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## Comparison of gut morphology and gut microflora of seven species of mud shrimp (Crustacea: Decapoda: Thalassinidea)

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**Abstract** The gut morphology is described for seven species of Thalassinidea; *Callianassa subterranea* (Montagu), *Jaxea nocturna* Nardo, *Axius stirhynchus* Leach, *Calocaris macandreae* Bell, *Upogebia pusilla* (Petagna), *U. deltaura* (Leach) and *U. stellata* (Montagu). Differences were observed in the structure of the dorsal and lateral teeth of the gastric mill. *Callianassa subterranea* and *A. stirhynchus* had simple robust dorsal teeth and proportionally larger lateral teeth with flexible spines. The three upogebiids had complex dorsal teeth that were highly ridged and proportionally smaller lateral teeth with inflexible spines. The dorsal and lateral teeth of *J. nocturna* were intermediate in form. The dorsal tooth of *Calocaris macandreae*, although relatively simple in design, possessed accessory projections, or “wings”, on either side of the main structure. The lateral teeth were proportionally quite large, but lacked ridges and spines. The epithelia surfaces of the digestive gland, midgut and posterior diverticulum were similar for all seven species. Differences were observed in the morphology of the hindgut. The hindgut lining was completely smooth for the three upogebiid species. The other thalassinidean species had four distinct rows of cuticular projections situated on top of the ridges formed by the longitudinal convolutions of the hindgut.

The arrangement of these projections varied between species. A gut flora was observed for six of the seven species, the exception being *C. macandreae*. The differences observed in the structure of the gut are discussed in relation to feeding and thalassinidean phylogeny.

### Introduction

Because of their fossorial lifestyle, thalassinideans have often been overlooked in benthic community studies, although they are one of the most numerous inhabitants of eulittoral and sublittoral soft sediments (Hailstone and Stephenson 1961; de Vaugelas 1985; Tunberg 1986; Murphy and Kremer 1992). The activities of thalassinideans have been shown to have many effects upon the sediment which they inhabit. During feeding and other activities they bioturbate sediment, increasing the rate of organic decomposition (Koike and Mukai 1983; Suchanek 1983; Branch and Pringle 1987) and redistributing nutrients and organic matter (Aller et al. 1983; Waslenchuk et al. 1983; Suchanek et al. 1986; de Vaugelas and Buscail 1990). Their burrows greatly increase the area of the sediment–water interface (Pemberton et al. 1976; Witbaard and Duineveld 1989), resulting in an increase in the aeration and ventilation of the sediment (Kioke and Mukai 1983; Waslenchuk et al. 1983; Colin et al. 1986).

The feeding methods of Thalassinidea are extremely flexible. Although one feeding mechanism will usually predominate, many species have been shown to utilize different methods, possibly in response to food availability (Nickell and Atkinson 1995). For example, *Callichirus jousseaumei* Nobili, *Neotrypaea* (as *Callianassa*) *californiensis* Dana and *Callianassa subterranea* are predominantly deposit-feeders but can also suspension-feed (Swinbanks and Murray 1981; de Vaugelas and de Saint-Laurent 1984; Nickell and Atkinson 1995). Conversely, *Upogebia stellata* is predominantly a suspension-feeder but can deposit-feed (Nickell and Atkinson 1995; Pinn 1995).

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Whilst feeding behaviour has been examined in a number of thalassinidean species, information on the complete gut anatomy is almost entirely absent from the literature. The morphology of the foregut has been described for *Upogebia africana* (Ortmann) (Schaefer 1970), *U. pugettensis* Dana and *Neotrypaea* (as *Callianassa*) *californiensis* (Powell 1974), *U. deltaura* (Ngoc-Ho 1984), *U. stellata*, *C. subterranea* and *Jaxea nocturna* (Nickell 1992). The midgut and hindgut morphology has been given even less attention, only having been studied in three species; *C. kraussi* Stebbing, *U. africana* (Harris et al. 1991) and *Lepidophthalmus louisianensis* (Schmitt) (Felder and Felgenhauer 1993). Harris (1993) described the hindgut morphology of *U. pugettensis*, *Neotrypaea* (as *Callianassa*) *californiensis* and *Trypaea* (as *Callianassa*) *australiensis* Dana. In the present study, the digestive system morphology is described for *C. subterranea*, *Jaxea nocturna*, *Axius stirhynchus*, *Calocaris macandreae*, *Upogebia pusilla*, *U. deltaura* and *U. stellata*.

## Materials and methods

*Callianassa subterranea* [ $11.3 \pm 1.4$  mm carapace length (CL),  $n = 5$ ] and *Jaxea nocturna* ( $13.9 \pm 1.2$  mm CL,  $n = 5$ ) were collected from a sheltered sea loch on the west coast of Scotland, Loch Sween, Argyll ( $56^{\circ}0'N$ ;  $05^{\circ}36'W$ ) from a depth of 10 to 25 m by SCUBA divers. The divers used an Alvey king-sized bait pump to suck the shrimp from their burrows, a technique similar to that described by Manning (1975). Because of its rarity, only a single preserved specimen of *Axius stirhynchus* (17.5 mm CL) was available for this study. This individual was kindly provided by Dr. N. Ngoc-Ho. Although known to have come from the Mediterranean Sea, no exact information was available on the actual site of capture. *Calocaris macandreae* specimens ( $18.7 \pm 1.4$  mm CL,  $n = 5$ ) were caught in the Main Channel off the Isle of Cumbrae ( $50^{\circ}46'N$ ;  $04^{\circ}58'W$ ) in the Clyde Sea area, from water depths down to 50 m, using a 2 m Agassiz trawl. The specimens of *Upogebia pusilla* ( $15.2 \pm 1.9$  mm CL,  $n = 3$ ) used in this study were collected intertidally from Arcachon on the south west coast of France ( $45^{\circ}40'N$ ;  $01^{\circ}15'W$ ). *U. deltaura* ( $11.7 \pm 1.6$  mm CL,  $n = 3$ ) and *U. stellata* ( $14.9 \pm 1.0$  mm CL,  $n = 5$ ) were collected from White Bay, Isle of Cumbrae in the Clyde Sea area ( $54^{\circ}47'N$ ;  $04^{\circ}54'W$ ) using a Forster anchor dredge in a water depth of 18 to 25 m.

The morphology of the digestive system was examined using scanning electron microscopy (SEM). The digestive tracts were dissected from formalin-preserved samples, as soon after capture as possible. The guts were placed in 2.5% EM-grade glutaraldehyde buffered with 0.2 M sodium cacodylate for at least 1 h and then passed through a graded acetone series. The samples were critical-point dried using carbon dioxide as the transitional fluid, and were mounted on aluminium stubs. During mounting, the digestive gland, midgut, posterior diverticulum and hindgut samples were split longitudinally to reveal both the contents and lining morphology. The foregut samples were placed dorsal side down and slit longitudinally through the cardio-pyloric valve to reveal the gastric armature. After coating with gold palladium, the samples were examined in a Joel JSM-5200 SEM.

## Results

### Foregut morphology

Some of the major differences between species were observed in the principal grinding structures of the

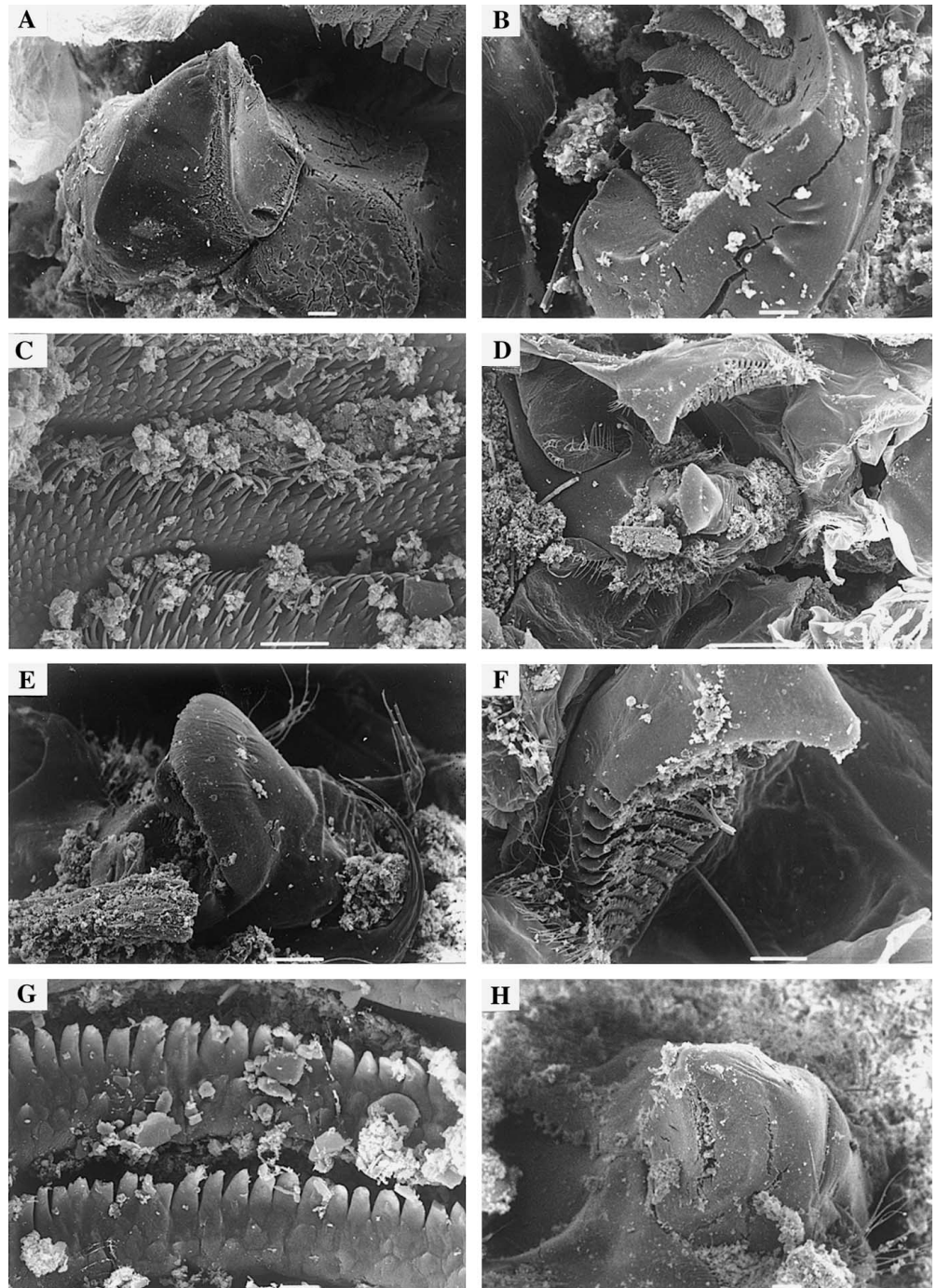
gastric mill, i.e. the dorsal and lateral teeth. The following descriptions have therefore concentrated on these structures. For a description of the structure and function of the decapod foregut (or proventriculus) see King and Alexander (1994).

The dorsal tooth of *Callianassa subterranea* was approximately pyramidal in shape (Fig. 1A), the lateral surfaces being triangular. The smooth anterior face was also triangular and keeled dorso-ventrally. The lateral teeth were approximately oval, tapering posteriorly (Fig. 1B). The medial surface of each lateral tooth was concave and had a large, smooth, anterior denticle that fitted neatly around the dorsal tooth (Fig. 1B). There was a distinct ventral crest on the anterior denticle. The surface of each lateral tooth was deeply grooved, with eight wide ridges that ran in a dorso-ventral direction but did not breach the ventral edge. The surface of each ridge bore numerous, horizontally arranged rows of slightly flexible projections which had a similar appearance to stout, cuspidate setae (Fig. 1C). These became worn in appearance as the dorsal edge of the tooth was approached.

The gastric mill of *Jaxea nocturna* is shown in Fig. 1D. The dorsal tooth was similar in shape to that of *Callianassa subterranea*; however, the anterior face was more concave with a distinct dorso-ventral keel. On either side of the central keel there were three deep grooves (Fig. 1E). The ridges formed were wide and flat and had small projections on their ventral edges. Although quite similar to those seen on the lateral teeth of *C. subterranea*, they were much less numerous. The lateral teeth were elongated, tapering posteriorly (Fig. 1F). They were approximately twice the length of the lateral faces of the dorsal tooth. The medial surface of each lateral tooth was concave and had a large, smooth, anterior denticle. The anterior ventral crest was less pronounced than that of *C. subterranea*. Traversing the lateral teeth were many grooves. The four anterior most grooves were widely spaced and extended to, but not through, the ventral crest. The remaining grooves ( $\approx 14$  or 15) crossed the entire width of the tooth and were more closely spaced posteriorly. The surface of the ridges between the grooves were rough and nodular, with the anterior edge of each bearing stout projections or spines. Many of these projections appeared to be damaged (Fig. 1G).

The dorsal tooth of *Axius stirhynchus* was similar in shape to that of *Callianassa subterranea* (Fig. 1H), but it had a distinct dorso-ventral keel and smooth lateral faces. The lateral teeth were elongate, similar in shape to those of *Jaxea nocturna* (Fig. 2A). The medial surface was concave and had a smooth anterior denticle, smaller than that of *J. nocturna*. There was also a well-defined ventral crest, which extended half way along each tooth. The medial surface of the lateral teeth had 12 dorso-ventral grooves, four of which were wide and stopped short of the ventral edge while the remainder traversed the tooth. The surface of the ridges between the grooves bore horizontally arranged projections,

**Fig. 1** A *Callianassa subterranea*, dorsal tooth; B *C. subterranea*, lateral tooth; C *C. subterranea*, lateral tooth ridges; D *Jaxea nocturna*, gastric mill; E *J. nocturna*, dorsal tooth; F *J. nocturna*, lateral tooth; G *J. nocturna*, lateral tooth ridges; H *Axius stirhynchus*, dorsal tooth (Scale bars for A, B, E, F, H = 100  $\mu\text{m}$ ; C = 50  $\mu\text{m}$ ; D = 500  $\mu\text{m}$ ; G = 10  $\mu\text{m}$ )



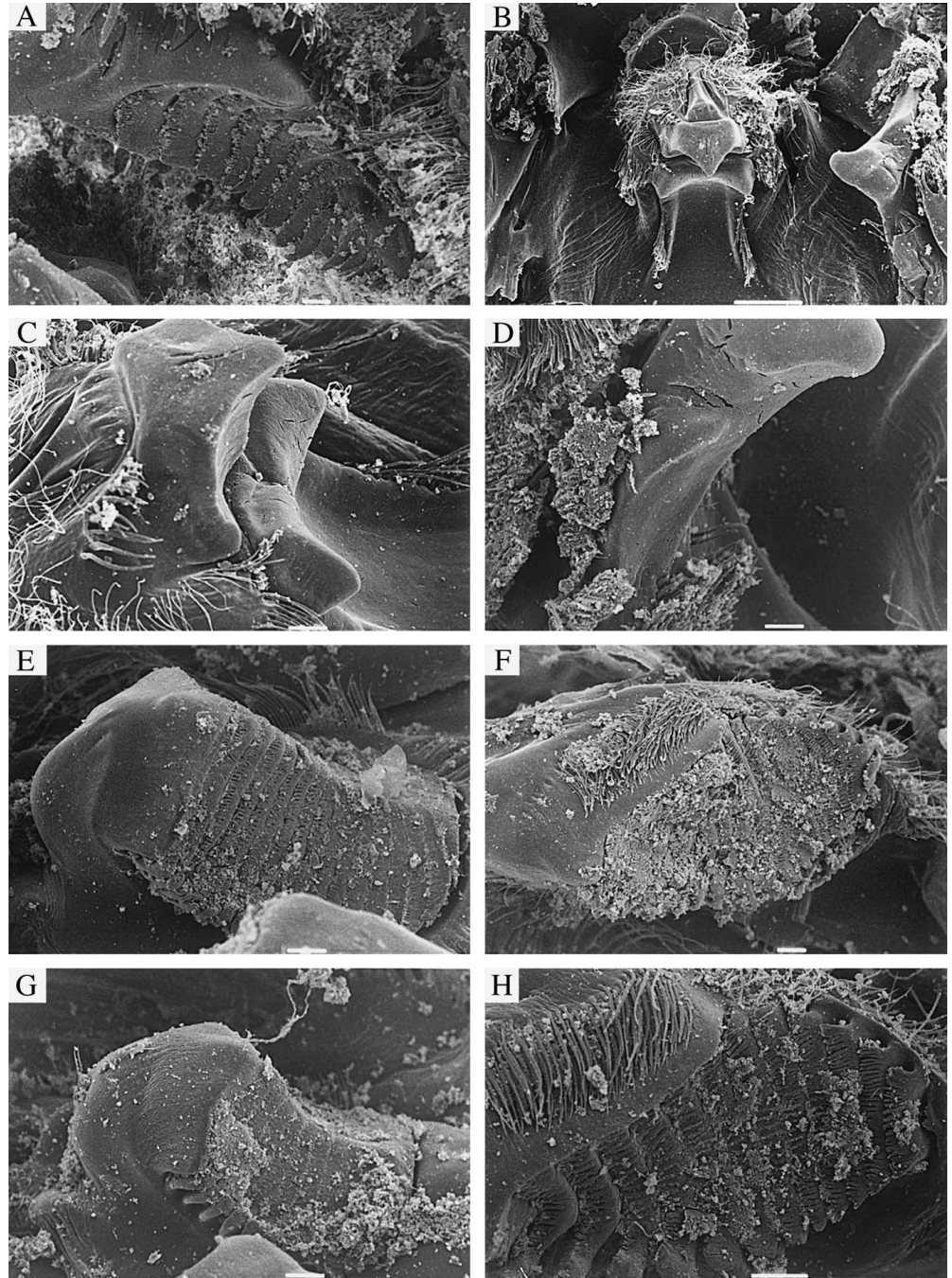
similar in shape to those of *J. nocturna* but smaller and more numerous.

The gastric mill of *Calocaris macandreae* is shown in Fig. 2B. The dorsal tooth had a hook-like appearance (Fig. 2C). The anterior surface was distinctly concave and keeled with a pointed ventral tip. As in *Callianassa subterranea*, the surface of the tooth was completely smooth and did not possess grooves or ridging. The dorsal tooth had two projections on either side of the keel, one small and the other larger and more robust.

The lateral teeth of *Calocaris macandreae* were also smooth in appearance (Fig. 2D), and had an anterior denticle and ventral crest which extended approximately half way along the tooth.

The dorsal tooth of *Upogebia pusilla* was pyramidal in shape but with a rounded apex (Fig. 2E). There was also a distinct dorso-ventral keel, on either side of which were  $\approx 15$  horizontal grooves which completely traversed the anterior face. The edge of each ridge was notched, giving it a comb-like appearance. The lateral teeth were

**Fig. 2** **A** *Axius stirhynchus*, lateral tooth; **B** *Calocaris macandreae*, gastric mill; **C** *C. macandreae*, dorsal tooth; **D** *C. macandreae*, lateral tooth; **E** *Upogebia pusilla*, dorsal tooth; **F** *U. pusilla*, lateral tooth; **G** *U. deltaura*, dorsal tooth; **H** *U. deltaura*, lateral tooth (Scale bar for **B** = 500  $\mu$ m; all other scale bars = 100  $\mu$ m)

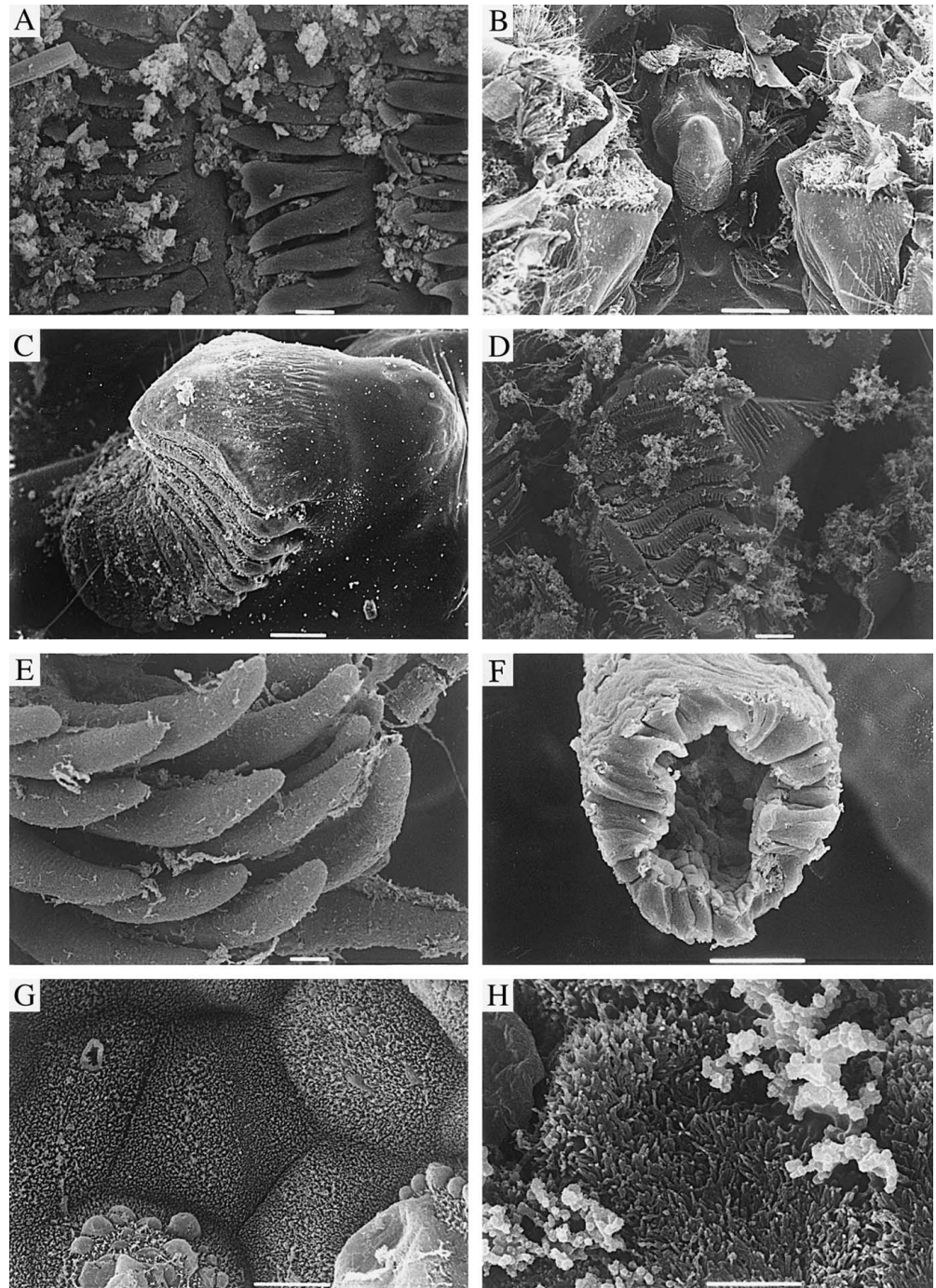


rhomboidal in shape (Fig. 2F), with each tooth having a well defined smooth anterior denticle and ventral crest. The medial face of the tooth was slightly concave and had 14 transverse grooves. Anteriorly on each lateral tooth, six wide grooves extended to the ventral crest, and posterior to this, eight narrower grooves traversed the tooth completely. As apparent on the dorsal tooth, the edges of the lateral teeth ridges had a comb-like appearance but the tips of the projections were more pointed.

The dorsal tooth of *Upogebia deltaura* was pyramidal in shape; however, the anterior face was con-

cave and had a keel, on both sides of which were horizontal grooves (Fig. 2G). The edge of each such "ridge" was comb-like in appearance, and the ridges themselves were apically flattened. As noted for *U. pusilla*, the lateral teeth were rhomboidal in shape, with a distinct ventral crest and smooth anterior denticle (Fig. 2H). Traversing each tooth were 12 grooves, the posteriormost six of which crossed the tooth completely whilst the anterior six stopped short of the ventral edge. The edges of these ridges were comb-like in appearance, with both pointed and blunt projections (Fig. 3A).

**Fig. 3** **A** *Upogebia deltaura*, lateral tooth ridges; **B** *U. stellata*, gastric mill; **C** *U. stellata*, dorsal tooth; **D** *U. stellata*, lateral tooth; **E, F** *U. stellata*, digestive gland; **G** *Callianassa subterranea*, digestive gland; **H** *Calocaris macandreae*, digestive gland (Scale bar for **A, G** = 10  $\mu\text{m}$ ; **B** = 500  $\mu\text{m}$ ; **C, D, E** = 100  $\mu\text{m}$ ; **F** = 50  $\mu\text{m}$ ; **H** = 5  $\mu\text{m}$ )



The gastric mill of *Upogebia stellata* can be seen in Fig. 3B. The dorsal tooth was stout and hook-shaped (Fig. 3C). The anterior face was distinctly concave and had a prominent central keel. Originating from each side of the keel were  $\approx 13$  horizontal deep grooves which ran to the edge of the tooth. The edge of each ridge was notched, with the same comb-like appearance as in *U. pusilla* and *U. deltaura*. The lateral teeth were approximately rhomboidal in shape (Fig. 3D), with a concave medial surface, a small anterior dent-

icle, and a ventral crest which extended half the length of the tooth. The medial face of each lateral tooth was grooved dorso-ventrally. Anteriorly, there were six grooves which stopped short of the ventral edge, whilst a further six posterior grooves extended over the entire width of the tooth. The ridges thus formed had a comb-like appearance due to blunt ended projections at their edges. These ridges exhibited the highest degree of apical flattening of any species examined. The grooves were very narrow, with the



ridges fitting closely together and forming a reticulated surface.

#### Digestive-gland morphology

The digestive gland was a large compact organ, made up of a series of blind-ending tubules (Fig. 3E). With the exception of *Callianassa subterranea* and *Upogebia deltaura*, the digestive gland was usually contained completely within the cephalothorax of the specimens. In *C. subterranea* and *U. deltaura*, the digestive gland occupied not only the cephalothorax but also extended into both the first and second abdominal somites. Extension of the digestive gland into the first abdominal somite, however, was occasionally observed for some ovigerous females of the other species examined.

The digestive-gland tubules were circular in cross-section and convoluted longitudinally, whilst the epithelium consisted of a single cell layer (Fig. 3F) with a microvillus surface which was similar in all thalassini-dean species examined (Fig. 3G, H). Secretion and cellular extrusion were apparent within the digestive gland (Fig. 3G). In all species examined, the presence of irregularly or abnormally shaped bacteria was also noted (Fig. 3H).

#### Midgut morphology

The midgut accounted for  $\approx 50\%$  of the post-gastric alimentary canal in the species examined, and in each case the midgut epithelium was relatively similar (Fig. 4A to E). Differences included the length of the microvilli of the midgut epithelium, which were longest in the specimens of *Calocaris macandreae* (Fig. 4A). There was no evidence of bacterial colonization in the midgut of *C. macandreae*; however, in the posterior regions of the midgut, unidentified coccoid bodies were noted,  $\approx 8 \mu\text{m}$  in diameter (Fig. 4B). The midgut epithelium of *Jaxea nocturna* was colonized by rod-shaped bacteria,  $1.5 \mu\text{m}$  in length (Fig. 4C) with no evidence of any coccoid bodies. The midgut epithelium of *Axius stirhynchus* was similarly colonized with rod-shaped bacteria. These, however, were slightly larger than those in *J. nocturna* ( $\approx 3 \mu\text{m}$  long). Coccoid bodies,  $\approx 10 \mu\text{m}$  in diameter, were observed in the posterior regions of the midgut of *A. stirhynchus*.

Within the posterior regions of the midgut of *Callianassa subterranea* was a patchy distribution of filamentous bacteria on the epithelium (Fig. 4D). Regions of the epithelial surface were also covered with unidentified coccoid bodies,  $\approx 6.5 \mu\text{m}$  in diameter. *Upogebia pusilla*, *U. deltaura* and *U. stellata* had filamentous and rod-shaped bacterial colonization in the posterior midgut (Fig. 4E). Coccoid bodies were also present, but were smaller than previously observed ( $\approx 5 \mu\text{m}$  diam for *U. pusilla* and *U. deltaura*,  $\approx 3 \mu\text{m}$  for *U. stellata*).

#### Posterior diverticulum morphology

Certain morphological features of the posterior diverticulum were common to all species examined. The posterior diverticulum arose immediately before the junction between the midgut and hindgut and was approximately equivalent in length to the midgut. In the majority of specimens examined, the diverticulum lay against the midgut, directed posteriorly. The microvillar lining of the diverticulum was similar to that observed for the midgut in the species examined (Fig. 4F to 5B). In *Callianassa subterranea*, numerous coccoid bodies, similar to those of the midgut, were seen in some regions of the diverticulum (Fig. 4F). These exhibited a greater range of size than those in the midgut and were, on average, smaller ( $\approx 5 \mu\text{m}$  diam compared with  $6.5 \mu\text{m}$  in the midgut). Secretion and extrusion of cells also appeared to be occurring in this region of the digestive system. Smaller coccoid bodies ( $\approx 3 \mu\text{m}$  diam) were observed within the diverticula of *Upogebia deltaura* and *U. pusilla* (Fig. 4G). Evidence of secretion and the apparent extrusion of dead cells was also noted (Fig. 4H). In *Jaxea nocturna*, the diverticulum had numerous pores in its wall (Fig. 5A, B) that were not found in the other species examined. No coccoid bodies were observed in the posterior diverticulum for this species.

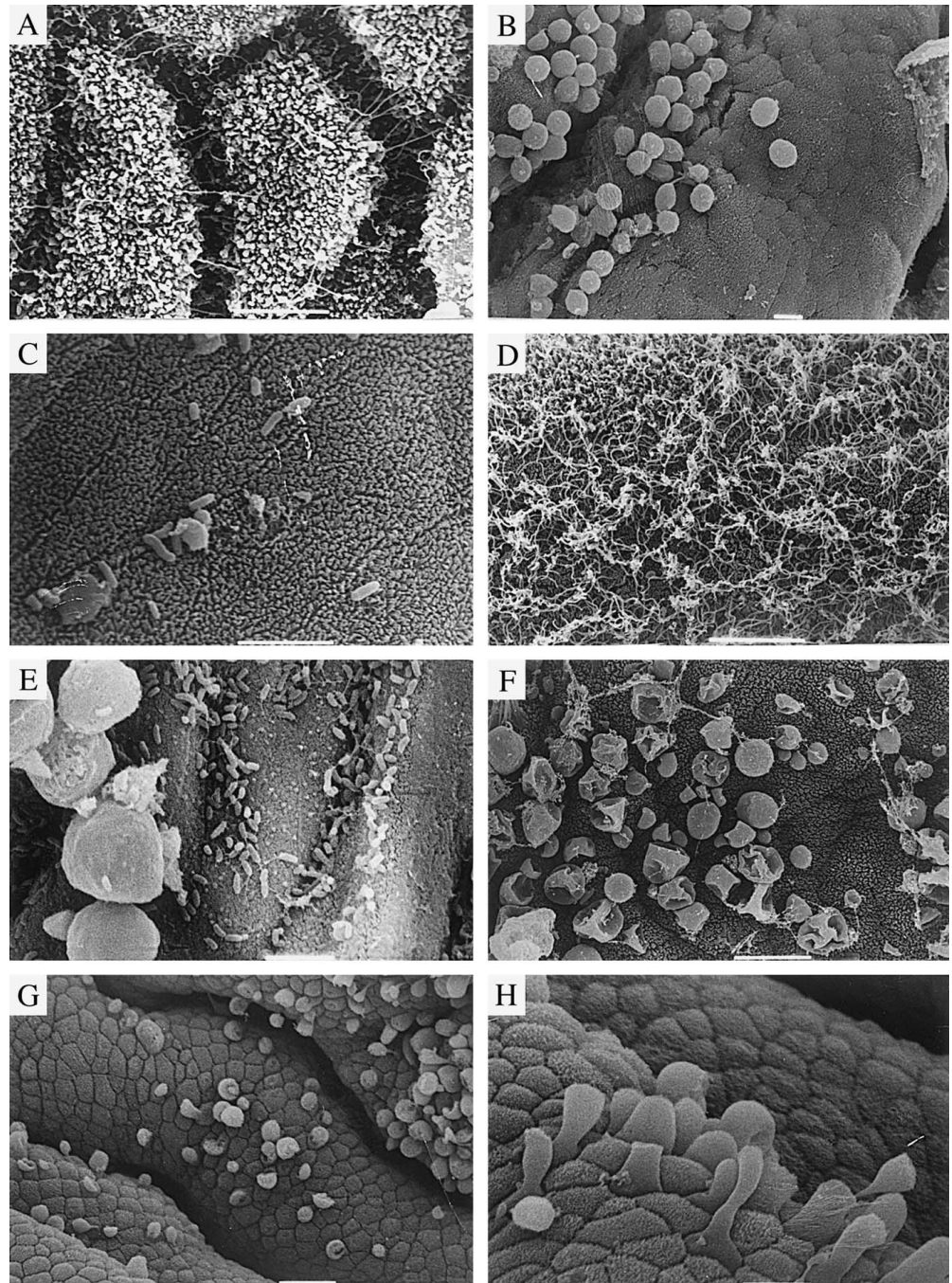
#### Hindgut morphology

The hindgut cuticle of *Callianassa subterranea*, *Jaxea nocturna*, *Axius stirhynchus* and *Calocaris macandreae* had four distinct rows of simple projections running along its length which were not found in the Upogebidae examined. These rows were situated on top of ridges formed by the longitudinal convolutions of the hindgut lining. The microdentition, i.e. the pattern and number of the projections, varied between the four species.

In *Jaxea nocturna*, the cuticular projections were simplest (Fig. 5C). They were arranged singly and were  $\approx 1 \mu\text{m}$  long. Evidence of extensive bacterial colonization was noted. Examination of the hindgut lining and outer face of the faecal rod, i.e. that lying against the lining, showed that they were coated with bacteria. Five bacterial morphotypes were identified (Fig. 5D). The most numerous type formed an extensive mat coating the faecal rod and were small, fat, rod-shaped bacteria up to  $2 \mu\text{m}$  long and  $1 \mu\text{m}$  wide. Overlaying these were a mixture of the other morphotypes. There were larger rods ( $4 \mu\text{m} \times 1.5 \mu\text{m}$ ), distinctly curved rods ( $4 \mu\text{m} \times 1.5 \mu\text{m}$ ), slender rods ( $6 \mu\text{m} \times 0.5 \mu\text{m}$ ), and clumps of coccoid bacteria ( $\approx 1.5 \mu\text{m}$  diam). The hindgut content, i.e. the faecal rod itself, was extensively invaded with slender rod-shaped bacteria ( $3 \mu\text{m} \times 0.5 \mu\text{m}$ ).

The hindgut lining of *Callianassa subterranea* had cuticular projections of  $3 \mu\text{m}$  length. They were more

**Fig. 4** A, B *Calocaris macandreae*, midgut; C *Jaxea nocturna*, midgut; D *Callianassa subterranea*, midgut; E *Upogebia stellata*, midgut; F *C. subterranea*, posterior diverticulum; G, H *U. deltaura*, posterior diverticulum (Scale bars for A, C, D, E, F = 5  $\mu$ m; B, G, H = 10  $\mu$ m)



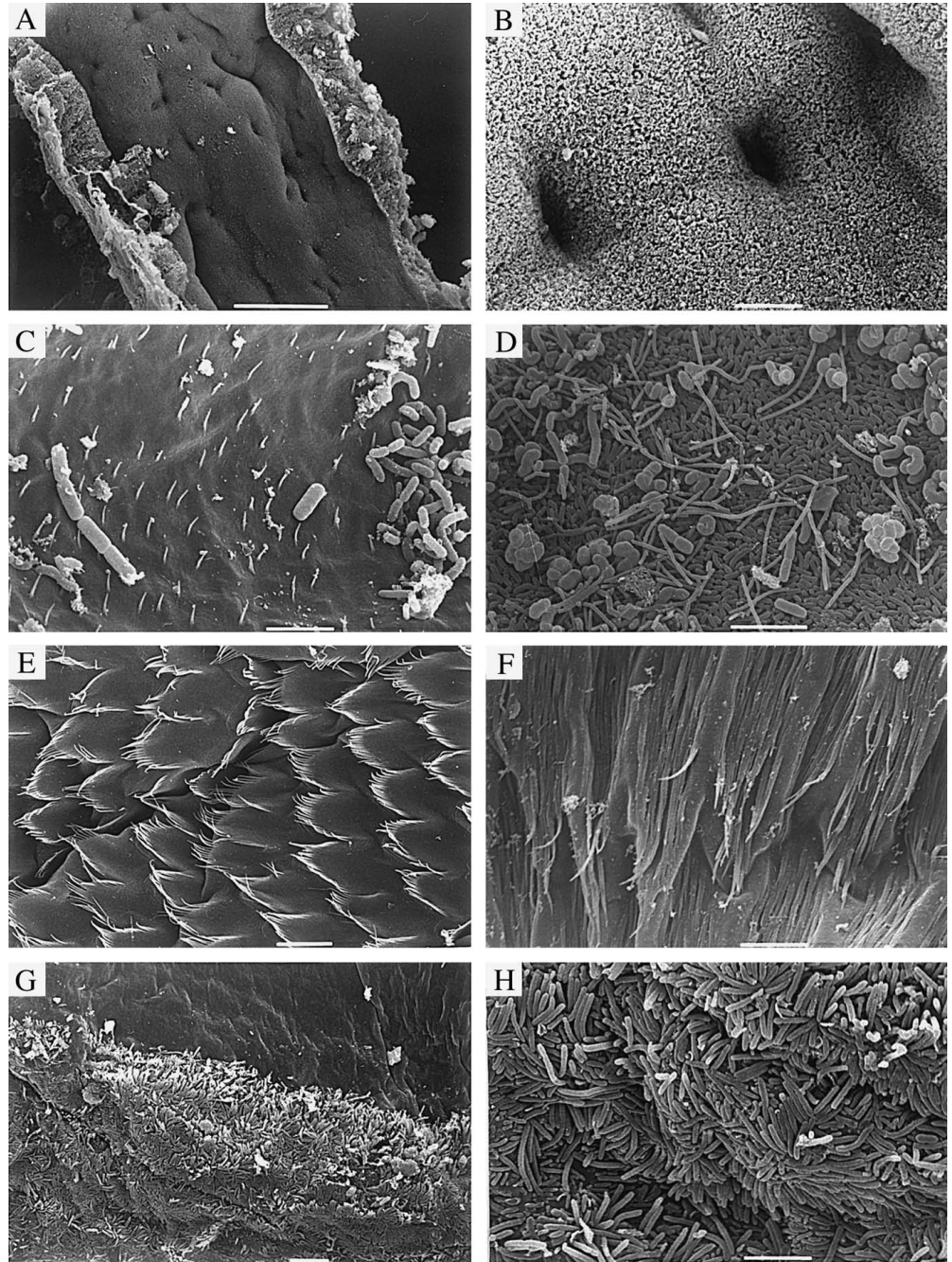
numerous than those of *Jaxea nocturna* and arranged in semicircles, each comprising  $\approx 19$  individual spines (Fig. 5E). The semicircles were parallel, with the projections directed towards the anus. There was little bacterial colonization of the cuticle, with only occasional rod-shaped bacteria noted beneath the projections. As with the midgut, a proliferation of rod-shaped bacteria was found on the internal surface of the peritrophic membrane surrounding the faecal rod.

The microdentition of the hindgut lining of *Calocaris macandreae* was the most complex observed. The spines were the most numerous and longest of the species ex-

amined, often  $> 5 \mu$ m long, and coated the ridges on which they were found (Fig. 5F). They occurred in oval shaped clumps of  $\approx 25$ . Some of these projections had forked tips. No evidence of any bacterial colonization was found within the hindgut. Although the arrangement of cuticular projections was similar in *Axius stirhynchus*, they were slightly shorter ( $\approx 4.5 \mu$ m long). There was little evidence of bacterial colonization in the hindgut of *A. stirhynchus*.

The hindgut lining of the three Upogebiidae species was completely smooth. The cuticular lining of *Upogebia pusilla* was colonized by patches of rod-shaped

**Fig. 5** A, B *Jaxea nocturna*, posterior diverticulum; C, D *J. nocturna*, midgut; E *Callinassa subterranea*, hindgut; F *Calocaris macandreae*, hindgut; G, H *Upogebia stellata*, hindgut; (Scale bars for A = 50  $\mu$ m; B, C, F, H = 5  $\mu$ m; D, E, G = 10  $\mu$ m)



bacteria,  $\approx 1 \mu\text{m}$  long. The patches predominantly occurred in or near folds of the lining. Similar colonization of the hindgut cuticle by rod-shaped bacteria was observed for *U. deltaura*. The hindgut of *U. stellata* exhibited the greatest degree of bacterial colonization of the three Upogebiidae examined (Fig. 5G). The majority of the bacteria noted were rod-shaped. Next to the lining was a layer of rod-shaped bacteria of a single morphotype,  $\approx 3 \mu\text{m}$  long (Fig. 5H). Some of these cells appeared to be dividing, suggesting that the populations were growing in situ. Although extensive, these mats of bacteria were patchy in distribution and, as for *U. pusilla* and *U. deltaura*, were usually located

around folds in the cuticular lining. Several other bacterial morphotypes were observed overlying these mats; the most conspicuous of these were filamentous.

## Discussion

The phylogenetic history of a given decapod plays an important role in the gross structure of the foregut. This basic structure, however, may be modified to varying degrees by diet and particle size of food (Schaefer 1970; Powell 1974; Icely and Jones 1978; Kunze and Anderson 1979; Ngoc-Ho 1984; Felgenhauer and Abele 1985;



Skilleter and Anderson 1986; Wolfe and Felgenhauer 1991; Nickell 1992). The finer the particle size of the diet, the more complex the dorsal tooth and the more setose the gastric mill. Such a gastric mill is typified by the suspension-feeding *Upogebia* spp. examined in the present study, although a graduation in complexity was noted even between these three species. The most complex structures were observed in *U. stellata*, the simplest in *U. pusilla*. This further differentiation of the gastric mill may result from a difference in the feeding mechanism used. For example, *U. pusilla* has a more robust dorsal tooth than the other species and may spend proportionally more of its time deposit-feeding than the other two species. However, *U. pusilla* is found in the littoral zone and in extremely shallow waters (<6 m: Dworschak 1987). In such environments, *U. pusilla* would be expected to encounter suspended material of more robust nature, through tidal and wind driven turbulence, than would *U. deltuara* or *U. stellata*, which inhabit deeper subtidal sediments.

The gastric mills of *Callinassa subterranea* and *Axius stirhynchus* are more typical of those with a crushing action. Both have relatively simple robust dorsal teeth and proportionally larger lateral teeth with flexible spines. Both species are considered to be deposit-feeders (Ellis and Baker 1972; Nickell and Atkinson 1995). The gastric mill of *Jaxea nocturna* shows intermediate adaptations, with a more complex dorsal tooth than either *C. subterranea* or *A. stirhynchus* but less complex than that of the Upogebiidae examined. Similarly, the spines of the lateral teeth of *J. nocturna* are less flexible than those of either *C. subterranea* or *A. stirhynchus*, but more flexible than those of the *Upogebia* species. *J. nocturna* is a re-suspension-feeder (Nickell and Atkinson 1995), and as such would be expected to have a gastric mill intermediate in form to the suspension- and deposit-feeders.

The exception to this link between diet and gastric mill complexity is *Calocaris macandreae*, which has a relatively simple dorsal tooth with no ridges; however, the tooth has a more complex gross morphology, with robust accessory projections on either side of the main structure. The lateral teeth are proportionally quite large, but lack any ridges or projections on their lateral face. *C. macandreae* has a much more flexible approach to feeding, although it is primarily a deposit-feeder, as indicated by the simple dorsal tooth and the large anterior denticle of the lateral teeth. It is known to be an opportunistic scavenger (Pinn 1995) and, as such, will encounter large food items of low mineral content. The gastric mill appears to be adapted to deal with this material by cutting or tearing it, as well as grinding sedimentary material with a high mineral content.

The descriptions of the digestive gland, midgut, and posterior diverticulum epithelia for the species examined here are consistent with those for other decapods (e.g. Lovett and Felder 1990a, b; Harris et al. 1991; Icely and Nott 1992). The presence of unidentified coccoid bodies within the midgut and posterior diverticulum of the

Thalassinidea examined, excepting *Jaxea nocturna*, has been previously reported for other invertebrates including members of the Crustacea (Pillai 1960; Harris et al. 1991), Orthoptera (Mead et al. 1988), Oligochaeta (Jolly et al. 1993), Polychaeta (Grémare 1988) and Ascidiacea (Seiderer and Newell 1988). Various origins have been proposed, including parasitic or fungal spores (Mead et al. 1988; Jolly et al. 1993), mucus droplets (Grémare 1988; Mead et al. 1988) and degraded phytoplankton cells (Seiderer and Newell 1988). Pillai (1960), Harris et al. (1991) and Jolly et al. (1993), however, all conclude that the coccoid bodies are of physiological origin. Lipid droplets were reported to be common in the diverticula of *Lepidophthalmus louisianensis* (Felder and Felgenhauer 1993), and it was proposed that these droplets provided an energy source for the midgut epithelia. Similar results were also observed in the midgut of larval penaeid shrimp (Talbot et al. 1972). Although not tested, the coccoid bodies observed in both the posterior diverticulum and midgut of the thalassinideans included in the present study could possibly be lipid droplets of physiological origin.

The three species of Upogebiidae examined had similar, smooth hindgut linings, as do *Upogebia africana* (Harris et al. 1991) and *U. pugettensis* (Harris 1993), suggesting that this feature may be consistent throughout the family. Modification of the hindgut lining, in the form of microdentition, in the other species in the present study appears to be a common phenomenon in crustaceans (e.g. Felgenhauer 1992; Harris 1993). Several functions have been proposed for these projections, the most common of which is to aid the movement of the faecal rod through the hindgut (Dall 1967; Bignell 1984; Felgenhauer 1992). Pillai (1960) proposed the reverse, in that the projections arrest the movement of the faecal rod through the hindgut, thus allowing concentration and compaction of the material before it is expelled. These cuticular projections may also provide sites for microbial attachment, as shown by Brecko and Štrus (1992) in the hindgut of terrestrial isopods, or shelter microbes from abrasion by the faecal rod (Harris 1993). Alternatively, long fine projections may prevent microbial attachment (Bignell 1984). The variation in microbial colonization in relation to the type of microdentition observed suggests that several of these suggestions may hold true. However, in the present study, projections only occurred on four longitudinal ridges rather than over the whole lining as might be expected, if preventing microbial colonization was the primary function. Felder and Felgenhauer (1993) proposed that *Lepidophthalmus louisianensis* used the projections to grip the faecal rod within the hindgut and to assist with its posterior progression. They also noted that the projections maintained contact with the peritrophic membrane or compacted rod even during antiperistaltic anterior movements of water. A similar conclusion regarding the function of these projections was reached in the present study. The absence of any

microdentition in the hindgut of the *Upogebia* spp. examined may be a feature connected with suspension-feeding. The diet of a suspension-feeder would have a higher water content than that of a deposit-feeder. The need for antiperistaltic movement of water in these species may therefore be reduced, and a mechanism for holding the faecal rod stationary within the hindgut during such activity would not be required.

Colonization of the gut environment is thought to be an almost ubiquitous phenomena in the animal kingdom. There was a dominance of rod-shaped bacteria within the hindgut of the thalassinideans examined, and similar morphological types have been noted for other Thalassinidea (Harris et al. 1991; Harris 1993). The bacterial populations were not very diverse in terms of appearance, suggesting that very specific conditions exist in the gut which are not suitable for a plethora of different microbes (Harris 1993).

The absence of microbial flora within the gut of *Calocaris macandreae* is surprising, considering the gut flora observed in other thalassinidean species during this and other studies (Harris et al. 1991; Harris 1993). The similarity in specimen preparation and the rapid processing of *C. macandreae* specimens (within 2 h of capture) in comparison to the *Upogebia pusilla* specimens (whole animal fixed 4 yr prior to processing), indicates it is not likely that the absence of microbial flora is an artifact of preparation. An examination of two marine wood-boring isopods *Limnoria tripunctata* Menzies and *L. lignorum* (Rathke), one terrestrial species *Oniscus asellus* L., and a wood-inhabiting amphipod *Chelura terebrans* Philippi, also revealed an absence of any microbial flora (Boyle and Mitchell 1978). Similar observations were reported by Sleeter et al. (1978) for *L. tripunctata*. Under certain conditions, *L. tripunctata*, however, does harbour a microbial flora, e.g. when boring into creosote-stained wood (Zachary and Colwell 1979; Zachary et al. 1983). More recently, Harris (1993) found only a few coccoid-shaped bacteria in the digestive system of the crab *Scylla serrata* (Forskål). Boyle and Mitchell (1978) and Sleeter et al. (1978) proposed that the isopods and the amphipod all produced antimicrobial substances that keep the gut free of microbial organisms. *Calocaris macandreae* could also produce such a substance to maintain its gut free of microbes.

The reasons for *Calocaris macandreae* not harbouring a gut flora are unclear. Sleeter et al. (1978) suggested that the absence of a gut flora was linked to the production of endogenous cellulases. Pinn (1995) demonstrated that *C. macandreae* does indeed produce endogenous cellulases. However, other thalassinideans with extensive bacterial colonization of the hindgut have also been shown to produce endogenous cellulase, e.g. *Callianassa kraussi* (Harris 1992), *C. subterranea* and *Jaxea nocturna* (Pinn 1995). Harris (1993) suggested that the degree and type of colonization of the decapod digestive system is related to diet; *Scylla serrata*, a carnivore, showed little evidence of bacterial colonization of

the gut, whilst the hindgut of detritivorous decapods showed extensive colonization. *Calocaris macandreae* is generally considered to be a detritivore; however, this thalassinidean is also a scavenger with cannibalistic and necrophagous tendencies (Buchanan 1963; Calderon-Perez 1981; Pinn et al. 1998). Although further research is required, the broad range of feeding modes and varied diet of *C. macandreae* may explain, in part, the absence of a gut flora.

In conclusion, *Callianassa subterranea* and *Axius stirhynchus* are predominantly deposit feeders and, as such, have a digestive system with a robust gastric mill. The three Upogebiidae species have a gastric mill designed for dealing with smaller particles obtained by suspension-feeding. *Jaxea nocturna* has a digestive system intermediate between these two opposites, as might be expected from its re-suspension method of feeding. The gut of *Calocaris macandreae* is designed to deal with material of a higher organic content than would be encountered by deposit-feeding alone. Whilst predominantly a deposit feeder, this thalassinid is also an opportunistic scavenger (Pinn 1995). In conclusion, the results of the present study demonstrate that digestive-tract morphology is modified to some extent by feeding mode and diet, and that certain features may be consistent within families. These features may have a useful role in phylogenetic studies.

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