Comparative morphology of the mouthparts, chelipeds and foregut of two kalliapseudid apseudomorphans (Crustacea: Tanaidacea)

DAVID T. DRUMM

Nova Southeastern University Oceanographic Center, 8000 North Ocean Drive, Dania Beach FL 33004, U.S.A. Present address: Academy of Natural Sciences, 1900 Benjamin Franklin Parkway, Philadelphia PA 19103, U.S.A. drumm@acnatsci.org

ABSTRACT—The mouthparts, chelipeds and foregut of two kalliapseudid apseudomorphan species, *Kalliapseudes mac-sweenyi* (subfamily Kalliapseudinae) and *Psammokalliapseudes granulosus* (subfamily Tanapseudinae), are described and compared using light and scanning electron microscopy. The setae on the mouthparts differ considerably between these two species and are directly related to the feeding mechanism, being in accord with the subfamilial kalliapseudid classification. *K. macsweenyi* possesses plumose setae on the chelipeds, maxillipedal palps, and mandibular palps. The females of *P. granulosus* possess simple setae on the chelipeds. The males possess plumose setae on the chelipeds, but are directed ventrally, and thus do not form a filter as in *K. macsweenyi*. Females and males of *P. granulosus* possess simple and serrate setae on the maxillipedal palps; the mandibular palp is reduced and bears one serrate seta; and both sexes of *P. granulosus* possess comb setae on the moveable endite of the maxilla. The mandibles of *K. macsweenyi* are more heavily calcified and have better developed molar processes than those of *P. granulosus*. Foregut morphology of these two species is nearly identical and could be attributed to their close phylogenetic relationships on the familial level, or to their similar, chiefly detritus-based diets.

INTRODUCTION

Tanaidacean crustaceans are among the most diverse and abundant organisms in many deep-water environments, and some shallow-water species reach population densities of 10^4 – 10^5 m⁻² (Sieg 1988). Though they are thus likely to be important components of marine food webs, little is known about their ecology.

No comparative studies of tanaidacean mouthpart and foregut morphology exist based on scanning electron microscopy (SEM). Kudinova-Pasternak (1991) used light microscopy to relate tanaidacean feeding types to mandible types. She demonstrated that more trophic groups exist than previously believed. The only studies of tanaidaceans by SEM concern systematics (Ishimaru 1985; Larsen & Wilson 1998; and Larsen 2001). The only investigation into tanaidacean foreguts is that of Siewing (1953). This is the first time that SEM has been used to study tanaidacean foreguts. Tanaidacean foregut features might prove useful in the elucidation of their phylogeny, as has been shown for the Amphipoda (Coleman 1992, 1994) and Mysida (Kobusch 1998).

Comparative morphological studies of species belonging to the same family should demonstrate how ecological adaptations contribute to morphological divergence and establish a basis for phylogenetic diversification. In this paper, I present observations on the mouthparts, chelipeds and foregut morphology of two species of the apseudomorphan family Kalliapseudidae: Kalliapseudes macsweenyi Drumm, 2003, and Psammokalliapseudes granulosus Brum, 1973 (= Cirratodactylus floridensis Gardiner, 1973), using light and scanning electron microscopy. These two confamilials, classified (Gutu 2001) in different subfamilies (Kalliapseudinae Lang 1956; and Tanapseudinae Băcescu 1978, respectively), were selected because they are locally abundant, live in different habitats and have different mouthpart morphologies. Both species construct semipermanent mucus-lined burrows in the sediment. Information on their feeding mechanisms is currently being prepared for publication.

MATERIALS AND METHODS

Kalliapseudes macsweenyi was collected from Whiskey Creek, a tidal sandy mangrove creek, in Dania Beach, Florida (26° 05'N, 80° 06'W, depth 0.5 m). Sediment samples from the creek bed were sieved through a 0.5-mm mesh sieve and washed in plastic bags. *P. granulosus* was collected with a box core off Hollywood, Florida, between the second and third reefs (25°59'14"N, 80°05'25"W, depth 20 m). Specimens intended for dissection were fixed in 10% formalin and later transferred to 70% ethanol. A total of 15 adult *K. macsweenyi* and 10 adult *P. granulosus* were prepared and examined by SEM. Dissections and gross examinations of mouthparts and appendages were first made using a stereomicroscope. To remove food material from the mouthparts, some specimens were sonicated for 10 sec in an aqueous surfactant solution (Tween-80). Detritus was also removed from the more concealed mouthparts using a fine brush. Some specimens were not sonicated so that food deposition on the mouthparts could be observed. Preparation followed the procedure of Felgenhauer (1987). Mouthparts were examined using an ISI-DS130 scanning electron microscope at an accelerating voltage of 20 kV.

Foreguts were placed in 15% KOH overnight to remove tissue and then transferred to glycerol. Drawings and detailed examinations were made with a Wild compound microscope and a camera lucida. Internal structures were easily seen through the transparent cuticle. However, gut contents had to be carefully removed in order to prevent damage. SEM micrographs were taken at the University of Miami, Florida on the cryo-transfer unit installed on the Phillips ESEM.

Terminology of mouthparts follows Larsen (2003); that of foreguts follows Coleman (1991) and Wallis and Macmillan (1998).

Abbreviations: Labrum, L; Mandible, M; Incisor process, I; Spine row, SR; Molar process, MO; Mandibular palp, MP; Labium, P; Maxillule, X1; Inner endite of maxillule, IE; Outer endite of maxillule, OE; Maxilla, X2; Inner lobe of fixed endite of maxilla, PE; Outer lobe of fixed endite of maxilla, FE; Inner lobe of moveable endite of maxilla, IL; Outer lobe of moveable endite of maxilla, OL; Maxilliped, MXP; Epignath, E; Cheliped, C.

RESULTS

Setal Types (Figs. 1, 2)

Because the functions of crustacean mouthparts are often directly related to the morphology of the setae found on the mouthparts, the different types of setae must be described before discussing mouthpart morphology.

In the current study, the classification system of Farmer (1974) is used, with some modifications. The scheme presented here includes four basic setal types: simple, plumed, serrate, and plumodenticulate. Each basic type may have several variations.

- 1) Plumed setae (Fig. 1A-C): only setules on shaft.
 - a) Plumose setae (fig. 1A): setules arise from the shaft in two opposite rows like barbs on a feather. Abundant in *K. macsweenyi* on the



Fig. 1. Setal types. A) Plumose. B) Pappose. C) Terminally setulate. D) Simple-pointed. Scale bars: A, B, D, 25 $\mu m;$ C, 50 $\mu m.$

mandibular palp, maxillipeds, and chelipeds, and on the maxillae in both species.

- b) Pappose setae (fig. 1B): most setules arise from the shaft at all angles. Found on the maxillipedal endites of both species. Often called "brushing" setae (Cannon & Manton 1929; Dennell 1937).
- c) Terminally setulate setae (fig. 1C): many long setules arise at the tip of the seta. Found on the inner endite of the maxillules of both species.
- 2) Simple setae (Fig. 1D): surface of setae smooth, without setules or denticles.
 - a) Simple-pointed (fig. 1D): pointed apically. Found, for example, on the maxillipedal palp in *P. granulosus*.
 - b) Simple-blunt: blunt apically. Found on the outer lobe of the fixed endite of the maxillae.
 - c) Hair-like: narrower than simple-pointed setae



Fig. 2. Setal types. A) Type A serrate. B) Type B serrate. C) Type C serrate (comb). D) Plumodenticulate. E) Microtrichs. Scale bars: A–D, 25 μ m; E, 10 μ m.

and same diameter the entire length. Numerous in *K. macsweenyi*. Found, for example, on the distal margin of the maxillipedal endites.

- 3) Serrate setae (Fig. 2A–C): only denticles on shaft.
 - a) Type A (fig. 2A): two rows of strong denticles on one side of shaft. Found on the outer lobe of the fixed endite of the maxillae in *K. macsweenyi*.
 - b) Type B (fig. 2B): two rows of denticles on one side of shaft, not as strong as in type A. Found on the moveable endite of the maxillae in *K. macsweenyi*.
 - c) Type C, or combed setae (fig. 2C): one row of strong denticles. Found on the moveable endite of the maxillae in *P. granulosus*.
 - d) Type D: one row of weaker denticles. Found on last article of the maxillipedal palp in *P*. *granulosus*.

- 4) Plumodenticulate setae (Fig. 2D): both setules and denticles on shaft.
 - a) Large, serrated along their distal half, with several long proximal setules (fig. 2D). Found on the outer lobe of the moveable endite of the maxillae of both species.

The faces of many of the appendages and the funnel of the foregut bear minute cuticular processes called microtrichs (fig. 2E), which are much smaller than ordinary setae (macrotrichs), and arranged in crescentic rows. Needham (1942) suggested that they may serve as exteroceptors sensitive to movements on the surface of the cuticle, but their function is still unknown.

Mouthpart Morphology

Kalliapseudes macsweenyi (Figs. 3-6, 10)

The labrum (L) (figs. 3 A–C) is a large, flap-like structure that forms the anterior boundary of the mouth opening. It bears numerous hair-like setae on the lateral margins of its ventral face. The mandibles (M in fig. 3A) (figs. 3A-D, 4A, B, 6D) are large and heavily calcified. The outer faces of the incisor processes are finely denticulate. The cutting edge of the right incisor process (fig. 3D) bears 5 blunt cusps, the posterior 2 larger than the 3 anterior ones. The left incisor process (I) (figs. 4A, B) bears 7 blunt cusps. The spine row (SR) (figs. 3D, 4A) of both mandibles bears a long peduncle with 4 distal serrate stiletto-shaped spines. The mandibular palp (MP) (figs. 3A, D, 4A, B) is uni-articulate, well developed, and is fringed with a series of long, plumose, dorso-medially curved setae on its inner margin. The molar surfaces on the left (fig. 4C) and right mandible (fig. 4D) are asymmetrical. The molar process (MO) of the right mandible is composed of about 16 longitudinal masticatory ridges that gradually flatten out anteriorly. Because the posterior ends of the ridges are elongated and extend beyond the edge of the mandible, the molar surface is slightly concave. The dorsal end bears several thornlike bristles. The left molar surface bears 11 longitudinal masticatory ridges that do not extend posteriorly and are covered anteriorly with bristle-like protrusions that together form a coarse brush. The posteriorly extended ridges of the right molar surface restrict the space between the molar surfaces and prevent loss of food particles.

The labium (P) (fig. 3B) has a pair of palps that bear numerous long hair-like setae along their margins. The ventral faces are finely setose (hair-like) on either side of the cleft between the labium.

The maxillules (X1) (figs. 3B, 5A) bear an inner (medial) endite (IE) armed with 4 terminally setu-



Fig. 3. *Kalliapseudes macsweenyi-* mouthparts. A) Ventral view of mouthparts with maxillipeds removed; maxilla (X2), maxillue (X1), mandible (M), labrum (L), and mandibular palp (arrows). B) Ventral view of mouthparts with maxillae removed; inner endite (*) of maxillule with anteromedially directed setae extending across cleft between labium (P), palp of labium (arrow), right mandible (RM), left mandible (LM). C) Posterior view of mandibles *in situ*; thickened portion of labrum (*). D) Right mandible; incisor process (I), spine-row (SR), molar process (MO), mandibular palp (MP). Scale bars: A–C, 100 µm; D, 50 µm.

late setae that extend toward each other (fig. 3B). The outer (lateral) endite (OE) bears 6 toothed spines and 4 simple spines, which bite against those of the apposing sides. On the posterior face, proximal to the terminal cluster of spines, are two type B serrate setae. The outer margin bears dense rows of long hair-like setae distally.

The maxilla (X2) (figs. 5B–C, 10A) has an inner lobe of the fixed endite (PE) (figs. 5B, 10A) bearing about 31 slender, plumose setae and a posterior row of 2 apically serrate spines (fig. 10A). The outer lobe of the fixed endite (FE) (fig. 5B, 10A) bears 4 type A serrate setae on the inner half of the distal margin and several type B serrate setae on the outer half of the distal margin. There is a short serrate seta on the posterior face of the endite. The inner lobe (IL) of the moveable endite (figs. 5C, 10A) bears several simple-blunt setae and a few type B serrate setae. The outer lobe (OL) bears 3 type B serrate setae and 2 large plumodenticulate setae. The outer margin of the maxilla bears dense rows of long hair-like setae distally. On the posterior and anterior faces of



Fig. 4. *Kalliapseudes macsweenyi-* mandibles. A) Medial view of left mandible; lacinia mobilis (LM). B) Left mandible, showing the long plumose setae of the mandibular palp. C) Molar process of left mandible. D) Molar process of right mandible. Other abbreviations as noted previously. Scale bars: A, B, 100 µm; C, 10 µm; D, 50 µm.



Fig. 5. *Kalliapseudes macsweenyi-* mouthparts. A) Ventral view of terminal portion of maxillule; outer endite (OE), inner endite (IE). B) Fixed endite outer lobe (FE) and inner lobe (PE) of maxilla. C) Moveable endite of maxilla; inner lobe (IL), outer lobe (OL). D) Ventral view of mouthparts with chelipeds removed, showing the maxillipeds (MXP) *in situ* with their anteriorly directed palps (*). Scale bars: A–C, 50 µm; D, 100 µm.

the maxilla are several rows of microtrichs arranged in crescentic rows (fig. 5B).

The maxillipeds (MXP) (figs. 5D, 6A) extend horizontally forwards, covering the other mouthparts with their tips beneath the labrum. The outer margin of the basis is fringed with a row of plumose setae. An endite (fig. 6C) extends from the median face of the basis as a flat plate ventral to the maxilla and extends anteriorly and dorsal to the main axis of the palp. Its dorsal, medial margin bears a row of pappose "brushing" setae (fig. 6C), and its distal and lateral margins bear long, hair-like setae. The lower medial margin bears two coupling hooks that lock the apposing endites together. The three distal articles of the 4-segmented palp bear two rows of long, plumose setae on their medial margins. The tips of these setae on apposing palps meet in the midline. The last article bears three long, simple,



Fig. 6. *Kalliapseudes macsweenyi-* mouthparts. A) Maxilliped with attached epignath (E). B) Ventral view of head *in situs*, cheliped (C) with long plumose setae cover the mouthparts. C) Maxillipedal endites. D) Distal portion of left mandible. Other abbreviations as noted previously. Scale bars: A, B, 100 µm; C, 50 µm; D, 10 µm.



Fig. 7. *Psammokalliapseudes granulosus*- mouthparts. A) Medial view of distal portion of left mandible. B) Molar process of left mandible. C) Molar process of right mandible. D) Ventral view of mouthparts with maxilla removed; inner endite (*) of maxillule with anteromedially directed setae extending across labium cleft. Other abbreviations as noted previously. Scale bars: A–C, 10 µm; D, 100 µm.

terminal setae with short, hair-like setae on the outer margin. The epignath (E) (fig. 6A) is a vaulted plate and bears a spiniform protuberance posteriorly and a round lobe anteriorly.

The chelipeds (C in fig. 6B) play a vital role in the feeding mechanism (Drumm in prep.), and therefore should be treated with the mouthparts. The carpus bears two rows of long, plumose setae along its entire length. The dorsal row of setae (not visible in fig. 6B) curves dorsomedially at the tips. The propodus bears a row of long, plumose setae that runs diagonally across its medial face. There is no exopodite.

Psammokalliapseudes granulosus (Figs. 7-10)

The labrum is similar to that of *K. macsweenyi* but bears stout simple setae on the posterior margins



Fig. 8. *Psammokalliapseudes granulosus*- mouthparts. A) Dorsal view of outer endite of maxillue. B) Moveable endite of maxilla; inner lobe (IL), outer lobe (OL). C) Fixed endite outer lobe (FE) and inner lobe (PE) of maxilla. D) Ventral view of mouthparts with chelipeds removed, showing maxillipeds (MXP) *in situ* with their anteriorly directed palps (*). Arrow indicates exopodite of right cheliped. Scale bars: A, D, 100 µm; B, C, 50 µm.



Fig. 9. *Psammokalliapseudes granulosus*- mouthparts. A) Dorsal view of maxillipedal endites. B) Distal setae of maxillipedal endites. C) Ventral view of male head *in situ*; chelipeds (C); arrow indicates ventrally-directed plumose setae on medial margin of propodus. D) Ventral view of female head *in situ*; maxillipedal palp (*), exopodites of chelipeds (white arrows), exopodite of first right pereopod (black arrow). Scale bars: A, 50 μm; B, 10 μm; C, D, 100 μm.

and short, slender simple setae on the anterior margins.

The mandibles (fig. 7A) are not as massive or heavily calcified as in K. macsweenyi. The cutting edge of both right and left mandibles (fig. 7A) bears 2 large distal teeth and 2 smaller proximal teeth. The lacinia mobilis (fig. 7A) of the left mandible bears 3 teeth. The spine row of both mandibles bears a peduncle with 6 forked and terminally serrate spines. The molar processes are not as strongly developed as those of K. macsweenyi. The molar processes of the left mandible (fig. 7B) bears several thorn-like bristles anterodistally and has 5 short longitudinal ridges. The same of the right mandible (fig. 7C) has about 8 ridges and a thick, smoothly rounded margin with several narrow grooves. The mandibular palp is strongly reduced and consists of a single small article bearing one long type B seta.

The labium (P in fig. 7D) has a pair of palps that bears 3 long distal simple setae and numerous hairlike setae along their lateral and medial margins. The ventral face is finely setose (hair-like) on either side of the cleft.

The maxillules (X1 in fig. 7D) bear an inner (medial) endite armed with 4 terminally setulate setae. The outer (lateral) endite (fig. 8A) bears 11 smooth spines, most of them shorter than in *K. macsweenyi*. Proximal to the terminal cluster of spines are two type B serrate spines. The outer margin bears rows of long hair-like setae, but not as dense as in K. macsweenyi.

The spiniform setae of the maxillae (figs. 8B, C, 10B) are strikingly different in comparison with those of K. macsweenvi. The outer lobe (OL) of the moveable endite (figs. 8B, 10B) terminates in 8 long type C serrate setae and 2 large plumodenticulate setae. The combs coarsen slightly from the outermost to the innermost seta. The inner lobe (IL) (figs. 8B, 10B) of the moveable endite bears 8 shorter type C serrate setae of the same nature but with stronger combs. Again, the combs coarsen slightly from outermost to innermost. The outer lobe of the fixed endite (fig. 8C) bears 2 heavy, trifid spines bearing several proximal setules, and several simple, blunt setae. The inner lobe of the fixed endite (figs. 8C, 10B) has an anterior row of 19 slender, plumose setae and a posterior row of 5 apically serrate spines.

The maxillipeds (MXP in fig. 8D) have a row of plumose setae on the lateral margins of the coxa and basis. The endite (fig. 9A) has a row of pappose "brushing" setae on its upper medial margin and 4 coupling hooks on its lower medial margin. The distal margin is armed as shown in fig. 9B. The second and third articles of the palp bear slender, simple setae along their medial margins. The last article bears a distal row of type D serrate setae. The epignath is similar in shape to that of *K. macsweenyi*, but has a larger posterior spine.



Fig. 10. Maxilla. A) Kalliapseudes macsweenyi. B) Psammokalliapseudes granulosus. Inner lobe (IL), outer lobe (OL). Scale bar: 0.05 mm.

The male chelipeds bear a medial row of plumose setae on the basis, merus, and carpus, and are directed ventrally (fig. 9C). The female chelipeds bear only simple setae (fig. 9D). The chelipeds and first pereopods both bear exopodites (arrows in figs. 8D and 9D).

Foregut Morphology (Figs. 11, 12)

The following is a preliminary comparison of foregut morphology of *K. macsweenyi* and *P. granulosus* that attempts to relate structure and function. The foreguts of both species are nearly identical, so only figures of *K. macsweenyi* are shown. The foregut is divided into three regions: anterior cardiac chamber, posterior pyloric chamber, and funnel (figs. 11A, B).

A short esophagus (figs. 11A, B), which bears setae on the lateral walls, opens into the cardiac chamber. Food is sucked through the esophagus and is macerated and pushed into the cardiac chamber by the lateralia (figs. 11A, B; 13A, C), which are lateral invaginations of the anterior foregut region. The lateralia bear spines, with the anterior ones directed medially, and the posterior ones directed obliquely posteriorly. It is possible to see the lateralia in live specimens viewed dorsally. As the muscles of the foregut contract, the spines of the lateralia meet in the midline and presumably crush hard food particles such as diatom frustules.

An unpaired anterior dorsal structure (figs. 11A, B) projects into the cardiac chamber and has been termed the 'median setose prominence' in syncarids (Smith 1909, Wallis & Macmillan 1998), the 'unpaired dorsal cardiac piece' in mysids (Storch 1989), and the '*dorsale hakenplatte*' in tanaids (Siewing 1953). It is equipped with strong spines directed posteriorly and presumably acts to push food in that direction (Siewing 1953).

The superolateralia (figs. 11A, B) are invaginations of the dorsolateral foregut wall that begin in the anterior cardiac chamber and end in the pyloric



Fig. 11. Foregut of Kalliapseudes macsweenyi. A) Dorsal view. B) Lateral view. Scale bar: 0.5 mm.

chamber. They bear spines and presumably push food down the foregut and crush hard food particles.

In *K. macsweenyi* and *P. granulosus*, the fine filter (figs. 11A, B) in the pyloric chamber consists of a midventral ridge with setae on its lateral walls. This ridge has been termed the 'inferomedianum' in mysids, amphipods, and isopods (Storch 1987, 1989; Coleman 1991; Ullrich et al. 1991), and the 'midventral pyloric ridge' (*pylorikales mittelstück*) in tanaids (Siewing 1953). Only the finest particles are able to pass through the filter and reach the midgut glands (Storch 1989). The pyloric region is followed by the funnel region (figs. 11A, B; 12B), which is thought to transport coarse unutilized particles directly into the hindgut (Ullrich et al. 1991).

DISCUSSION

Scanning electron microscopy should greatly facilitate our understanding of the mouthpart structure of tanaidaceans and their adaptations for various feeding habits. This, in turn, will help us understand the actual mechanisms used to capture food.

The setae on the mouthparts and chelipeds differ considerably between K. macsweenyi and P. granulosus, and are directly related to the different feeding mechanisms employed by each species (Drumm in prep.). K. macsweenyi bears abundant plumose setae on its chelipeds, maxillipeds, mandibular palps, and on the inner lobe of the fixed endite of its maxillae. Both sexes of P. granulosus possess plumose setae only on the inner lobe of the fixed endite of the maxillae. These setae also occur on the chelipeds of males, but they are directed ventrally and do not form a filter as in K. macsweenyi. Both sexes of P. granulosus possess simple and serrate setae on the maxillipeds, comb setae on the moveable endite of the maxillae and complex setae on the distal edge of the maxillipedal endites. Even though the feeding mechanisms may be different, observations on the feeding behavior and gut content analysis indicate that both species primarily ingest detritus (Drumm in prep.).

The mandibles of both species have wide incisor processes that bear short and blunt teeth, as well as broad grinding molar processes, which reflects the negligible amount of cutting required for the main food source of small detrital particles. The mandi-



Fig. 12. Foregut of *Kalliapseudes macsweenyi*. A) Internal view of foregut showing spines of the lateralia. Note diatom (arrow) in the background. B) Funnel. C) Lateralia and its spines. Scale bars: A, C, 5 μ m; B, 10 μ m.

bles of *K. macsweeni*, however, are more heavily calcified with better developed molar processes than *P. granulosus*. This may be due to the need to crack diatom shells (Drumm in prep.). These features are in accord with subfamilial classification (Guţu 2001).

In a series of cross sections of the foregut of the tanaidacean, *Heterotanais oerstedi* (Krøyer 1842), Siewing (1953) figured a lateralia (*lateralfalten des kaumagens* 1) equipped with spines in the anterior cardiac chamber, as well as a midventral cardiac ridge (*cardiakales ventralstück*). Two ventrolateral ridges (*lateralfalten des kaumagens* 2) are equipped with spines that point medially, overlaying the midventral cardiac ridge and forming a filter that allows fine material to enter two ventral channels while directing coarser food items into the dorsal channel. I was able to see two parallel rows of setae (figs. 12A, B), forming the filter in *K. macsweenyi* and *P. granulosus* but was unable to see the midventral

ridge and ventrolateral ridges. Cross sections may reveal their presence.

Mysids and amphipods have a two-storied filter on each side of the midventral pyloric ridge (Schmitz & Scherrey 1983; Icely & Nott 1984; Storch 1989; Kobusch 1998). Isopods, cumaceans, and tanaids have only one filter on each side (Siewing 1953), which adds support to the close relationships between these peracarid groups (Siewing 1963; Watling 1981; Jarman et al. 2000; Richter & Scholtz 2001). Confirmation that there is only one filter on each side in specimens of *K. macsweenyi* and *P. granulosus* that I examined awaits the study of foregut cross sections. The filtratory mechanisms would easily deal with the main food source of small detrital particles.

In a study on the foregut morphology of Antarctic amphipods, Coleman (1991) discovered that the cuticle appeared to be stronger in detrital feeders than in carnivores and tissue ingestors. He also noticed that the foreguts were smaller in the detritivores due to limited storage ability afforded by the continous passage and filtration of food particles. Ullrich et al. (1991) found that the foregut armament is strong in the herbivorous euphausiid, Euphausia superba, while a carnivorous species, Nematobrachion boöpis, lacks spines. Kobusch (1998) discovered that the foregut armature of some mysid species differed in relation to diet. The foregut armature of the two tanaidacean species examined in this study are nearly identical, which may be attributed to their similar, chiefly detritus-based diets or to their close phylogenetic relationships. However, this cannot be confirmed until the foregut morphology of additional tanaidaceans with demonstrably different diets and systematic positions are studied.

ACKNOWLEDGMENTS

I wish to acknowledge Dr. Charles Messing (Nova Southeastern Univ., Oceanographic Center) for his critical reading of the manuscript, and for his constant encouragement, suggestions, and guidance during this investigation. Also, I thank Drs. James Thomas (NSU) and Richard Heard (Univ. Southern Mississippi) for their constructive criticism and guidance, and Dr. Patricia Blackwelder (NSU) for her invaluable aid with the scanning electron microscope. Insightful comments on the manuscript were provided by Dr. Modest Gutu and one anonymous reviewer.

LITERATURE CITED

Cannon, H. G.,and S. M. Manton. 1929. On the feeding mechanism of the syncarid Crustacea. Transactions of the Royal Society of Edinburgh 56:175–189.

- Coleman, C. O. 1991. Comparative fore-gut morphology of Antarctic Amphipoda (Crustacea) adapted to different food sources. Hydrobiologia 223:1–9.
- Coleman, C. O. 1992. Foregut morphology of Amphipoda (Crustacea). An example of its relevance for systematics. Ophelia 36:135–150.
- Coleman, C.O. 1994. Comparative anatomy of the alimentary canal of hyperiid amphipods. Journal of Crustacean Biology 14:346–370.
- Dennell, R. 1937. On the feeding mechanism of *Apseudes talpa* and the evolution of the peracaridan feeding mechanisms. Transactions of the Royal Society of Edinburgh 59:57–78.
- Farmer, A. S. 1974. The functional morphology of the mouthparts and percopods of *Nephrops norvegicus* (L.) (Decapoda: Nephropidae). Journal of Natural History 8:121–142.
- Felgenhauer, B. 1987. Techniques for preparing crustaceans for scanning electron microscopy. Journal of Crustacean Biology 7(1):71–76.
- Guţu, M. 2001. New changes in the systematics of the suborder Apseudomorpha (Crustacea: Tanaidacea). Travaux du Museum National d'Histoire Naturelle "Grigore Antipa", 43:65–71.
- Icely, J. D., and J. A. Knott. 1984. On the morphology and fine structure of the alimentary canal of *Corophium volutator* (Pallas) (Crustacea: Amphipoda). Philosophical Transactions of the Royal Society of London 306: 49–78.
- Ishimaru, S-I. 1985. A new species of *Leptochelia* (Crustacea, Tanaidacea) from Japan, with a redescription of *L. savignyi* (Krøyer, 1842). Publications of the Seto Marine Biological Laboratory 30(4–6):241–267.
- Jarman, S. N., S. Nicol, N. G. Elliott, and A. McMinn. 2000. 28S rDNA evolution in the Eumalacostraca and the phylogenetic position of krill. Molecular Phylogenetics and Evolution 17:26–36.
- Kobusch, W. 1998. The foregut of the Mysida (Crustacea, Peracarida) and its phylogenetic relevance. Philosophical Transactions of the Royal Society of London B. 353: 559–581.
- Kudinova-Pasternak, R. K. 1991. Trophic groups of Tanaidacea (Crustacea, Peracarida). Zoologicheskii Zhurnal 70:30–37.
- Larsen, K. 2001. Morphological and molecular investigation of polymorphism and cryptic species in tanaid

crustaceans: implications for tanaid systematics and biodiversity estimates. Zoological Journal of the Linnean Society 131:353–379.

- Larsen, K. 2003. Proposed new standardized anatomical terminology for the Tanaidacea (Peracarida). Journal of Crustacean Biology 23(3):644–661.
- Larsen, K., and G. D. F. Wilson. 1998. Tanaidomorphan systematics- is it obsolete? Journal of Crustacean Biology 18(2):346–362.
- Needham, A. E. 1942. Microanatomical studies on Asellus. Quarterly Journal of Microscopical Science 84:49–72.
- Richter, S., and G. Scholtz. 2001. Phylogenetic analysis of the Malacostraca (Crustacea). Journal of Zoological Systematics and Evolutionary Research 39:113–136.
- Schmitz, E. H. and P. M. Scherrey. 1983. Digestive anatomy of *Hyalella azteca* (Crustacea, Amphipoda). Journal of Morphology 175:91–100.
- Sieg, J. 1988. Tanaidacea. In: Higgins R.P. and H. Thiel H. (eds), Introduction to the study of meiofauna, pp. 402–404. Washington, D.C.
- Siewing, R. 1953. Morphologische Untersuchungen an Tanaidaceen und Lophogastriden. Zeitschrift f
 ür wissenschaftliche Zoologie 157:333–426.
- Siewing, R. 1963. Studies in malacostracan morphology: results and problems. In: H. B. Whittington and W. D. I. Rolfe (eds), Phylogeny and evolution of Crustacea, pp. 85–103. Museum of Comparative Zoology, Cambridge.
- Smith, G. 1909. On the Anaspidacea, living and fossil. Quarterly Journal of Microscopical Science 53:489– 578.
- Storch, V. 1987. Microscopic anatomy and ultrastructure of the stomach of *Porcellio scaber* (Crustacea, Isopoda). Zoomorphology 106:301–311.
- Storch, V. 1989. Scanning and transmission electron microscopic observations on the stomach of three mysid species (Crustacea). Journal of Morphology 200:17–27.
- Ullrich, B., V. Storch, and H. P. Marschall. 1991. Microscopic anatomy, functional morphology, and ultrastructure of the stomach of *Euphausia superba* Dana (Crustacea, Euphausiacea). Polar Biology 11:203–211.
- Wallis, E. J., and D. L. Macmillan. 1998. Foregut morphology and feeding strategies in the syncarid malacostracan *Anaspides tasmaniae*. correlating structure and function. Journal of Crustacean Biology 18:279–289.
- Watling, L. 1981. An alternative phylogeny of peracarid crustaceans. Journal of Crustacean Biology 1:201–210.