

# Mouthpart and digestive tract structure in four talitrid amphipods from a translittoral series in Tasmania

Matthew D. Johnston\*<sup>‡</sup>, Danielle J. Johnston<sup>†</sup> and Alastair M.M. Richardson<sup>‡</sup>

\*School of Aquaculture, University of Tasmania, Locked Bag 1-370 Launceston, TAS. 7250, Australia.

<sup>†</sup>Department of Fisheries, Western Australian Marine Research Laboratories, GPO Box 20 North Beach, WA. 6020, Australia.

<sup>‡</sup>School of Zoology, University of Tasmania, GPO Box 252C Hobart, TAS. 7001, Australia.

<sup>‡</sup>Corresponding author, e-mail: mdjohnst@cyllene.uwa.edu.au

Structural adaptations of the mouthparts and digestive tract of four talitrid amphipods were examined in relation to diet, habitat and phylogeny. The species differed in their habitat relative to the shoreline and also in their diet: a 5-dentate 'sandrunner', *Talorchestia* species II (a mid to low shore intertidal diatom feeder), a 5-dentate sandhopper, *Talorchestia marmorata* (a strandline kelp feeder); a 4-dentate sandhopper, *Talorchestia* species I (extreme high shore, feeding on spinifex grasses), and a 4-dentate landhopper, *Keratroides vulgaris* (forest leaf litter, litter feeding). Gross structural characteristics of the mouthparts were similar among all three *Talorchestia* species reflecting their phylogenetic relatedness. Increased setation and minor structural differences among the *Talorchestia* species could be attributed to dietary differences, reflecting the zones across the shoreline that they inhabit. Mouthparts of *K. vulgaris* were elongate, with markedly different setation to the *Talorchestia* species, reflecting its more distant phylogenetic position and its diet of decaying leaf litter. Digestive tract structure was more conserved among all species due to their phylogenetic relatedness. The gross digestive structure conformed to the general plan exhibited by most gammaridean amphipods. However, an additional pair of lateral pyloric caeca was evident in all species, the function of which is uncertain.

## INTRODUCTION

Amphipods inhabit a diverse range of aquatic and terrestrial habitats. They are most abundant and diverse in marine and freshwater environments, but they also extend across intertidal zones to cryptozoic habitats in the leaf litter of forests, woodlands and grassland. Talitrid amphipods (Amphipoda: Talitridae) are unique among the order Amphipoda as they are the only family to have successfully made the transition onto land, and they are also more generally accepted as a trans-littoral family: having representatives at all levels of the intertidal zone, in fully terrestrial habitats and in freshwaters (Richardson & Swain, 2000). They are therefore a valuable group for investigating evolutionary changes in their mouthparts and digestive tract associated with the colonization of land.

The sandy beaches of Tasmania comprise a substantial proportion of the coastline, including beaches of various degrees of exposure, which subside to a range of native vegetation types inland, ranging from dry grasslands to wet eucalypt forests and temperate rainforest. Shepherd (1994) described the distribution of three species of sandhopper at Fortescue Bay, a moderately exposed sandy beach in south-east Tasmania and detailed their stomach contents. The taxonomy of the Australian sandhoppers and beachfleas is poorly known (Bousfield, 1982), and no sandhoppers have been described since Haswell (1885), despite the presence of a diverse fauna (Richardson, 1996). Two of the three sandhoppers at Fortescue Bay are undescribed, while the other can be referred to as *Talorchestia marmorata* (Haswell). The redefinition of the

genus *Talorchestia* by Morino & Miyamoto (1998) technically excludes the three species used here from the genus, but since no other generic name is available we have used *Talorchestia* in this work. Taxonomic work in progress (Richardson, unpublished data) suggests that one of these species will be placed in a separate genus (see below).

Closest to the sea at Fortescue Bay can be found an undescribed 5-dentate species of sandhopper (Bousfield, 1984), *Talorchestia* species II that emerges onto the wet sand to forage and feed mainly on surf diatoms. At the zone of seaweed and kelp deposition at the mean high water mark another 5-dentate sandhopper (Bousfield, 1984), *Talorchestia marmorata* (Haswell), is abundant in and around piles of cast kelp. At the very highest levels on the shore an undescribed 4-dentate sandhopper (Bousfield, 1984), *Talorchestia* species I, emerges on calm dewy evenings to forage and feed on high strandline plants. Immediately inland in closed eucalypt forest, *Keratroides vulgaris* (Friend), a common talitrid landhopper, feeds upon decayed forest leaf litter (Morton & Richardson, 1984). This ecological series of four talitrid amphipods represents four stages of increasing terrestrial adaptation, but it is important to stress that these particular talitrid species are not from a single evolutionary lineage, and that sandy shores are unlikely to have been the route which talitrids used to colonize land (Richardson et al., 1991; Richardson & Swain, 2000). Phylogenetic relationships within the Talitridae are not yet clearly understood, but the shared possession of a 5-dentate (Bousfield, 1984) left lacinia mobilis on the mandibles of *Talorchestia* species II and *T. marmorata* suggest that they are more closely

related to each other than to *Talorchestia* species I. All three *Talorchestia* species are phylogenetically closer to each other than to the landhopper *K. vulgaris*, since landhoppers are thought to have arisen from beachflea-like ancestors, not sandhoppers (Bousfield, 1984).

Among the various challenges for talitrid amphipods as they colonized the intertidal zone and terrestrial forests was the necessity to alter their diet according to the availability of food items in these habitats. The diets of the four talitrid species examined in this study are substantially different. Specialized structures of the mouthparts and digestive tract of amphipods have commonly been explained as adaptations to the physical and chemical characteristics of their diet. Although a considerable amount of evidence is available in the amphipod literature to support this link (Agrawal, 1964; Icely & Nott, 1984) many authors have failed to recognize that morphological differences of the mouthparts and digestive tract may also be attributed to a species' phylogenetic history (Keith, 1974). Few studies have provided evidence to separate the influences of phylogeny and diet on the mouthparts and digestive tract (Kunze & Anderson, 1979; Coelho & Rodrigues, 2001a,b). This study will identify structural differences of the mouthparts and digestive tract structure between four species of talitrid amphipod, and interpret these structural differences in terms of their diet, habitat and phylogeny. It will also help to understand the degree to which structures associated with the mouthparts, which are often used in taxonomic and phylogenetic studies, are likely to be modified by diet.

## MATERIALS AND METHODS

### *Collection*

*Talorchestia* species II and *T. marmorata* (N=20) were collected using an aspirator at low tide at the lower and strandline zones of the sandy shore at Binalong Bay on Tasmania's east coast, 3–4 hours after sunset. *Talorchestia* species I (N=20) was hand collected from spinifex grasses on the fore-dunes at Fortescue Bay on calm dewy evenings, and *Keratroides vulgaris* (N=20) was collected using an aspirator, during the day at Lilydale Falls Reserve.

### *Scanning electron microscopy*

The morphology of the mouthparts was investigated using scanning electron microscopy. Freshly dissected mouthparts were fixed in 2.5% glutaraldehyde in 0.1 M phosphate buffer pH 7.4, for 2–3 hours, washed in phosphate buffer then dehydrated in an ethanol series, critical point dried, gold sputter coated, and examined on an Electro Scan 2020 environmental scanning electron microscope at 15 kV. Mouthpart terminology is based on that of Bousfield (1973).

### *Histology and histochemistry*

Prior to dissection each talitrid amphipod was placed on ice for 20–30 min to induce a chill coma. Dissected digestive tracts were fixed for at least 48 h in Bouin's. After fixation, digestive tracts were washed in 70% ethanol and embedded in paraffin wax. Transverse serial sections were taken at 6 µm on a Microm HM 340 microtome. Sections were stained in Mallory–Heidenhain trichrome (Winsor,

1984) and mercuric bromophenol blue (Chapman, 1975) to determine the structure of the digestive tract and the location of proteins, respectively.

## RESULTS

### *Structure of the mouthparts*

#### *Position in situ*

At rest, the *in situ* positions of the mouthparts are similar among all species examined. The opening to the oesophagus is situated ventrally, and is bounded anteriorly by the upper lip, posteriorly by the lower lip, and laterally by the mandibles. The first and second maxillae are situated a considerable distance behind the opening of the oesophagus, and are flexed toward the centre of the mouth. The maxillipeds are positioned behind the second maxillae, with both left and right palps completely opposed at rest (Figure 1A).

#### *Description of setal types*

In an effort to standardize setal terminology, setal classification in this study has been based on that of Watling (1989) as a consistent setal classification system of Amphipoda is lacking.

#### *Maxilliped*

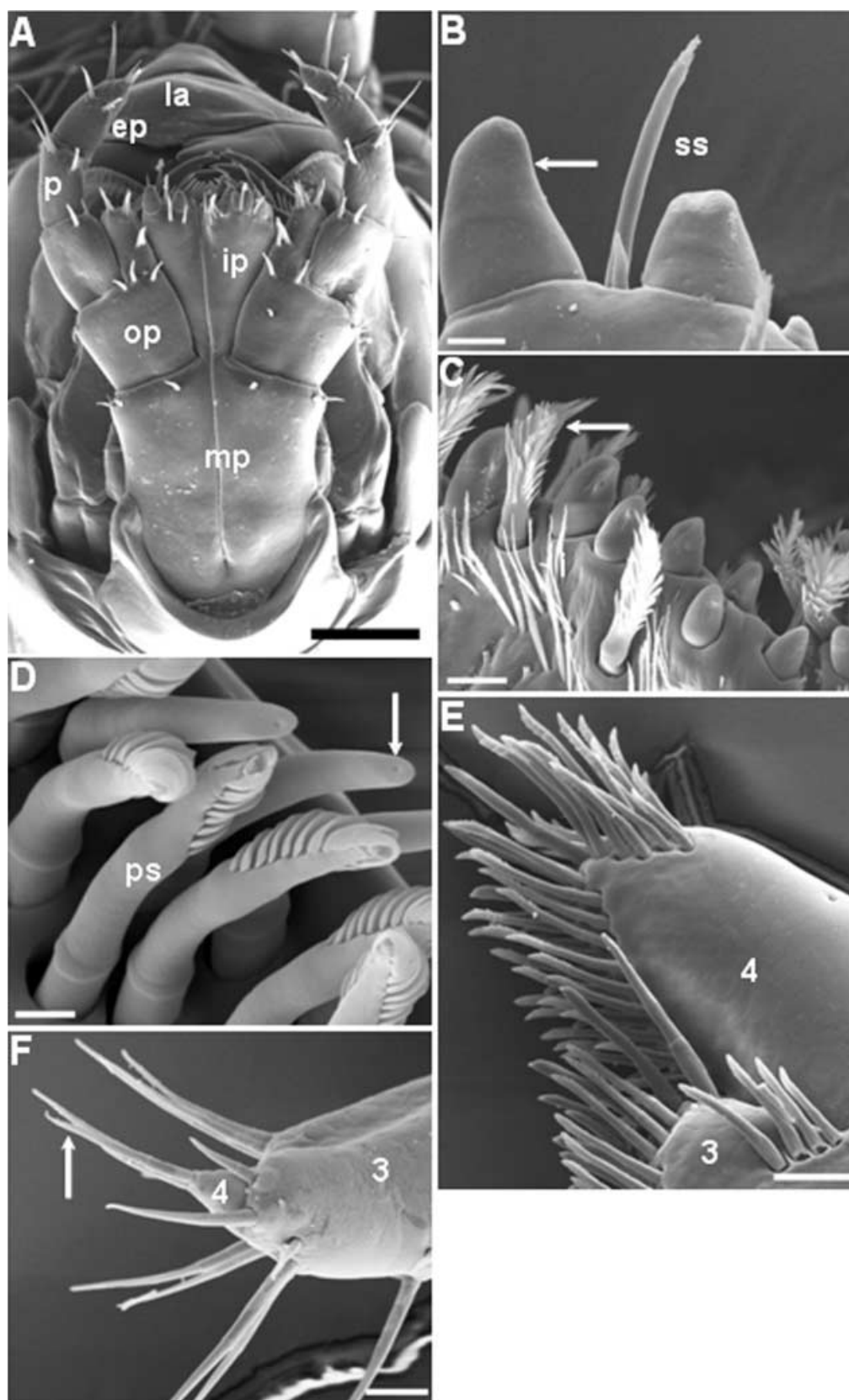
The distal margin of the maxilliped inner plate of all species bears 3–7 calcified apical spine teeth. The three apical spine teeth of *Keratroides vulgaris* are the largest of the four species, but are blunted distally (Figure 1B). The three apical spine teeth of *Talorchestia marmorata* and *Talorchestia* species I are similar in size, however, *Talorchestia* species II has seven smaller teeth, which form two distinct rows across the distal margin (Figure 1C).

The maxilliped outer plate of all three *Talorchestia* species is broad and distally rounded, whereas the outer plate of *K. vulgaris* is narrow, and tapers distally, giving rise to two branching elongated simple setae. The outer plate setal arrangement of *Talorchestia* species I, *Talorchestia* species II and *T. marmorata* is similar, with both dorsal margins bearing a single row of short simple setae and simple petal setae. The short simple setae of *Talorchestia* species II bear a chemoreceptive pore on their distal tip (Figure 1D).

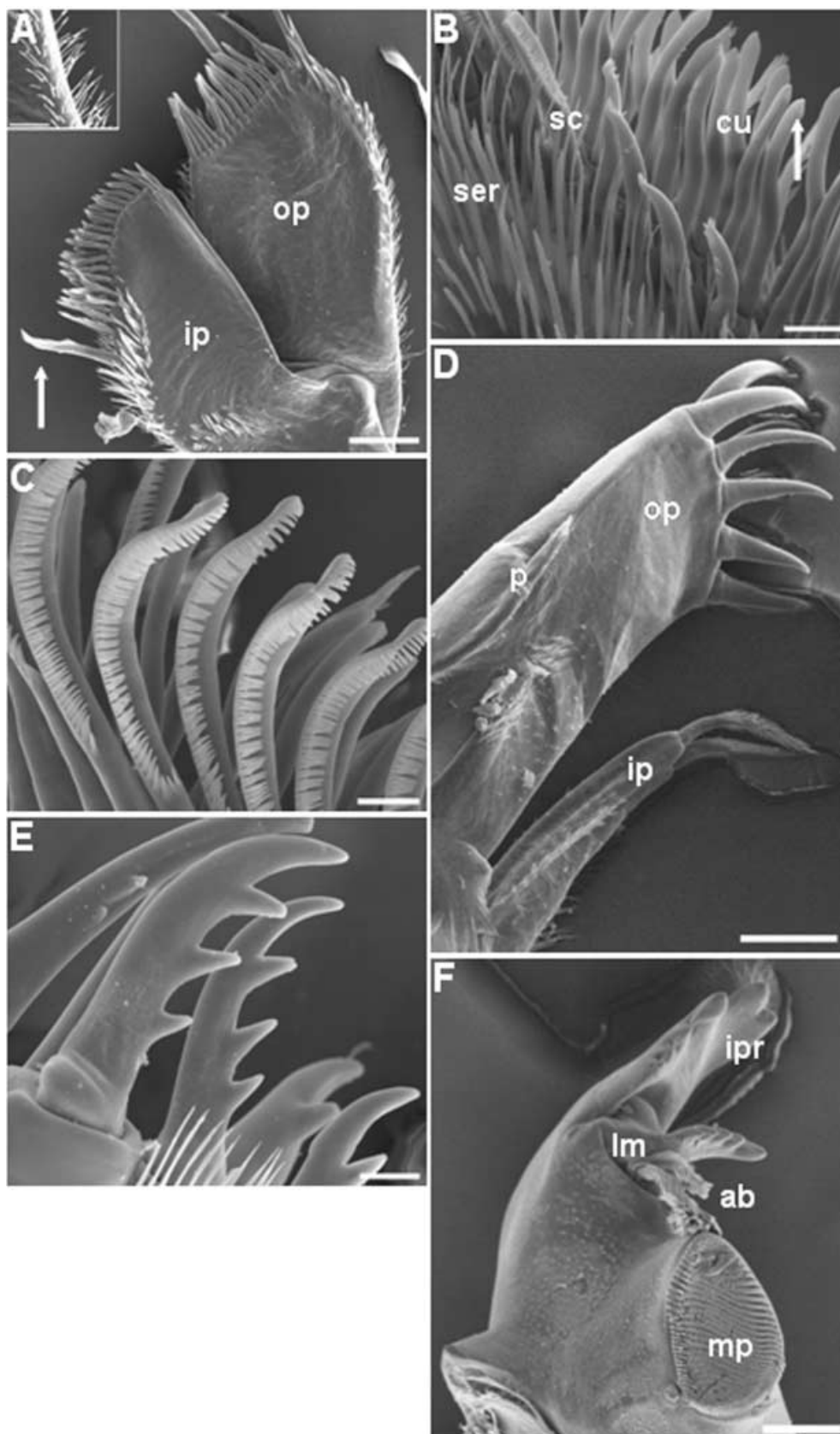
The palp is the longest and most prominent structure of the maxillipeds. The palps of all species are 4-segmented, although the fourth segment is very small in the three sandhoppers. Palp setation of all three *Talorchestia* species is similar, with dense clusters of 2–3 simple petal or simple setae extending from each segmental articulation (Figure 1E). In comparison, palp setation of *K. vulgaris* is distinctly different, with elongated simple setae extending from each articulation (Figure 1F).

#### *Second maxillae*

The maxilliped inner plates of all species are rounded distally, bearing prominent dorso-lateral pappose setae (Figure 2A). Serrate, cuspidate and small comb setae line the distal margin in all species (Figure 2B). A chemoreceptive-like pore is located on the distal tip of each cuspidate seta (Figure 2B). Arising from the aboral distal surface of the outer plate of all species are two setal rows; an inner row comprising short serrate setae, and an outer row of long comb setae, which increase in length dorso-laterally (Figure 2C).



**Figure 1.** Scanning electron micrographs of maxillipeds: (A) *In situ* position of mouthparts of *Keratroides vulgaris*. Ventral view; (B) inner plate dorsal margin setal arrangement of *K. vulgaris*. Arrow indicates blunt apical spine teeth. Oral view; (C) inner plate of *Talorchestia* species II showing seven apical spine teeth positioned in two rows. Arrow indicates robust serrulate setae. Oral view; (D) petal and simple setae positioned on maxilliped outer plate of *Talorchestia* species II. Arrow indicates chemoreceptive pore. Aboral view; (E) maxillipedal palp segments 3 and 4 showing intermeshed simple and elongated petal setae of *Talorchestia* species II. Aboral view; (F) maxillipedal palp segments 3 and 4 of *K. vulgaris*. Arrow indicates branched elongated simple setae. Aboral view. ep, epistome; ip, inner plate; la, labrum; mp, maxilliped; op, outer plate; p, palp; ps, petal setae; ss, simple setae; 3, 3rd palp segment; 4, 4th palp segment. Scale bars: A, 143  $\mu\text{m}$ ; B, 15  $\mu\text{m}$ ; C, 14  $\mu\text{m}$ ; D, 4  $\mu\text{m}$ ; E, 35  $\mu\text{m}$ ; F, 22  $\mu\text{m}$ .



**Figure 2.** Scanning electron micrographs of second and first maxillae and mandibles: (A) outer and inner plate of second maxillae of *Keratroides vulgaris*. Arrow indicates robust pappose setae. Oral view. Inset, inner plate lateral setal margin showing simple setae. Scale, 19  $\mu\text{m}$ ; (B) second maxillae outer plate of *Talorchestia* species I, showing dorsal setal margin. Arrow indicates chemoreceptive pore. Aboral view; (C) long comb setae positioned on the dorsal margin of second maxillae of *Talorchestia* species II. Oral view; (D) first maxillae of *K. vulgaris*, showing palp and outer and inner plate. Oral view; (E) robust apical setae on first maxillae of *K. vulgaris*. Aboral view; (F) left mandible of *T. marmorata*. Lateral view. ab, accessory blades; cu, cuspidate setae; ip, inner plate; ipr, incisor process; lm, lacinia mobilis; mp, molar process; op, outer plate; p, palp; sc, short comb setae; ser, serrate setae. Scale bars: A, 68  $\mu\text{m}$ ; B&C, 12  $\mu\text{m}$ ; D, 78  $\mu\text{m}$ ; E, 18  $\mu\text{m}$ ; F, 130  $\mu\text{m}$ .

**Table 1.** Structural characteristics of the mouthparts of four species of talitrid amphipod.

	<i>Talorchestia</i> species II	<i>Talorchestia marmorata</i>	<i>Talorchestia</i> species I	<i>Keratroides vulgaris</i>
Habitat	Low shore	Strandline	High shore	Forest
<b>Maxilliped</b>				
Inner plate	7 apical spine teeth	3 apical spine teeth	3 apical spine teeth	3 apical spine teeth
Outer plate	Broad, distally truncate	Broad, distally truncate	Broad, distally truncate	Narrow, tapering distally
<b>Mandible</b>				
Left lacinia mobilis	Symmetrical 5-dentate	Symmetrical 5-dentate	Symmetrical 4-dentate	Symmetrical 4-dentate
Incisor process	7-teeth	6-teeth	5-teeth	5-teeth
Molar process	173 $\mu\text{m}$ (W) $\times$ 99 $\mu\text{m}$ (L) 31 transverse spine ridges	198 $\mu\text{m}$ (W) $\times$ 114 $\mu\text{m}$ (L) 34 transverse spine ridges	207 $\mu\text{m}$ (W) $\times$ 113 $\mu\text{m}$ (L) 24 transverse spine ridges	266 $\mu\text{m}$ (W) $\times$ 149 $\mu\text{m}$ (L) 21 transverse spine ridges

#### First maxillae

The first maxillae are located anterior to the second maxillae, and consist of an inner and outer plate, the latter bearing a short palp (Figure 2D). The prominent feature of the first maxillae is the presence of apical setae on the distal margin of the outer plate (Figure 2E). The apical setae of all species are morphologically similar and curve distally toward the centre of the oral cavity (Figure 2E).

#### Mandible

The mandibles lie between the upper and lower lip, forming a transverse biting mechanism. As in all talitrid amphipods, the mandibles lack a mandibular palp, and the medial surface of all species bear well-developed molar (proximal) and incisor (distal) processes. Lying between these tritulative structures are a series of accessory blades and a lacinia mobilis (Figure 2F).

The incisor processes of all four species are highly calcified, consisting of a series of lateral and dorsal teeth. The incisors of *Talorchestia* species I and *K. vulgaris* are similar in structure with five teeth in total, all of which are distally rounded. The number of incisor teeth of both *T. marmorata* and *Talorchestia* species II are both reduced to four (Table 1); however, the teeth are considerably sharper than that of *Talorchestia* species I and *Keratroides vulgaris*.

The right lacinia mobilis of *Talorchestia* species I and *Talorchestia* species II branches into two overlapping tritulative structures (Figure 3A,B). The distal and proximal branch of both species carries an inner arrangement of small teeth, which are bordered laterally by two larger teeth (Figure 3A,B). The teeth of *Talorchestia* species II are considerably sharper and are more abundant on both branches than that of *Talorchestia* species I (Figure 3B).

#### Upper lip (labrum)

The labrum of all species is shallow and broad, forming the anterior margin of the oral cavity. Similar morphology is displayed by all species; except that cuspidate setae are confined to the epistome of *Talorchestia* species I rather than emerging from the labrum as in the other three talitrid species examined (Figure 3D).

#### Lower lip (paragnath)

The lower lip lies ventrally to the mandibles; the outer lobes form the posterior margin of the oral cavity. The

outer lobes are broad and the apical and medial margins are heavily setose with a combination of both simple and serrate setae. The general morphology of the lower lip is similar among all species, except that emerging from the lateral surface of the inner plate of *K. vulgaris* are distinct hamate setal clusters (Figure 3E).

#### Structure of the digestive tract

The digestive tract of talitrid amphipods can be divided into three distinct regions, the foregut, midgut and hindgut. The foregut is subdivided into an oesophagus and proventriculus, the latter being divided further into cardiac and pyloric chambers (Figure 4A). The midgut is the longest region of the digestive tract, consisting of an anterior dorsal caecum, a pair of lateral pyloric caeca, two pairs of digestive caeca, and one pair of posterior caeca. From the termination of the midgut the hindgut extends through the abdomen to a posteriorly positioned anus.

#### Foregut (oesophagus)

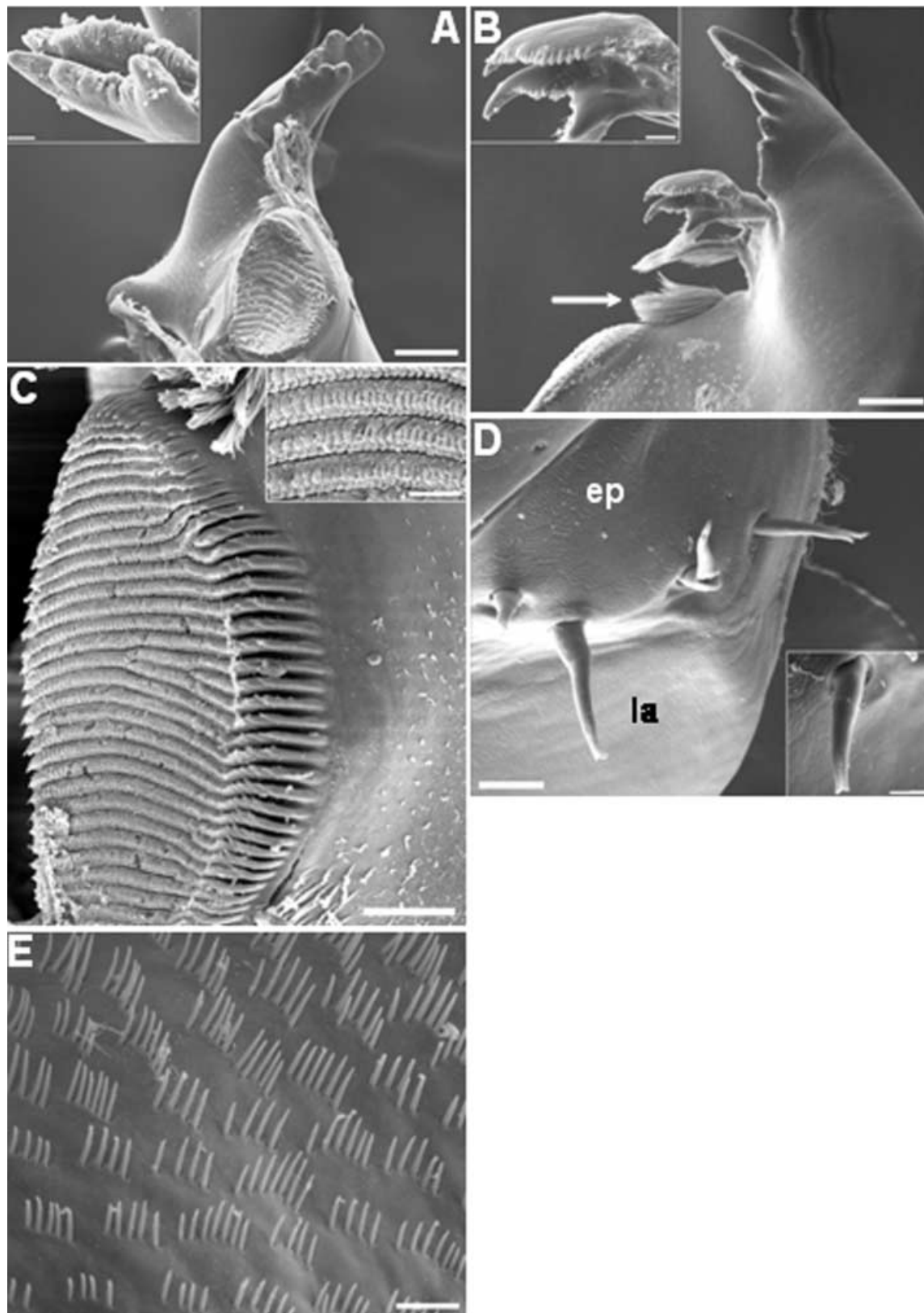
The oesophagus leads from the mouth to the anterior end of the cardiac stomach. The cuticle and underlying epithelium of the oesophagus are elaborated at the oesophagus–cardiac chamber junction to form a pair of lateral folds. These folds, the ampullae, bear stout spines (Figure 4B). The spines are arranged in two parallel rows, with smaller spines positioned anteriorly and larger more robust spines posteriorly (Figure 4B). Positioned posteriorly to the ampullae at the anterior region of the cardiac chamber are long dorsally directed setae, which extend from the cuticle, creating a setose screen (Figure 4C).

#### Cardiac stomach

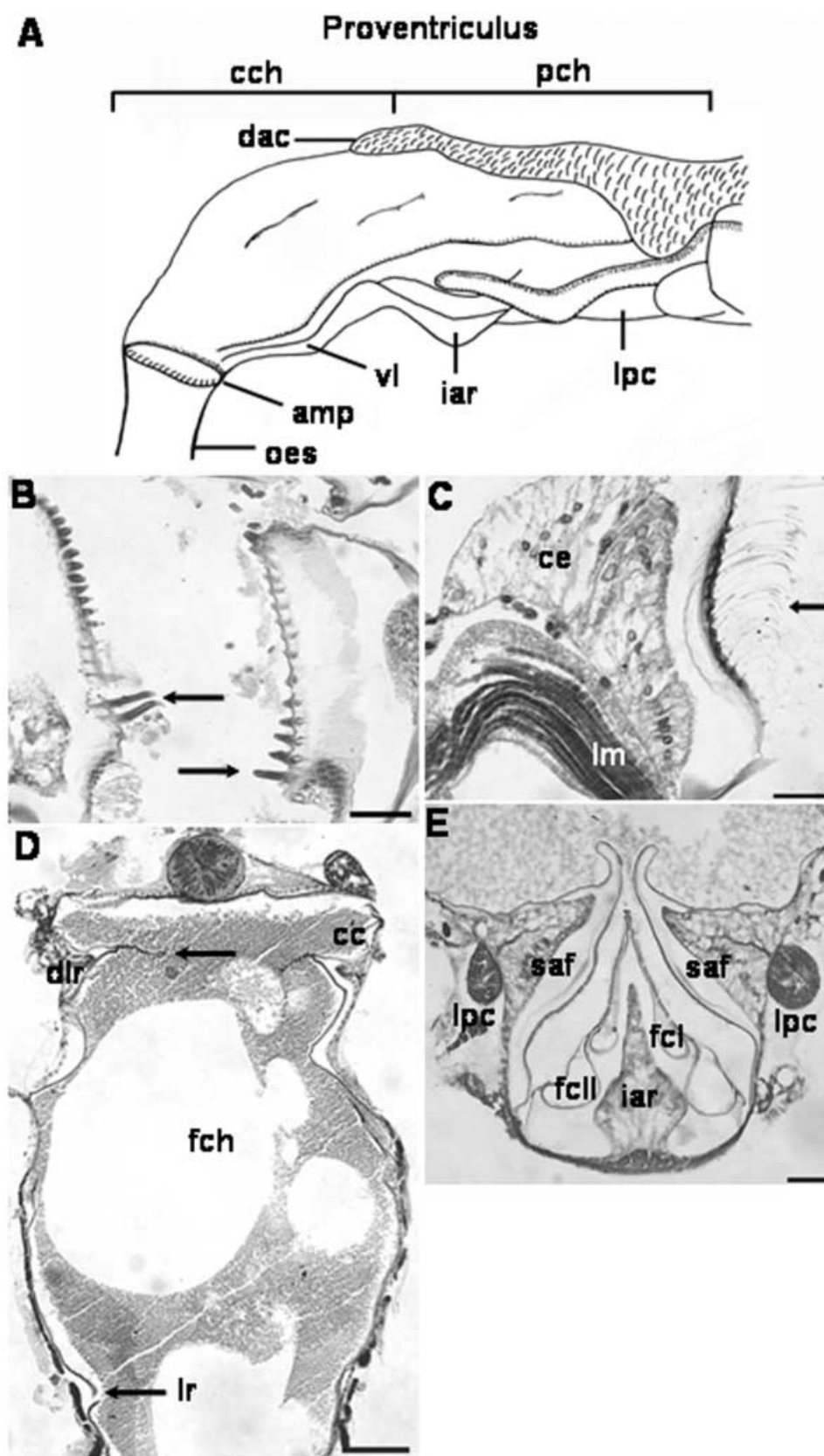
The cardiac stomach is divided into food and circulation channels, formed by infoldings of the cardiac epithelial wall, primarily paired lateral, and dorso-lateral ridges (Figure 4D). The dorso-lateral ridges arise from the anterior cardiac stomach and extend into the midgut. The dorso-lateral ridges bear a single long calcified spine which separates the food channel from adjacent circulation channels (Figure 4D).

#### Pyloric stomach

The pyloric stomach is separated into dorsal and ventral chambers by interlocking setae of the ventro-lateral ridge. The filter press, positioned ventrally, is formed by a

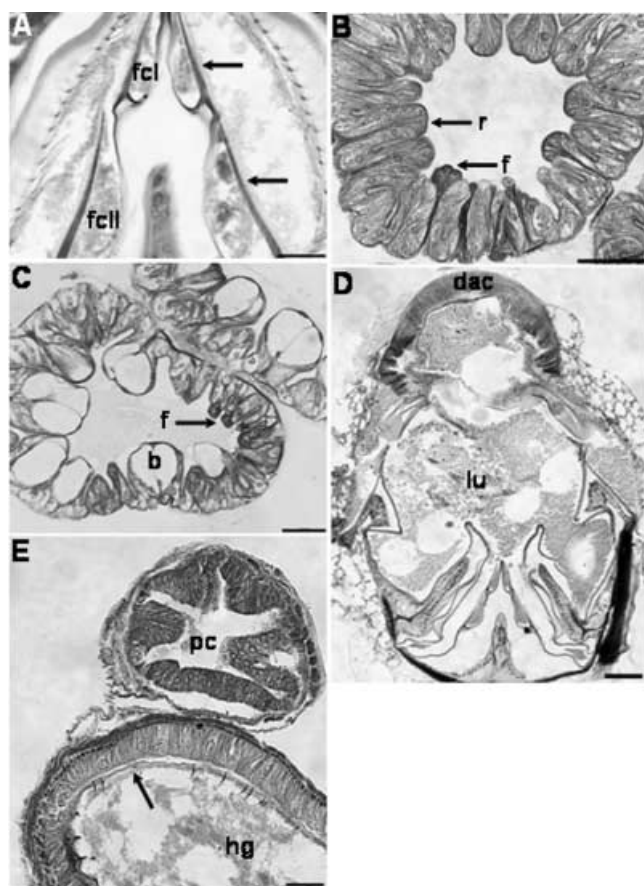


**Figure 3.** Scanning electron micrographs of mandibles and upper and lower lip: (A) left mandible of *Talorchestia* species I. Lateral view. Inset, right lacinia mobilis. Scale, 10  $\mu\text{m}$ ; (B) right mandible of *Talorchestia* species II. Arrow indicates simple setal tuft enveloping molar process. Lateral view. Inset, right lacinia mobilis. Scale, 12.5  $\mu\text{m}$ ; (C) molar process of *T. marmorata*. Lateral view. Inset, triturative area of molar process. Scale, 9  $\mu\text{m}$ ; (D) epistome and labrum of *Talorchestia* species I. Dorsal view. Inset, robust cuspidate setae. Scale 7  $\mu\text{m}$ ; (E) hamate setal clusters of the lower lip of *Keratroides vulgaris*. Dorsal view. ep, epistome; la, labrum. Scale bars: A, 99  $\mu\text{m}$ ; B, 58  $\mu\text{m}$ ; C, 35  $\mu\text{m}$ ; D, 13.5  $\mu\text{m}$ ; E, 8  $\mu\text{m}$ .



**Figure 4.** Histological sections of cardiac and pyloric stomach: (A) lateral internal view of anterior region of the foregut. Left is anterior (Not to Scale); (B) transverse section (TS) through oesophagus of *Talorchestia marmorata*. Arrows indicate ampullae spines; (C) TS through posterior oesophagus, showing columnar epithelium of *Talorchestia* species I. Arrow indicates filtering setae; (D) TS through anterior cardiac stomach, showing dorso-lateral and lateral ridges of *Keratroides vulgaris*. Arrows indicate dorso-lateral spine and positioning of lateral ridge; (E) TS through filter press of *Talorchestia* species II. amp, ampullae; cc, circulation channel; cch, cardiac chamber; ce, columnar epithelium; dac, dorsal anterior caecum; dlr, dorso-lateral ridge; fch, food channel; fcl, first filter channel; fcll, second filter channel; iar, interampullary ridge; lpc, lateral pyloric caeca; lr, lateral ridge; lm, longitudinal muscle; oes, oesophagus; pch, pyloric chamber; saf, supra-ampullary fold; vl, ventro-lateral ridge. Scale bars: B, 30  $\mu$ m; C, 20  $\mu$ m; D&E, 100  $\mu$ m.

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**Figure 5.** Histological sections of filter press, midgut caeca and hindgut: (A) TS of filter press of *Keratroides vulgaris*. Arrows indicate arrangement of setae on interampullary ridge; (B) TS through posterior digestive caeca of *Talorchestia* species I (mercuric bromophenol blue). Arrows indicate R- and F-cells; (C) TS showing F-cells and B-cells of *Talorchestia* species I (mercuric bromophenol blue). Arrow indicates F-cells; (D) TS through posteriorly positioned dorsal anterior caecum of *Talorchestia* species I; (E) TS through distally positioned posterior caeca and hindgut of *T. marmorata*. Arrow indicates cuticle integument. b, B-cell; cut, cuticle; dac, dorsal anterior caecum; f, F-cell; fcl, first filter channel; fcII, second filter channel; hg, hindgut; lu, lumen; pc, posterior caeca; r, R-cell. Scale bars: A, 25  $\mu\text{m}$ ; B, 75  $\mu\text{m}$ ; C, 70  $\mu\text{m}$ ; D, 100  $\mu\text{m}$ ; E, 50  $\mu\text{m}$ .

prominent interampullary ridge and paired supra-ampullary folds (Figure 4E). Both dorsal and ventral epithelial borders of the supra-ampullary folds are covered with fine setae (Figure 5A). The lining of the interampullary ridge is folded, giving rise to two longitudinal groves or filter channels (Figures 4E & 5A). The outer lateral surfaces of both filter channels are guarded by dense short setae, which typically form a setal screen (Figure 5A). Circular and longitudinal muscle bounds the lateral and ventral walls of the filter press.

#### Midgut and caeca

The midgut is a straight tube, with two pairs of digestive caeca arising from its junction with the foregut. Each digestive caecum is lined with columnar epithelium, bearing a thin microvillous brush border. Three of four cell types were identified according to the scheme of Jacobs (1928): 'Embryonic' cells (E), 'Retzell' cells (R), 'Fibrillar' cells (F) and 'Blasenzell' cells (B). E-cells were

not positively identified in any of the species' but are likely to be present at the distal tips of each of the tubules. F-cells were distinguished from R-cells by an intense dichromatic blue/red colour when stained with mercuric bromophenol blue, indicating large quantities of protein within the cytoplasm (Figure 5B,C) while B-cells were characterized by the presence of a single large central vacuole, which occupied most of the cell volume (Figure 5C).

The dorsal anterior caecum is positioned dorso-laterally to the cardiac and pyloric stomach of the foregut, and extends anteriorly to the junction of the oesophagus and cardiac stomach in all species. The dorsal anterior caecum becomes enlarged anteriorly, enveloping the anterior region of the pyloric stomach, prior to the midgut proper (Figure 5D).

Paired lateral pyloric caeca lie along each side of the pyloric chamber, just lateral to the supra-ampullary folds (Figure 4E). These caeca have only previously been reported in two other gammaridean species of amphipod both in different families and neither from the family Talitridae.

#### Hindgut

The hindgut is lined by a thin cuticle and surrounded by a thick band of circular muscle. Posteriorly, the inner wall of the hindgut bears a large number of small spines, which protrude from the cuticle into its luminal space (Figure 5E).

## DISCUSSION

### *Structure and function of the mouthparts*

Gross structural differences of the mouthparts among the four talitrid species are likely to be associated with their phylogenetic divergence, while setal differences are possibly associated with different dietary preferences. The similarity in the short broad maxilliped segments in the three *Talorchestia* sandhoppers is likely to reflect their close phylogenetic relatedness. Short broad palps characterize all the beachfleas and sandhoppers illustrated by Bousfield (1982), whereas within the Tasmanian landhoppers illustrated by Friend (1987), maxilliped palps range from the narrow elongated form seen in *Keratroides vulgaris* to shorter broader palps similar to those seen in the sandhoppers examined here, and in species such as *Orchestia neambulans* (Friend). It is significant that short broad palps are confined to those landhoppers showing the cuspidactylate condition (i.e. the presence of small cusps on the dactyls of the walking legs (Bousfield, 1984)) since this character has been proposed by Bousfield (1984) to mark a relatively deep phylogenetic division within the landhoppers. This supports the suggestion that the form of the maxilliped palp in these species reflects phylogenetic history rather than recent adaptation to different diets. Nevertheless differences in setation do reflect diet preferences between the three *Talorchestia* species and *K. vulgaris*. The elongated simple setation of the maxilliped palp of *K. vulgaris* may aid in lifting leaf litter off the forest floor by gripping the epidermal tissue of leaves. The presence of short, simple and petal setae on the maxilliped palp on all three *Talorchestia* species suggests an additional role of these setal types to simply acquiring food items. It is possible that they have a brushing and sorting function to prevent sand from entering the preoral cavity, a role described for similar setae in slipper lobster (Johnston, 1995).



The number of apical spine teeth on the maxilliped inner plate differed between the low shore diatom feeding talitrid, *Talorchestia* species II, in which seven sharp teeth were observed, to three broader apical spine teeth in *T. marmorata*, *Talorchestia* species I, and *K. vulgaris*. The greater number of apical spine teeth in *Talorchestia* species II is likely to be a derived phylogenetic trait that evolved in response to its specialized diatom diet through the need to pierce the hard outer siliceous frustule of diatoms.

The triturative surface of all species' mandibular molars consisted of a series of transverse spine ridges. The relative length and width of the triturative surface of the molar process increased in each of the species with increasing landward habitat, whilst the number of spine ridges decreased (Table 1). This suggests that structural changes in the molar process are likely to be associated with diet. The reduction in size of the molar process and increased number of spine ridges in *Talorchestia* species II compared with the other species may reflect a need to further triturate the siliceous frustule of diatoms. The smaller area of the triturative surface would also increase the internal pressure that the spine ridges exert on one another, allowing harder food materials to be adequately triturated via a crushing action. A reduction in spine ridge number in *T. marmorata*, *Talorchestia* species I and *K. vulgaris*, coinciding with both an increase in length and width of the molar surface suggests that there is a shift from crushing to a grinding action, which is likely to be associated with the shift in diet. A grinding action would collectively promote an efficient breakdown of the cellulose matrix of both spinifex grasses and leaf litter; diets that are typical of terrestrial habitats where cellulose is the primary component of their chemical composition.

Variation in structure of the mandibular laciniae occurred only on the right lacinia mobilis of *K. vulgaris* and *T. marmorata*. As in all talitrid amphipods the left and right laciniae mobiles of these species were asymmetrical, the left bearing four or five blunt, regular teeth while the right carried sharper, more complex dentition. The variation in structure of the right laciniae mobiles between species appears to be related to dietary differences among the species and not influenced by their evolutionary lineage. The lack of sharp dentition on the right laciniae mobiles of both *K. vulgaris* and *T. marmorata* appears to reflect the softer food items ingested by both these species, while the stout denticulations on the anterior edge of the right laciniae mobiles of *Talorchestia* species I and *Talorchestia* species II perhaps produce greater laceration in response to physically harder dietary items such as spinifex and diatoms.

The upper and lower lips of all species were morphologically similar. However, distinct hamate setal clusters ranging from 4–7 setae were evident on the lateral surface of the lower lip of *K. vulgaris*. It is likely that these setal clusters aid in the retention of food particles which may otherwise be lost from the triturative process of the mandibles.

Pores with chemoreceptive characteristics (McIver, 1975) were observed on the distal tips of the simple cuspidate setae lining the maxilliped outer plate of *Talorchestia* species II and second maxillae outer plate of *Talorchestia* species I. The presence of chemoreceptive pores suggests that these talitrids are not feeding indiscriminately on any marine or terrestrial debris that has washed or blown into their respective habitats.

#### Structure and function of the digestive tract

Unlike the mouthparts, the structure of the digestive tract was highly conserved, presumably a result of the four species' close phylogenetic lineage. The posterior region of the oesophagus of each species was lined by a complex array of ampullae spines. It would appear from their calcified structure and their close association with the surrounding musculature that the ampullae spines constitute a mechanism by which food particles are further triturated (Martin, 1964). This would collectively benefit filtration and assimilation, as each of these species has a distinct lack of triturative structures within their cardiac stomach, especially on the lateral ridge, compared with freshwater amphipods such as *Hyalella azteca* (Saussure) (Schmitz & Scherrey, 1983). The spines of the lateral ridge are assumed to be the primary triturative component of the cardiac stomach in most gammaridean species of amphipod. Crustacean species which have well developed triturative structures within the cardiac chamber presumably do not need to achieve efficient trituration by their mouthparts (Vonk, 1960). Thus, all four talitrid species appear to have compensated for this structural deficiency by developing well equipped mouthparts which have become modified accordingly to each species' dietary preference. They also have an elaborate array of ampullae spines to reduce further the food particles for efficient filtration and assimilation within the pyloric stomach and digestive caeca. Thus, the absence of spines on the lateral ridge appears not to reflect specific dietary preferences of these four closely related species, but rather is influenced by their close phylogenetic lineage.

The structure of the filter press of the pyloric stomach was similar to that described by Icery & Nott (1984) in the amphipod *Corophium volutator* (Pallas). However, the musculature associated with filtration was different and similar to the filtration processes described in the amphipod *Hyalella azteca* (Schmitz & Scherrey, 1983). The thin layer of circular muscle on the ventral wall of the filter press, which previously has only been described in the amphipod *Hyalella azteca* (Schmitz & Scherrey, 1983) would appear to aid the laterally inserted V-shaped muscle groups by reducing the total free area within which the food particles can move within the filtration chamber, therefore maximizing filtration efficiency within the pyloric stomach.

Enzyme secreting F-cells were distinguished in each of the four talitrid species from R-cells by an intense positive reaction of the F-cells to mercuric bromophenol blue, a histochemical stain for protein. Cytological evidence suggests that the F-cells, located within the digestive caeca of amphipods secrete the digestive enzymes, as they show an abundance of rough endoplasmic reticulum and free ribosomes, organelles associated with the secretion of digestive enzymes (Schultz, 1976; Schmitz & Scherrey, 1983).

The dorsal anterior caecum is characteristic of the amphipod digestive tract (Agrawal, 1964). A possible salt resorptive function for the dorsal anterior caecum was suggested by Schmitz (1967), due to the presence of densely arranged columnar epithelium. Such a functional role for this caecum has not been proved, but it appears from a negative reaction of the cells within this caecum to mercuric bromophenol blue that it is not secretory in function.

Paired lateral pyloric caeca have been documented previously in only two other amphipod species, *Hyaella azteca* and *Gammarus lacustris lacustris* (Say) (Schmitz, 1967; Schmitz & Scherrey, 1983). Positioned on opposing sides of the filter press the presence of such caeca in the species studied here differs from the typical gammaridean body plan. The cells within this caecum, when stained with mercuric bromophenol blue, produced a negative reaction; therefore they are not secretory in function. Schmitz (1967) and Schmitz & Scherrey (1983) both postulated that these caeca may be salt resorptive in function as the epithelium was densely packed. Whilst freshwater amphipods, such as *Hyaella azteca* and *Gammarus lacustris lacustris*, and also fully terrestrial amphipods such as *K. vulgaris* would benefit from a salt resorption system based in these caeca in order to retain ions in these ion-depleted habitats, this would be less problematic for supralittoral species, such as the three *Talorchestia* species investigated here. Indeed for some of the high shore amphipod species, periodic hyperosmotic stress and thus excess ions, due to desiccation, for example, may be equally problematic. Further cytological evidence of the epithelium and surrounding cell types within this caecum is needed to gain a further functional understanding of the role this caecum.

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