

## Feeding, tentacle and gut morphology in five species of southern African intertidal holothuroids (Echinodermata)

Greg G. Foster\* and Alan N. Hodgson

Department of Zoology and Entomology, Rhodes University, Grahamstown, 6140 South Africa  
Tel.(461)318526, Fax(461)24377, e-mail: g87f2768@giraffe.ru.ac.za

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Light, scanning and transmission electron microscopy were used to compare the structure of the tentacles and digestive tracts of four species of intertidal dendrochirote (*Roweia stephensoni*, *Pseudocnella sykion*, *Aslia spyridophora*, *R. frauenfeldi frauenfeldi*), and one species of aspidochirote holothuroid (*Neostichopus grammatus*). In addition, gut lengths and contents of the five species were compared. Gut contents were sieved to determine the size of the particulate matter ingested. *Roweia stephensoni*, *P. sykion* and *A. spyridophora* were found to be suspension feeders using dendritic tentacles to capture and ingest food particles mostly <53 µm in size. *Roweia f. frauenfeldi* was also a suspension feeder but, had atypical (reduced) dendritic tentacles which captured food particles between 250 µm–1.18 mm in size. *Neostichopus grammatus* was a deposit feeder, ingesting sediments mostly between 106–500 µm using tentacles which are peltate with ramified processes. The gut lengths of the four suspension-feeding species were found to be significantly ( $p < 0.001$ ) longer than that of the deposit feeder. The digestive tract of all species was composed of four tissue layers, with the digestive epithelial layer of the anterior and posterior ends of the intestine of suspension feeders being significantly thicker (52 to 57 µm) than that of the deposit feeder (about 19 to 29 µm). In addition, the epithelial layer of the intestine of suspension feeders contained more highly vesicular enterocytes than that of the deposit feeder.

\*To whom correspondence should be addressed

Holothuroids are chiefly deposit or suspension feeders (Massin 1982). Members of the order Dendrochirotida use finely branched dendritic tentacles to feed on particles suspended in the water column whereas the Aspidochirotida are deposit-feeding holothurians which push sediments into the mouth using peltate tentacles (Massin 1982). Moore & Roberts (1994) have suggested that interspecific differences in tentacle morphology reflect different feeding mechanisms in abyssal holothuroids.

Although the structure of the digestive system of holothuroids is well known (Féral & Massin 1982; Smiley 1994) there have been few studies which have compared the digestive tract structure of holothuroids with different feeding habits. Within southern Africa, except for the work of Velimirov (1984) and Barkai (1991) who both examined aspects of holothuroid ecology, there have been no published studies on the feeding biology of holothuroids despite the fact that they often occur in high densities (Foster 1994).

Five species of holothuroids, the dendrochirotes *Roweia stephensoni* (John), *Pseudocnella sykion* (Lampert), *Aslia spyridophora* (Clark), *Roweia frauenfeldi frauenfeldi* (Ludwig) and the aspidochirote *Neostichopus grammatus* (Clark), are particularly abundant in rocky intertidal regions of the Eastern Cape Province of South Africa (Foster 1994), and are sympatric in their distribution from Cape Agulhas (34°50'S/20°00'E) to East London (32°56'S/28°02'E) (Thandar 1985, 1987a, 1987b, 1991). Furthermore, along the Eastern Cape these species overlap in their distribution within the intertidal zone (Foster 1994). These animals must play a significant role in energy transfer in Eastern Cape intertidal communities. As a first step towards a greater understanding of the role of holothuroids in South African intertidal communities we describe and compare the structure of the feeding and digestive apparatus of the above species and relate this to the type of food ingested.

### Materials and methods

Animals were collected from the intertidal region of rocky shores at Port Elizabeth (33°58'S/25°38'E) and Port Alfred (33°36'S/26°54'E) in the Eastern Cape Province of South Africa.

### Anatomy of the feeding and digestive apparatus

The tentacles of three similarly sized individuals of each species were examined by scanning electron and light microscopy. To fix and examine tentacles in an extended state, an animal was placed in a darkened container and just covered with seawater. Once the tentacles were extended into a feeding position, the container was flooded with an excess of liquid nitrogen. This successfully captured the tentacles in their extended state. The frozen animal was then thawed in either aqueous Bouin's or 2.5% glutaraldehyde in filtered sea water, and allowed to fix for up to 4 h before the tentacles were amputated. Tentacles were then prepared for scanning electron microscopy using a graded acetone series, which also removed surface mucus, and critical-point drying. Samples were sputter coated in gold and photographed with a Jeol JSM 840 scanning electron microscope. Preparation for light microscopy followed standard procedures of dehydration and embedding of tissues in Paraplast. Longitudinal and transverse sections (5–7 µm thickness) were stained in haematoxylin and eosin, and toluidine blue for mucous secretions (Humason 1967).

To determine whether the different species had similar or dissimilar gut lengths, 100 individuals of different sizes of each species were collected. Sizes were based on drained volume in order to eliminate the influence of water in the coelomic cavity. Animals were housed in aerated aquaria and starved for 2–3 days, by which time the gut contents had been voided. Guts were removed, extended to their full length and measured to the nearest millimetre. Linear regressions were

used to determine if a relationship existed between gut length and body size in each species, and a one-way-analysis of variance (ANOVA) using standardization values (gut length: volume ratios) coupled with a Sheffe's comparison of range test was performed to determine if the gut lengths differed significantly between the species (Sokal & Rohlf 1981).

### Structure of the digestive system

The guts of similarly sized individuals of *R. stephensoni* and *R. f. frauenfeldi* (examples of suspension feeders), and *N. grammatus* (a deposit feeder) were removed and small portions of the stomach, and the anterior and posterior ends of the intestine were prepared for both light and transmission electron microscopy. Tissues for light microscopy were fixed for 24 h in aqueous Bouin's, embedded in Paraplast, sectioned at 5–7  $\mu\text{m}$  thickness and stained in haematoxylin and eosin. For TEM, tissues were fixed in 2.5% glutaraldehyde in 35‰ seawater for 12 h at 4°C, and postfixed in 1% osmium tetroxide in 0.1 mol.dm<sup>-3</sup> sodium cacodylate buffer and seawater for 90 min. Tissues were then dehydrated and embedded in a Taab/Araldite resin mixture (Cross 1989). Sections 110–130 nm thick were cut on an RMC MT-7 microtome, stained in uranyl acetate and lead citrate and viewed under a Jeol 1210 transmission electron microscope at 80 kV.

The digestive epithelial thickness in each region of the gut was determined from histological sections using a Nikon filar micrometer eyepiece. Thirty measurements were taken from each gut region of four individuals of each species. To determine if the digestive epithelial thickness in the different gut regions within and between species varied, an ANOVA coupled with a Sheffe's comparison of range test was used (Sokal & Rohlf 1981).

### Gut content analysis

The gut contents of 100 individuals of each species were removed, pooled and the particle size composition analysed. After removal, gut contents were placed in 70% alcohol. In addition, the top 10 mm layer of sediment was collected from areas where all the species co-occurred. Ingested particles were wet sieved, using a series of graded Endecotts sieves. The contents remaining in each sieve were then dried at 60°C to constant weight and expressed as a percentage of the cumulative dry weight. In addition, the gut contents of five individuals of each species were examined in an attempt to identify ingested food particles. In *R. f. frauenfeldi* and *N. grammatus* the ingested food particles were sufficiently large enough to be identified under a Wild M5A stereo dissecting microscope. In the remaining three species, sub-samples of the gut contents were analysed using scanning electron microscopy. The samples were dehydrated through a graded ethanol series, critical-point dried, gold coated and examined. After each ethanol series the samples were centrifuged to form a pellet thus ensuring that no particles remained in suspension. All the component food material was identified into the highest taxonomic group possible.

## Results

### Anatomy of the feeding and digestive apparatus

Three morphological forms of tentacles were recognized. The

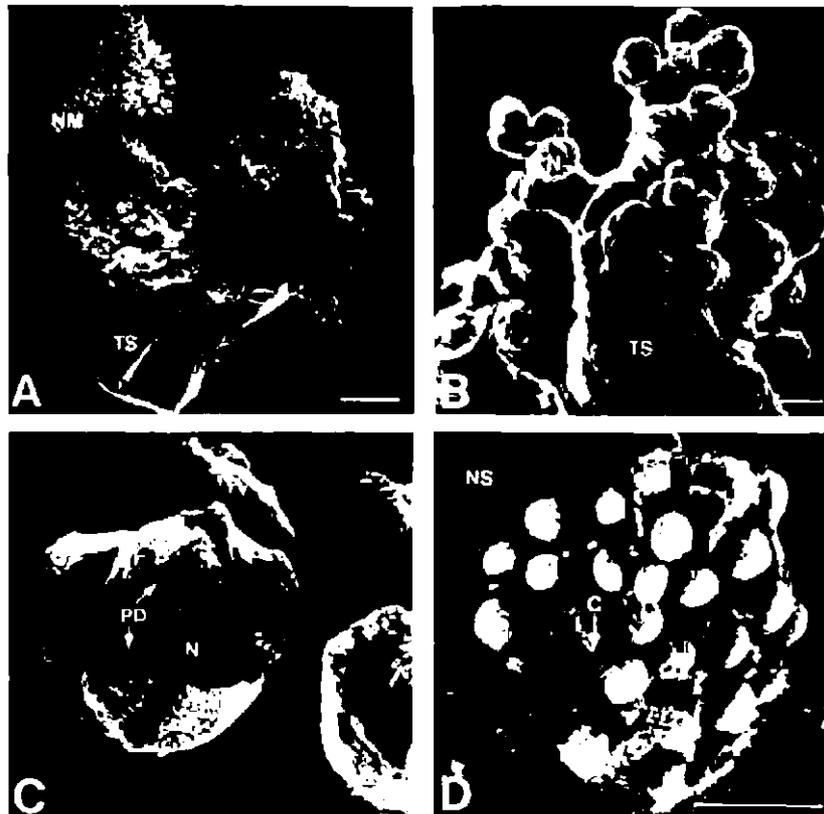
first type is a true dendritic form, which is similar in *Roweia stephensoni*, *Pseudocnella sykion* and *Aslia spyridophora*, and hence only that of *R. stephensoni* is illustrated (Figure 1). The tentacle crown is composed of 10 dendritically branched tentacles of equal length arranged pentamerously around the mouth. Each tentacle is thickest at its base and branches several times into secondary, tertiary and sometimes quaternary branches (Figure 1A). The distal branches terminate in numerous swellings or nodes, measuring between 80–120  $\mu\text{m}$  in diameter in *R. stephensoni* (Figure 1B), 60–100  $\mu\text{m}$  in *P. sykion* and 100–140  $\mu\text{m}$  in *A. spyridophora*. In *R. stephensoni*, each node has 4–7 circular areas or discs of papillate projections, each with 25–39 papillae (Figure 1C). In *P. sykion*, each node has 5–11 discs of papillate projections each with 6–15 papillae, whereas in *A. spyridophora*, each node has 4–12 discs of papillate projections each bearing 5–17 papillae. The discs vary in diameter from 15–30  $\mu\text{m}$  in *R. stephensoni* and 10–15  $\mu\text{m}$  in *P. sykion* and *A. spyridophora*. In all three species, small stout cilia, measuring about 3  $\mu\text{m}$  in length in *R. stephensoni*, and about 2  $\mu\text{m}$  in *P. sykion* and *A. spyridophora*, are situated amongst the papillae, often occurring in small tufts (Figure 1D).

The second type of tentacle possessed by *R. frauenfeldi* is a modified dendritic form. The tentacle crown consists of 10 modified dendritic tentacles of equal length. Each tentacle is thickest at its base (Figure 2A) but unlike the typical dendritic tentacles of *R. stephensoni*, *P. sykion* and *A. spyridophora*, in *R. f. frauenfeldi* tentacle branching is reduced to secondary branches only. The branches are thick and robust, the distal ends forming large bulbous nodes, measuring between 230–325  $\mu\text{m}$  in diameter (Figure 2B, C). The nodes lack discs of papillate projections (Figure 2C), but are covered with numerous microvilli and cilia which are about 2  $\mu\text{m}$  in length and often occur in pairs or tufts (Figure 2D).

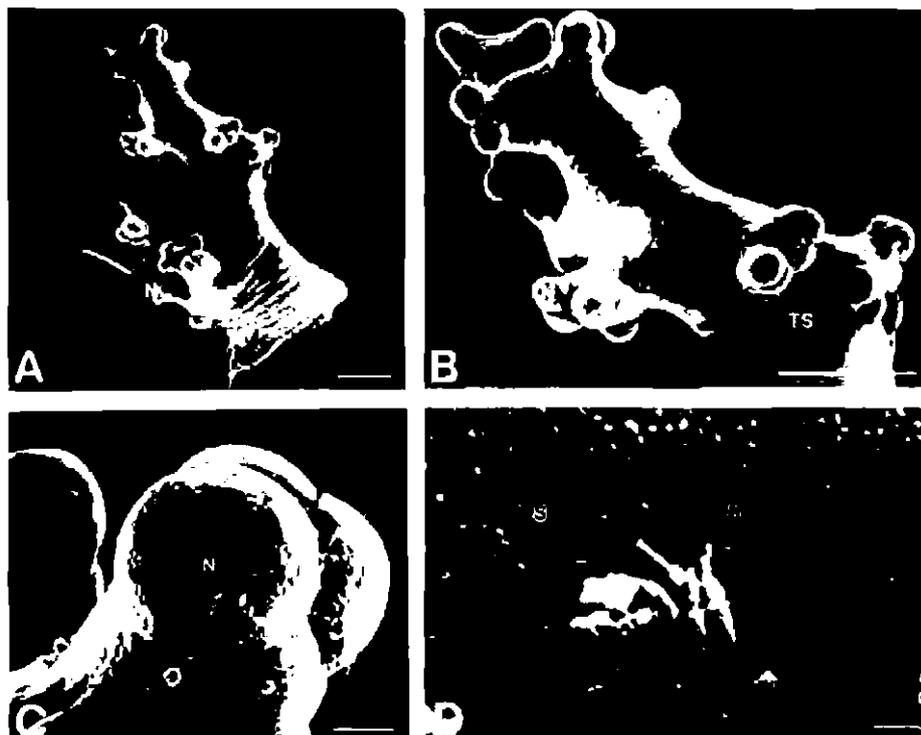
The third type of tentacle, possessed by *Neostichopus grammatus*, is peltate with ramified processes. The tentacle crown is composed of 20 branched tentacles of equal length arranged around the mouth. Each tentacle is thickest at its base and branches several times forming secondary, tertiary and sometimes quaternary branches (Figure 3A). The distal branches terminate in numerous nodes, measuring from 80–110  $\mu\text{m}$  in diameter (Figure 3B). These form the functional surface of the tentacle when splayed against the substratum during feeding. No discs of papillate projections occur on the tentacle nodes (Figure 3C), but the surface is interspersed with cilia, measuring about 2  $\mu\text{m}$  in length (Figure 3D).

The histological structure of the tentacles of all the species studied is as described for other holothuroids (Bouland, Massin & Jangoux 1982; Smith 1983) and therefore only a brief description follows. Each tentacle is comprised of four well defined tissue layers; an external pigmented epithelial layer, underlying which is a layer of muscle, connective tissue and an inner layer of endothelium which surrounds the water-vascular system of the tentacle. On the nodes, the epithelial layer consists of columnar epithelial cells which are about 35  $\mu\text{m}$  long in all species. Only the node areas in all species stained positively for mucus, indicating a secretory function (Humason 1967).

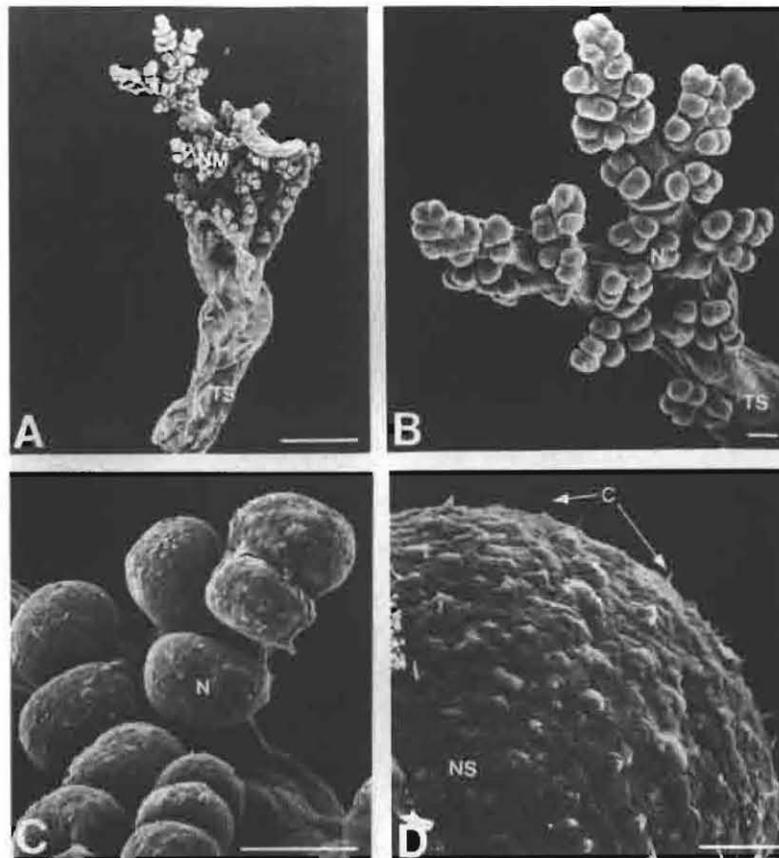
The gut of all four dendrochirotes consisted of the follow-



**Figure 1** *Roweia stephensoni*. (A) Tentacle showing the shaft and the distal branching (Scale bar = 1 mm); (B) distal portion of extended tentacle showing the nodes (Scale bar = 100  $\mu$ m); (C) tentacle node covered with discs of papillate projections (Scale bar = 10  $\mu$ m); (D) papillate disc on node surface showing papillae interspersed with cilia (Scale bar = 10  $\mu$ m). C: cilia; N: node; NM: node mass; NS: node surface; P: papillae; PD: papillate disc; TS: tentacle shaft.



**Figure 2** *Roweia frauenfeldi frauenfeldi*. (A) Tentacle showing the shaft and the distal branching (Scale bar = 1 mm); (B) distal portion of extended tentacle showing the nodes (Scale bar = 1 mm); (C) tentacle node lacking discs of papillate projections (Scale bar = 100  $\mu$ m); (D) cilia cluster and numerous microvilli on the node surface (Scale bar = 10  $\mu$ m). C: cilia; M: microvilli; N: node; NS: node surface; TS: tentacle shaft.



**Figure 3** *Neostichopus grammatus*. (A) Tentacle showing the shaft and the distal branching (Scale bar = 1 mm); (B) distal portion of extended tentacle showing the nodes (Scale bar = 100 µm); (C) tentacle nodes lacking discs of papillate projections (Scale bar = 100 µm); (D) node surface bearing numerous cilia (Scale bar = 10 µm). C: cilia; N: node; NM: node mass; NS: node surface; TS: tentacle shaft.

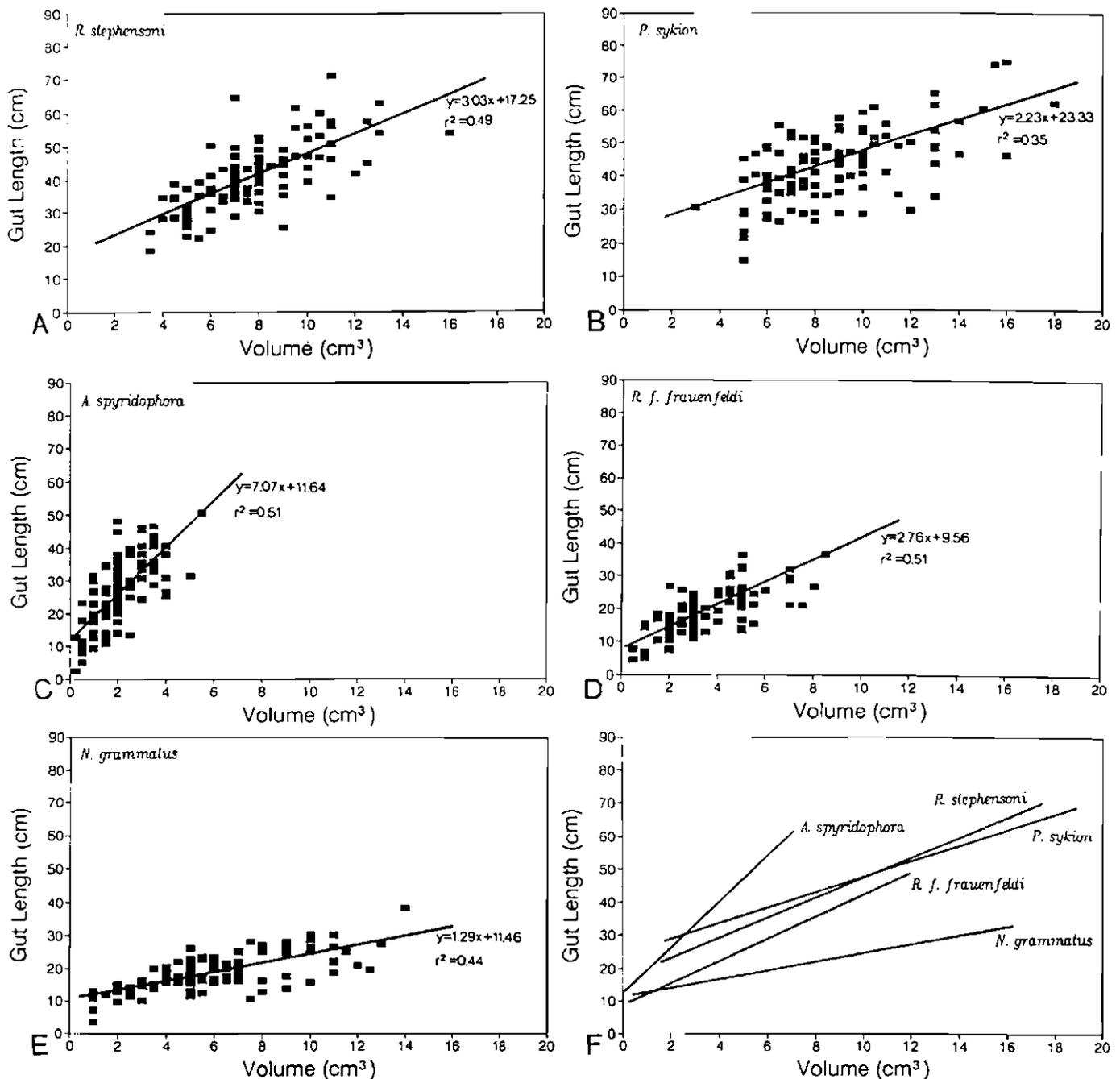
ing regions: pharyngeal bulb, stomach, small intestine, and a rectum/cloaca. Although all these regions could be recognized, in *N. grammatus* the stomach region is not well defined. There was a positive relationship between gut length and drained body volume in all species (Figure 4): *R. stephensoni* ( $p < 0.0001$ ,  $r^2 = 0.49$ ); *P. sykion* ( $p < 0.0001$ ,  $r^2 = 0.35$ ); *A. spyridophora* ( $p < 0.0001$ ,  $r^2 = 0.51$ ); *R. f. frauenfeldi* ( $p < 0.0001$ ,  $r^2 = 0.51$ ) and *N. grammatus* ( $p < 0.0001$ ,  $r^2 = 0.44$ ), with larger individuals having longer guts than smaller individuals (Figure 4). Statistical analysis shows that there is a significant difference ( $p < 0.001$ ) in the gut length:volume ratios of all the species, except between *R. stephensoni* and *P. sykion*. The dendrochirote holothuroids have significantly longer ( $p < 0.001$ ) gut lengths to body size (volume) than the aspidochirote holothuroid (Figure 4F).

### Structure of the digestive system

The histological structure and ultrastructure of the guts of *R. stephensoni*, *R. f. frauenfeldi* and *N. grammatus* are similar to those described for other holothuroids (see Féral & Massin 1982; Smiley 1994 for reviews) and therefore only a brief description follows. Throughout the length of the guts of all three species, the gut wall consists of four tissue layers. From outside to inside: a single layer of peritoneal epithelial cells, circular and longitudinal muscles, a connective tissue layer of collagen and amoebocytes, and a digestive epithelial layer. Statistical analysis shows that there is a significant difference

in the thickness of the digestive epithelial layer in different gut regions both within and between species ( $p < 0.001$ ). In *R. stephensoni*, the mean thickness of the epithelial layer of the stomach ( $\bar{x} = 32.15 \pm \text{S.D. } 2.37 \mu\text{m}$ ) is significantly greater than that of *R. f. frauenfeldi* ( $28.34 \pm 2.13 \mu\text{m}$ ) (Figure 5). There is no significant difference between epithelial layer thickness of the anterior end of the intestine of *R. stephensoni* ( $57.75 \pm 5.67 \mu\text{m}$ ) and *R. f. frauenfeldi* ( $57.29 \pm 4.26 \mu\text{m}$ ). However, the epithelium of the posterior end of the intestine of *R. stephensoni* ( $57.10 \pm 4.74 \mu\text{m}$ ) is significantly thicker than that of *R. f. frauenfeldi* ( $52.76 \pm 3.65 \mu\text{m}$ ) (Figure 5). In *N. grammatus*, the epithelial layer of the anterior end of the intestine ( $28.96 \pm 2.14 \mu\text{m}$ ) is significantly thicker than the posterior end ( $19.23 \pm 1.63 \mu\text{m}$ ), but the epithelial layer of the entire intestine is significantly thinner than that of both *R. stephensoni* and *R. f. frauenfeldi* (Figure 5).

The digestive epithelial layer of the different gut regions of all three species consists of the same cell types described for other holothuroids (Féral & Massin 1982; Smiley 1994). In *R. stephensoni* and *R. f. frauenfeldi* the fine structure of the digestive epithelial cells of all gut regions is very similar. The stomach consists almost entirely of glandular enterocytes, the apical surfaces of which bear microvilli 1.1–1.3 µm long in *R. stephensoni* and *R. f. frauenfeldi* (Figure 6A). The anterior part of the intestine of both species consists mainly of very elongated vesicular enterocytes with microvilli 1.6–2.5 µm long in *R. stephensoni* and 1.5–1.9 µm long in *R. f. frauen-*



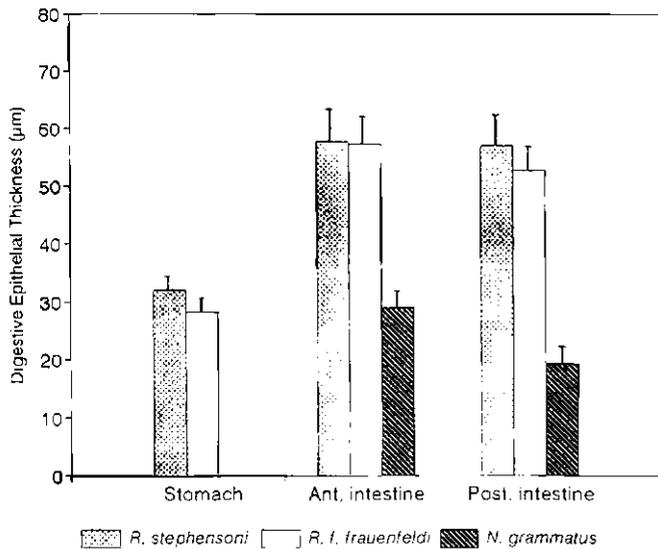
**Figure 4** Relationship between gut length and drained body volume for (A) *Roweia stephensoni* ( $n = 100$ ); (B) *Pseudocnella sykion* ( $n = 100$ ); (C) *Aslia spyridophora* ( $n = 100$ ); (D) *Roweia frauenfeldi frauenfeldi* ( $n = 100$ ); (E) *Neostichopus grammatus* ( $n = 100$ ); and (F) comparison of all five species.

*feldi* (Figure 6B). In the posterior portion of the intestine, the vesicular enterocytes have fewer vesicles and the cells have fewer microvilli (1.5–2.0  $\mu\text{m}$  long in *R. stephensoni* and *R. f. frauenfeldi*; Figure 6C).

In *N. grammatus* the enterocytes of the anterior end of the intestine are mainly of the vesicular type with microvilli 3–3.5  $\mu\text{m}$  long. However, the enterocytes contain few vesicles and are not as elongated as in the *Roweia* species (Figure 6D). The posterior end of the intestinal epithelium is very similar to the anterior and consists of enterocytes with numerous microvilli, 2.4–2.9  $\mu\text{m}$  long (Figure 6E).

#### Gut content analysis

Although all species were found to be omnivorous, they could be divided into one of three feeding groups based on the type and size of the food particles ingested. *Roweia stephensoni*, *P. sykion* and *A. spyridophora* are all suspension feeders. The guts contained mainly unidentifiable organic matter, together with unicellular and filamentous algae, macroalgal fragments, diatoms, dinoflagellates, sponge spicules, fragmented urchin spines, and fragments of arthropod exoskeletons. *Roweia stephensoni* ingested particles ranging from <53  $\mu\text{m}$ –1 mm, with the greatest component (51%) less than 53  $\mu\text{m}$  and the second largest component (35%) from 106–500  $\mu\text{m}$  (Figure



**Figure 5** Mean thickness ( $\pm$  S.D.) of the digestive epithelial layer in the different gut regions of *Roweia stephensoni*, *Roweia frauenfeldi* and *Neostichopus grammatus* ( $n = 4$  for all species).

7A). *Pseudocnella sykion* ingested particles ranging from  $<53$ – $500$   $\mu\text{m}$ , with the largest component (51%) less than  $53$   $\mu\text{m}$ , and the second largest component (23%) from  $106$ – $250$   $\mu\text{m}$  (Figure 7A). *Aslia spyridophora* ingested particles ranging from  $<53$ – $500$   $\mu\text{m}$ , with the largest component (72%) less than  $53$   $\mu\text{m}$ , and the second largest component (15%)  $106$ – $250$   $\mu\text{m}$  (Figure 7A).

*Roweia f. frauenfeldi*, although a suspension-feeder ingested larger particles when compared to the other dendrochirotes. The gut contents consisted of gastropod shells, fragments of red (including coralline), green and brown algae, whole amphipod and other crustacean exoskeletons and appendages, polychaete worm tubes, sea urchin spines and sand grains. The ingested particles ranged in size from  $<53$   $\mu\text{m}$ – $3.35$  mm (Figure 7B), the greatest component (54%) being in the range of  $250$   $\mu\text{m}$ – $1.18$  mm.

*Neostichopus grammatus* is a deposit feeder. Its gut contents consisted of a large spectrum of sand grains, unidentifiable algae, coralline algae, bacteria, crustacean appendages, sea urchin spines, other calcareous fragments, and gastropod and bivalve shells. The size of ingested particles ranged from  $<53$   $\mu\text{m}$ – $3.35$  mm (Figure 7B), with the most abundant fraction (64%) being  $106$ – $500$   $\mu\text{m}$  in size. Analysis of the grain sizes of the sediments of the habitat of *N. grammatus* (Figure 7C) revealed that a large component of sediment (46%) is greater than  $3.35$  mm, and consisted mainly of pebbles and shell fragments. Another large component (35%) ranged from  $106$   $\mu\text{m}$ – $1.18$  mm, and consisted mainly of sand grains and shell fragments.

## Discussion

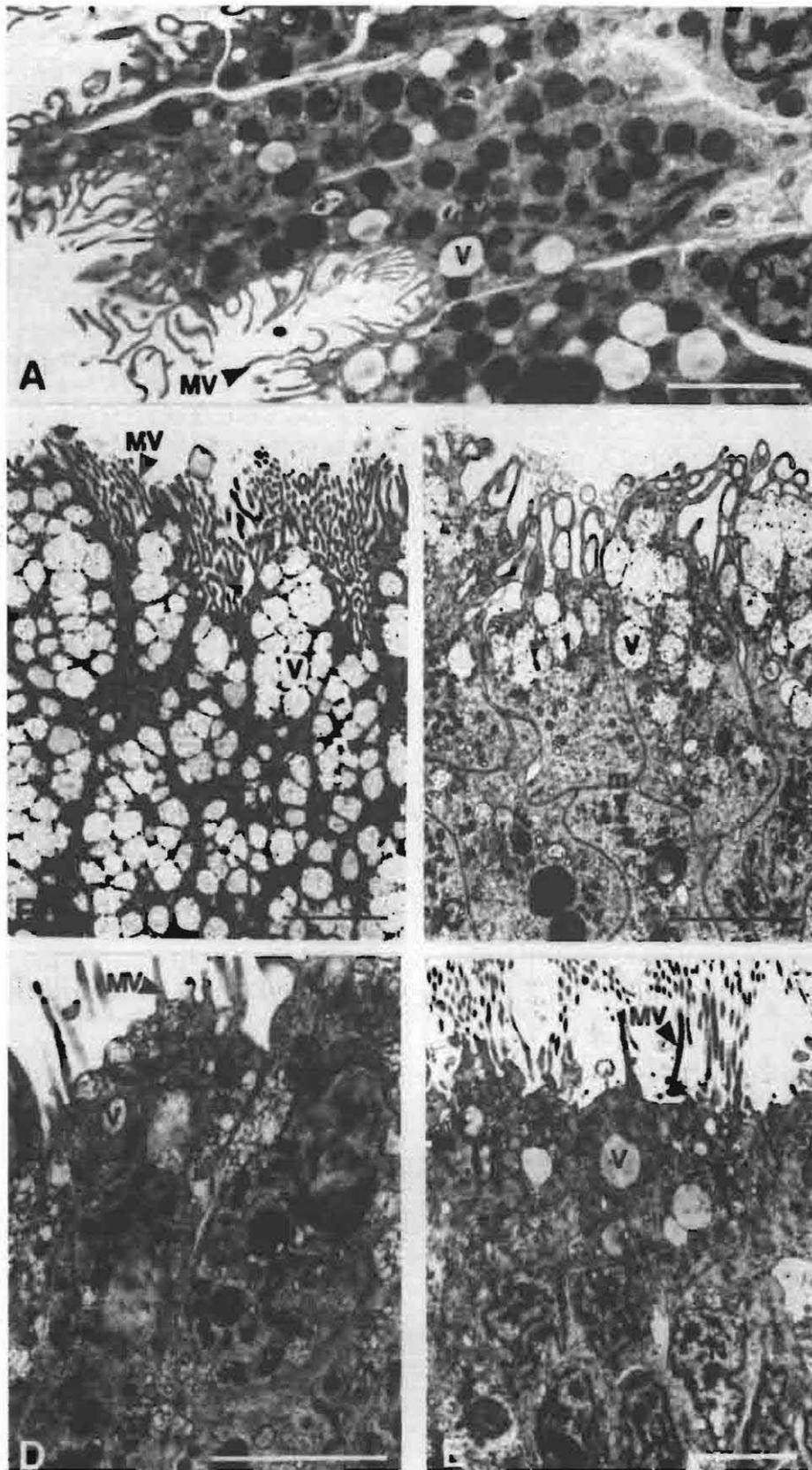
Holothuroids feed by means of their tentacles, with the aspidochirotes having the greatest adaptive radiations in feeding mechanisms with a correspondingly high variability in tentacle form (Roberts 1979; Hammond 1982; Roberts & Bryce 1982). By contrast the dendrochirotes, which include the most primitive holothuroids (Roberts 1982), exhibit little var-

iability in feeding mechanisms and tentacle form. This study however, has shown that variability can occur in dendrochirotes, since the tentacles of *Roweia f. frauenfeldi* differ markedly from those of *R. stephensoni*, *Pseudocnella sykion*, *Aslia spyridophora* and other dendrochirotes previously studied (e.g. Fankboner 1978; Smith 1983; Costelloe & Keegan 1984). We propose that the tentacles of *R. f. frauenfeldi* are sufficiently distinct to warrant a separate category or sub-category of tentacle — viz. reduced dendritic. This also supports the suggestion that *R. f. frauenfeldi* and *R. stephensoni* are not particularly closely related (Deichmann 1948; Thandar 1985).

The mucus of echinoderm tube feet has an important adhesive function (Hermans 1983). Since tentacles are modified buccal tube feet (Hyman 1955), mucous secretion may be an important pre-adaptation for capturing of food particles. Histological examination indicated that the nodes were the only secretory surfaces on the tentacles as suggested for other holothuroids (Fankboner 1978; Smith 1983; Costelloe & Keegan 1984). Entrapment of seston on the adhesive papillae in *R. stephensoni*, *P. sykion*, *A. spyridophora*, or on the nodes of *R. f. frauenfeldi*, is the most likely mode of food capture as mechanical entrapment of particles in the inter-papillar spaces of holothuroid tentacles plays a minor role in the uptake of suspended food (Fankboner 1978). However, it has been observed that the large nodes of *R. f. frauenfeldi* have some mechanical role, and act as 'hooks' to assist in pushing food into the mouth (Foster 1994).

The nodes at the tip of each tentacle are morphologically distinct from other tentacle areas by having elongated epithelial cells that give rise to papillae containing cilia in *R. stephensoni*, *P. sykion* and *A. spyridophora*, or simply bearing short cilia or clusters of microvilli as in *R. f. frauenfeldi* and *N. grammatus*. The cells of the papillae have been proposed as functioning as sensory receptors for feeding (Fankboner 1978; Smith 1983). Precisely what stimulates feeding in the species examined in this study remains to be determined, as the tentacles of holothuroids have been shown to respond to both chemical and mechanical stimuli (Sloan & Campbell 1982; Costelloe & Keegan 1984; Hamel, Himmelman & Dufresne 1993).

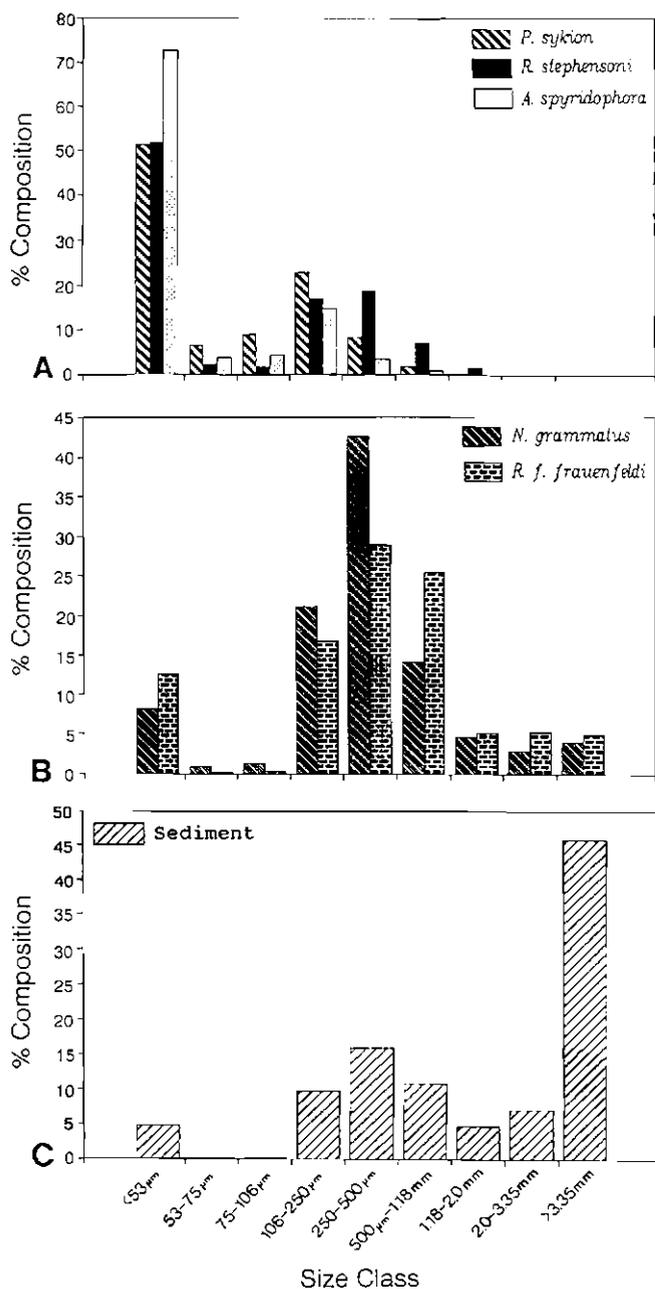
*Roweia stephensoni*, *P. sykion*, and *A. spyridophora* are most common under boulders in areas of high water motion, a feature essential to ensure a continuous supply of seston (Barkai 1991; Foster 1994). They feed predominantly on particles less than  $53$   $\mu\text{m}$  in diameter, consisting of diatoms, unicellular and filamentous algae, and other organic matter suspended in the water column, a diet which is similar to that of most dendrochirote holothuroids (Massin 1982; Costelloe & Keegan 1984; Hamel *et al.* 1993). The other large component of material ( $106$ – $250$   $\mu\text{m}$ ) observed in the guts of these three species may be acquired from organic matter resuspended from the substratum by wave action. The numerous fine branches of the tentacles present a large surface area with which to capture small food particles. When aggregated in high densities, neighbouring conspecifics of *R. stephensoni*, *P. sykion* and *A. spyridophora*, allow their tentacles to intermesh without apparently interfering with the feeding process (Foster, pers. obs.). Such aggregations may benefit individuals by enhancing particle capture, the baffle effect



**Figure 6** Transmission electron micrographs of the enterocytes from the different gut regions of *Roweia stephensoni*, *Roweia frauenfeldi frauenfeldi* and *Neostichopus grammatus*. Enterocytes from (A) the stomach of *R. stephensoni*; (B) anterior end of the intestine of *R. f. frauenfeldi*; (C) posterior end of the intestine of *R. f. frauenfeldi*; (D) anterior end of the intestine of *N. grammatus*; (E) posterior end of the intestine of *N. grammatus*. (Scale bars = 5  $\mu$ m). L: lysosome; M: mitochondria; MV: microvilli; N: nucleus; V: vesicle.

produced by the expanded tentacle crowns promoting the near-bottom concentration and precipitation of suspended

materials (Keegan 1974). Therefore the clumping behaviour of holothuroids is perhaps an adaptation which enhances their



**Figure 7** The particle size composition of the ingested food, pooled from 100 individuals of each species. (A) *Roweia stephensoni*, *Pseudocnella sykion* and *Astia spyridophora*; (B) *Roweia frauenfeldi* and *Neostichopus grammatus*; and (C) particle size composition of the sediments from the region in which the five species were found.

ability to survive in regions that are continuously subjected to wave action.

By contrast, *R. f. frauenfeldi* is a more solitary species and the tentacles of conspecifics never intermesh. It is seldom seen under boulders and prefers to remain buried in the sediment with only the tentacles protruding into the water currents (Foster 1994). *Roweia f. frauenfeldi* feeds predominantly on particles greater than 106  $\mu\text{m}$  in diameter, consisting of macroalgal fragments and dead invertebrates (whole or fragments), using robust tentacles with few branches. The solitary nature of this species may indicate that the adhesive property of the node surface is resilient, facilitating the cap-

ture of larger particles of food. Similarly, in *Neopentadactyla mixta*, which avoids physical contact with its conspecifics (Könnecker & Keegan 1973), papillar adhesion is very resilient (Smith 1983).

Deposit-feeding holothuroids play an important role in the reworking of surface sediments and are capable of processing large quantities per annum (Pawson 1966; Hauksson 1979; Coulon & Jangoux 1993). *Neostichopus grammatus* consumes particles similar in size to those of the bottom sediments (Figure 7B, C), although it avoids the larger particles (>3.35 mm). This may be a result of physical constraints (particle weight, tentacle structure, etc.) experienced by the holothurian in handling particles of that size. As the quantity of sediment processed by *N. grammatus* is not known, the role of this species in sediment reworking on South African shores has still to be determined.

The differences in gut length relative to body size, and thickness of the digestive epithelial layer of the gut between the aspidochirote and dendrochirote holothuroids may be of phylogenetic origin, or a functional adaptation to the food type ingested. Bacteria are the main food of deposit-feeding holothuroids (Bakus 1973; Yingst 1976; Massin 1982; Baird & Thistle 1986), while diatoms, unicellular algae, suspended organic matter and small invertebrates are the main food of suspension-feeding holothuroids (Fankboner 1978; Massin 1982; this study). Hence, the short gut length relative to body size and thinner digestive epithelial layer in *N. grammatus* may indicate a faster gut passage time than the dendrochirote species, bacteria being easier to digest (Hargrave 1970; Adams & Angelovic 1970; Calow & Fletcher 1972; in Yingst 1976). Lawrence (1982), has indicated that extracellular digestion by enzymatic activity is most active in the intestinal region of the gut. Hence, the significantly longer gut length (consisting mainly of intestine) relative to body size in the dendrochirotetes studied, and thicker digestive epithelial layer with its abundance of vesicular enterocytes (as observed in *R. stephensoni* and *R. f. frauenfeldi*) may be necessary to cope with the high cellulose content of the organic matter ingested, which requires longer to digest. Hamel *et al.* (1993) have reported that *Psolus fabricii* (Dendrochirotida) also has a remarkably long intestine relative to its body size, and this may be an adaptation to its diet of diatoms which are protected by siliceous frustules.

Species with very similar ecological requirements are frequently capable of existing together without having significant negative effects upon each other (e.g. Harger 1972; Underwood 1978; Menge 1979; Creese & Underwood 1982). Kohn (1978) suggested that particle feeders partition the habitat rather than food resources and habitat partitioning is thought to occur in some holothuroids (Sloan & von Bodungen 1980; Roberts & Bryce 1982). Habitat partitioning probably occurs in *R. stephensoni*, *P. sykion* and *A. spyridophora*. Although these species use similar feeding methods (all suspension feeders) they have different microhabitats on the shore (Foster 1994). *Neostichopus grammatus* and *R. f. frauenfeldi* have sufficiently different feeding techniques and diets to maintain a distinct niche separation from the suspension feeders.

*Neostichopus grammatus* appears to be the only intertidal deposit-feeding holothuroid on the eastern Cape coast (Than-

dar 1987a), and is therefore able to spread into a variety of habitats and exploit various deposits as reported for *Isoistichopus badionatus* on the Bermudan coast (Sloan & von Bodungen 1980).

In conclusion it appears that there is a relationship between tentacle morphology and the size and type of food ingested. Similarly, gut length, the thickness of the digestive epithelial layer and the number of vesicles present in the enterocyte cells of the digestive epithelium also differ in relation to the food ingested.

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