to rest near the middle or tips of the fringe spines before dropping to the substrate. An estimated 80% of particles (by number) reaching the ambitus via ciliary currents were lost in this manner. It was not possible to determine what proportion, if any, of the small particles successfully passed around the ambitus and were subsequently ingested. They could not be carried to the mouth by oral surface ciliary currents. Capture of particles from aboral ciliary currents by ambital or oral surface podia was not seen. Nearly all podium-particle contacts were with particles lying on the floor of the aquarium, only rarely with suspended particles.

Podia on the oral surface and at the ambitus picked up particles and pulled them

towards the test where they were passed from podium to podium to the food grooves. In the food grooves they were similarly passed towards the mouth by podia. During this transportation, particles became progressively more aggregated by mucus, probably from the tips of the podia, which are known to have secretory cells (Mooi, 1983). Particles which had hitherto not stuck together, such as *Artemia* cysts, were aggregated with other particles after they had been carried along the food grooves. At the mouth, buccal podia pushed food clumps and diatom-covered sand grains into the opening. Food groove podia (60–80 μm diameter at the tip) were seen to extend to about the length of the oral surface locomotory spines, almost 1 mm. Ambital and aboral podia (100 μm tip diameter) can extend 5 mm or more from the test. Non-food groove podia on the oral surface (80–100 μm diameter) extend about 1.5–2 mm from the test, which allows them to reach the underlying sediment.

When concentrated diatoms or sand grains with numerous attached diatoms were offered as food, the rate of collection by podia and transport along the food grooves increased markedly. If concentrated diatoms were offered in only one ambulacrum, the podial activity in that ambulacrum increased while in the others it ceased. When this response occurred, the food grooves filled up with diatoms faster than they could be ingested. Sand grains covered with diatoms, bacteria, and debris were often ingested, as were clumps of filamentous diatoms and small adherent organisms. On two occasions nematodes in clumps of organic debris were masticated by pedicellariae and then passed to the mouth by podia. However, it appears that the contribution of pedicellariae to feeding is small and possibly accidental. Nothing comparable to the pedicellarial activity nor the spine-cone traps of *Dendraster* (Timko, 1976) was ever observed in *E. parma*.

Gut contents consisted of sand grains, diatoms, broken diatom frustules, sponge spicules, crustacean fragments (parts of zoeae, ostracods, bits of exuviae, etc), and unidentifiable amorphous organic debris. The distribution of inorganic particle sizes in the gut was almost identical to that in the sediment. There were fewer large particles (>230 μm) but all other particles were represented in the same proportions. For small and intermediate sized particles, a Mann-Whitney U-test showed that there was no statistically significant difference between the proportions in the gut and sediment. The same non-parametric test showed that the proportion of the very largest particles (>230 μm) in the gut was significantly smaller than in the substrate ($P < 0.05$).

DISCUSSION

This study has demonstrated that in *Echinarachnius parma*: ciliary currents flow perpendicular to the orientation of cilia; aboral surface currents flow centrifugally to the ambitus but oral surface currents flow anterior to posterior; most particles carried by aboral ciliary currents are lost at the ambitus; podial collection of particles on the oral surface is a major source of food and the process is stimulated by the presence of diatoms; the inorganic particle size distribution in the gut is almost identical to the sediment except for the under-representation of particles greater than 230 μm . These observations indicate that the aboral sieving mechanism contributed little or nothing to feeding during these experiments.

The relationship between the orientation of cilia and the ciliary currents was described by Mooi and Telford (1982) but their description of centripetal ciliary flow on the oral surface was inaccurate. These currents are quite feeble and particles readily drop out of them. This makes it difficult to trace the flow by observing suspended material. Compared to the diameter of a sand dollar (about 50 mm), the field of view

in a dissecting microscope at high magnification is quite small (about 4 mm) and this makes the significance of small differences in angle of flow difficult to perceive. Moreover, in the anterior ambulacra flow is towards the mouth or food grooves, thus appearing to support the centripetal current hypothesis when flow is not mapped over the entire surface. Most recently, Ghiold (1983) appears to have been misled in the same way when he reported centripetal oral surface currents in *E. parma*. There can be no doubt that many of the discrepancies in the literature and the sometimes warmly held differences of opinion, are due to the extreme difficulty of observing particle and current movements in the spine fields of sand dollars. Nonetheless, Parker and van Alstyne (1932) detected the anterior to posterior flow. In the present study the flow was first observed in small sand dollars, <10 mm diameter. It was subsequently confirmed by direct observation for all sizes. Precise mapping of the orientation of ciliary bands on oral surface spines provided a convincing morphological explanation of current flow. Mooi and Telford (1982) based their account on spines in the anterior region or too close to the food grooves and were misled by subtle changes of angles. The lunulate sand dollars might be quite different in this respect. Goodbody (1960) and Smith and Ghiold (1982) have reported centripetal oral ciliary currents in *Leodia sexiesperforata* and *M. quinquiesperforata* respectively. However, the observations made here that cilia are oriented with respect to the position of spines on the test, and not directly to the shapes of the spines, casts considerable doubt on currents inferred from spine orientation alone, as it has been for fossil species.

The conventional aboral rocking sieve mechanism initially postulated by Goodbody (1960) can be visualized in three steps: aboral collection and transport of particles to the ambitus, passage around the ambitus, and then transport across the oral surface to the mouth. Centrifugal aboral ciliary currents have been observed by all investigators. Hyman (1958) and Bell and Frey (1969) suggest that centripetal movement on the oral surface might rely more on podial activity than ciliary currents (except, of course, in *Arachnoides*, which lacks food groove podia). Our observations of the oral surface show that transport of food to the food grooves and mouth of *E. parma* is accomplished entirely by podia. Particles are passed from one podial tip to the next, "like a tiny bucket brigade," to borrow an expression from Mooi (1983). Thus, if the rocking sieve mechanism is to work, this leaves the crucial question of passage around the ambitus. No previous authors have explicitly stated that they observed it. Goodbody (1960) and Mooi and Telford (1982) clearly saw aboral and oral movement of particles but they viewed the two surfaces separately and only inferred that the flow of particles was continuous. There is no direct evidence in any report (Ghiold, 1979; Seilacher, 1979; Alexander and Ghiold, 1980; Lane and Lawrence, 1982; Smith and Ghiold, 1982) to confirm that transfer around the ambitus from aboral to oral surface really does occur. In this study we found that a very high proportion of particles was lost at the ambitus, especially those over 20 μm which tended to move out onto the fringe spines and fall off. Initial observations suggest, in fact, that the basal circlet of cilia around fringe spines might contribute a final thrust, ensuring the ejection of particles. Since the biggest particles are lost at the ambitus there would have to be a mechanism to catch the remaining particles (<20 μm) if this is, indeed, the feeding mechanism. Retrieval of such particles by podia near the ambitus was not observed. Podia were seen picking up particles from the substrate but not capturing them out of the ciliary flow. If a mechanism does exist for selection of such small particles, it should be reflected in the particle sizes of the gut contents.

Analysis of the gut contents indicates that for inorganic particles at least, there is no selection at all for small sizes (<100 μm) but there is some selection against large ones (>230 μm). The number of larger particles (230–500 μm) in the gut is about 60% that of the sediment. The hypothesis "there is a bias against large particles

in the gut" can be distinguished from the alternative "there is a bias in favor of small particles in the gut." A real bias in favor of small particles would greatly inflate their representation because they make up such a large proportion by number of substrate particles. Conversely, a bias against large particles would change the proportion of small particles by number only slightly. The data support the hypothesis that there is a bias against large particles, not a selection for small ones. The gut content analysis, together with the failure to detect aboral to oral transfer of particles, clearly indicates that no aboral feeding mechanism was active in these animals. Certainly the frequent occurrence in the gut of particles ($>100 \mu\text{m}$) which could not be accommodated within the interspine spaces (25% by number, 45% by volume) indicates that the oral surface collection of particles by podia is a very important part of the feeding mechanism. Although this has not been detected previously, it should be noted here that Ghiold (1983) reported that particles, presumably suitable for ingestion, were collected by the ambital podia of *E. parma* and that the gut contained particles from 50 to 200 μm . It appears from the data of Lane and Lawrence (1982) that in *M. quinquesperforata*, where interspine distances are similar to those of *E. parma* (Ghiold, 1983), as much as 30% by weight of the gut material is too large for the proposed sieve mechanism. Particles less than 100 μm could be collected directly by podia of *E. parma*, or, perhaps, trapped in mucus or adhering to larger particles. Jumars *et al.*, (1982) cite work by Valiella *et al.*, (1979) which describes deposit feeding mechanisms for dealing with cohesive sediments. This is probably important for *E. parma* also, because the sediments in which they live show some cohesive properties. For example, diatoms stick to sand grains, unidentifiable organic debris coats inorganic particles, and clumps of filamentous diatoms were found entangled with sand grains and debris. Many of these complex particles including diatoms, organic debris, and probably bacteria, were collected by the podia of *E. parma* and ingested. As in other deposit feeders, the rate of collection depends on the organic content, and in this particular case, the diatom concentration. In *Oreaster reticulatus* (L.), a sand-dwelling sea star, Schiebling (1980) reported that the rate of podial raking of the microphyte-rich layer was related to chlorophyll concentration and substrate particle size. Possibly oral surface feeding activity in *E. parma* is controlled in a similar way. It appears that the ambulacra can respond differentially because when only one ambulacrum is given diatoms, its activity level goes up while the other ambulacra may stop processing particles entirely.

Oral surface collection of substrate particles by *E. parma* is much like the mechanism described by Telford *et al.*, (1983) for *Echinocyamus pusillus* and does not differ radically from that of *D. excentricus* (Timko, 1976). Podia gather particles either by sucker action or by sticky mucus. Mucus is secreted from the tips of many podia (Mooi, 1983; Telford *et al.*, 1983) and may aid in forming a seal for the sucker. Podial collection and transport provides a viable alternative hypothesis to the aboral rocking sieve mechanism of feeding. It explains the enormous numbers of podia on the oral surface and is independent of surface ciliary currents, which might best be regarded as ventilatory and cleansing. The rapid response of podia to the presence of diatoms, the filling of the food grooves, and the visible ingestion of diatoms leaves no possible doubt that this is a major feeding mechanism in *Echinarachnius parma*.

ACKNOWLEDGMENTS

This work has been supported by the Natural Sciences and Engineering Research Council of Canada through Operating Grant #A4696. We are indebted to Eric Lin, Department of Zoology, University of Toronto, for technical assistance with SEM,

to the Huntsman Marine Laboratory, St. Andrews, New Brunswick, for use of facilities, and to our colleague, Rich Mooi, who drew the diagrams and offered many useful criticisms.

LITERATURE CITED

- ALEXANDER, D. E., AND J. GHIOLD. 1980. The functional significance of the lunules in the sand dollar, *Mellita quinquesperforata*. *Biol. Bull.* **159**: 561-570.
- BELL, B. M., AND R. W. FREY. 1969. Observations on ecology and the feeding and burrowing mechanisms of *Mellita quinquesperforata* (Leske). *J. Paleontol.* **43**: 533-560.
- CHIA, F. S. 1969. Some observations on the locomotion and feeding of the sand dollar, *Dendraster excentricus* (Eschscholtz). *J. Exp. Mar. Biol. Ecol.* **3**: 162-170.
- GHIOLD, J. 1979. Spine morphology and its significance in feeding and burrowing in the sand dollar, *Mellita quinquesperforata* (Echinodermata: Echinoidea). *Bull. Mar. Sci.* **29**: 481-490.
- GHIOLD, J. 1983. The role of external appendages in the distribution and life habits of the sand dollar *Echinarachnius parma* (Echinodermata: Echinoidea). *J. Zool.* **200**: 405-419.
- GOODBODY, I. 1960. The feeding mechanism in the sand dollar, *Mellita sexiesperforata* (Leske). *Biol. Bull.* **119**: 80-86.
- HAROLD, A. S., AND M. TELFORD. 1982. Substrate preference and distribution of the northern sand dollar *Echinarachnius parma* (Lamarck). *Proc. Int. Echinoderm Conf., Tampa Bay (1981)*: 243-249.
- HYMAN, L. H. 1958. Notes on the biology of the five-lunuled sand dollar. *Biol. Bull.* **114**: 54-56.
- JUMARS, P. A., R. F. L. SELF, AND A. R. M. NOWELL. 1982. Mechanics of particle selection by tentaculate deposit feeders. *J. Exp. Mar. Biol. Ecol.* **64**: 47-70.
- LANE, J. M., AND J. M. LAWRENCE. 1982. Food, feeding and absorption efficiencies of the sand dollar, *Mellita quinquesperforata* (Leske). *Estuarine Coastal Shelf Sci.* **14**: 421-431.
- MACGINITIE, G. E., AND N. MACGINITIE. 1949. *Natural History of Marine Animals*. McGraw-Hill, New York, 473 pp.
- MOOI, R. 1983. Morphology, diversity and function of non-respiratory podia of clypeasteroids (Echinodermata: Echinoidea). M.Sc. Dissertation, Department of Zoology, University of Toronto, Ontario.
- MOOI, R., AND M. TELFORD. 1982. The feeding mechanism of the sand dollar *Echinarachnius parma* (Lamarck). *Proc. Int. Echinoderm Conf., Tampa Bay (1981)*: 51-57.
- MORTENSON, T. 1948. *A Monograph of the Echinoidea, IV. 2. Clypeasteroidea*. C. A. Reitzel, Copenhagen. 471 pp.
- O'NEILL, P. L. 1978. Hydrodynamic analysis of feeding in sand dollars. *Oecologia* **34**: 157-174.
- PARKER, G. H., AND M. A. VAN ALSTEYN. 1932. Locomotor organs of *Echinarachnius parma*. *Am. J. Psychol.* **39**: 167-180.
- SCHEIBLING, R. E. 1980. The microphagous feeding behaviour of *Oreaster reticulatus* (Echinodermata: Asteroidea). *Mar. Behav. Physiol.* **7**: 225-232.
- SEILACHER, A. 1979. Constructional morphology of sand dollars. *Paleobiology* **5**: 191-221.
- SMITH, A. B., AND J. GHIOLD. 1982. Roles for holes in sand dollars (Echinoidea): a review of lunule function and evolution. *Paleobiology* **8**: 242-253.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. 2nd. Ed., W. H. Freeman and Co., San Francisco. 859 pp.
- TELFORD, M. 1981. A hydrodynamic interpretation of sand dollar morphology. *Bull. Mar. Sci.* **31**: 605-622.
- TELFORD, M. 1983. An experimental analysis of lunule function in the sand dollar, *Mellita quinquesperforata* (Leske). *Mar. Biol.* **76**: 125-134.
- TELFORD, M., AND A. S. HAROLD. 1982. Lift, drag and camber in the northern sand dollar, *Echinarachnius parma* (Lamarck). *Proc. Int. Echinoderm Conf., Tampa Bay (1981)*: 235-241.
- TELFORD, M., A. S. HAROLD, AND R. MOOI. 1983. Feeding structures, behavior and microhabitat of *Echinocyamus pusillus* (Echinoidea: Clypeasteroidea). *Biol. Bull.* **165**: 745-757.
- TIMKO, P. L. 1976. Sand dollars as suspension feeders: a new description of feeding in *Dendraster excentricus*. *Biol. Bull.* **151**: 247-259.