Comparative Morphology of Cephalothoracic Feeding Appendages of Three Co-occurring Mysids (Crustacea: Mysidacea) from South-Eastern Tasmania

EPHRIME B. METILLO

Abstract

The endopods and mouthparts morphological data from three co-existing mysid species indicate three major feeding adaptations: predominantly macrophagous feeding on tough macrophyte particles (type a) for ***Tenagomysis tasmaniae,*** *predominantly macrophagous feeding on large animal prey/detritus (type b) for* ***Paramesopodopsis rufa****, and mainly microphagous and/or suction feeding on smaller animal prey and fine particulate matter (type c) for* ***Anisomysis mixta australis****. These feeding specializations are evidence of feeding niche partitioning which in part explain the co-occurrence of the three mysids.*

Introduction

According to the ***Bauplân*** (the German word for a structural design) concept, invertebrates are constrained by their structural plans particularly in their functioning, behaviour, and overall interaction with the environment (Brusca and Brusca 1990). These sets of body plans have allowed invertebrates to exploit almost all types of habitats and the food items present in those habitats. For instance, the feeding mechanisms of invertebrates vary considerably particularly in capture and digestion (Levinton, 1982; Barnes *et al.*, 1988). The competition theory assumes that competition influences phenotypic variations in organisms during their evolution (Schoener, 1974, 1982, 1989). Therefore, the ***Bauplâne*** of invertebrates may be perceived as a consequence of competition. Although similarities of basic and/or gross structures could be expected, subtle morphological differences would also be apparent particularly among

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competing species that require a very similar range of food types, and are found in similar habitats. As a means of alleviating competition, the feeding niche dimension may be partitioned by obvious and slight differences in feeding structures and associated feeding mechanisms (Schoener, 1974; Caine, 1974, 1977; Wagner and Blinn, 1987).

Studies of mysid diets by gut content analysis have generally revealed a broadly omnivorous feeding habit however with tendencies toward carnivory, herbivory and/or detritivory (e.g. Nath & Pillai, 1973; Siegfried and Kopache, 1980; Mauchline, 1980; Wooldridge and Bailey, 1982; Zagursky and Feller, 1985; Webb and Wooldridge, 1989). In addition to qualitative accounts of food items by gut content analysis, morphological investigation of feeding apparatus is required to fully understand feeding habits and ecology of organisms (Anraku and Omori, 1969; Kunze and Anderson, 1979; Webb and Wooldridge, 1989; Ohtsuka and Onbe, 1991). Webb and Wooldridge (1989) noted the strong relationship between mouthparts, foregut morphology, and the feeding habits of two co-occurring mysids.

Information from studies dealing with single species cannot readily be applied to other mysid species (Cannon and Manton, 1927; Crouau, 1987, 1989; Mauchline, 1980). As in the case for marine amphipods (Caine, 1977) and in copepods (Vanderploeg, 1990), feeding morphology and behaviour of the group are not expressed in any single species because different species most likely reflect a diversity of feeding mechanisms and feeding structures. A comprehensive comparative study is required to determine their functional significance (Mauchline, 1980).

The Structure of Cephalothoracic Feeding Appendages

Mysids were previously thought to be the closest relatives of euphausiids (the two previously belonged to the same Order Schizopoda), but have now been separated with mysids belonging to Peracarida and euphausiids to the Eucarida. However, mysids show a similar form of feeding appendages with those in euphausiids (Mauchline 1980). One major difference between these groups is that setules and microsetules on the setae on most mysid thoracic endopods are not as elaborate as in euphausiids. In *Mysis relicta*, the setae on the endopods have been suggested to increase efficiency of these appendages in grasping and manipulating large prey (Sierszen *et al.* 1982). The majority of setae with elaborate setulations are found on the mouthparts of mysids. These setae are similar to those in copepods (Tiselius and Jonsson, 1990) with setules concentrated on the base of each seta. This has led previous investigators to conclude that most processing of fine particles may only be occurring in the mouthparts, in particular the first and second maxillipeds (first and second endopods *sensu* Tattersall and Tattersall, 1951), maxillae, maxillules, the labial paragnaths, labrum and the mandibular palps (Mauchline, 1980; Crouau, 1989).

The potential size range of food particles that may be captured by suspension feeding crustaceans may be predicted from the intersetal and intersetular gap measurements. This has been demonstrated in calanoid copepods which utilize their bristled second maxilla in capturing suspended food particles (Boyd, 1976). A similar approach has been useful in elucidating the potential sizes of food particles that can be captured by the thoracic appendages of euphausiids (McClatchie and Boyd, 1983; Hamner, 1988; Mauchline, 1989). The microsetular gaps which can be as fine as 1 to 2 um in euphausiids indicate efficiency at capturing nanoplanktonic cells (McClatchie and Boyd, 1983; Dalley and McClatchie, 1989). Webb and Wooldridge (1989) observed a marked difference in intersetular gap ranges in two co-occurring mysid species which differ in diet.

A close relationship between feeding types and the dentition of the mandible has been shown in calanoid copepods (Anraku and Omori, 1963; Itoh, 1970; Sullivan *et al.*, 1975; Schnack, 1989; Ohtsuka and Onbe, 1991). These studies have shown that the herbivorous species have mandibles with cutting edges provided with grinding teeth, the predatory species possess very sharp teeth, and the omnivorous species possess mandibular dentition intermediate between the other feeding types, i.e. the teeth are heavier than those of the herbivores, but they are not as stout as for predators. The face of the mandibles of mysids and euphausiids show almost identical characteristics except that the spine row and the *lacinia mobilis* are lacking in most adults of the latter and in some lophogastrid mysids (Mauchline 1980). Using scanning electron microscopy, McClatchie and Boyd (1983) examined, the fine structure of the *pars molaris* of *Euphausia superba*. Mauchline (1980) noted that herbivorous feeding in euphausiids is correlated with a large *pars molaris*, and highly predatory with small. This relationship has been demonstrated in some mysids (Mauchline, 1980). In contrast to the well studied Order Euphausiacea, the mouthparts of the more diverse Mysidacea are little studied (Mauchline, 1980; Crouau, 1989).

In the present study, scanning electron (SEM) and light microscopy were used to describe and compare the morphology of the thoracic endopods, and mouthparts of three co-existing Tasmanian mysid species, *Paramesopodopsis rufa* Fenton 1985, *Tenagomysis tasmaniae* Fenton 1991, and *Anisomysis mixta australis* Zimmer 1910. Feeding specializations which may explain food resource partitioning and co-occurrence of these mysid species are examined in detail.

Materials and Methods

Mysid Field Collection and Laboratory Maintenance

The collection and laboratory maintenance of the three mysid species used in the present study are described in detail by Metillo and Ritz (1993).

General Morphological Methods

Adult individuals were cold narcotised before dissections of feeding structures under a binocular dissecting microscope. Mouthparts and stomachs for SEM and whole animals for serial sectioning were fixed for two hours in a solution of 2.5% glutaraldehyde, 0.2M phosphate buffer (pH = 7.3), and 0.14M NaCl. Fixed specimens were each washed three times for 10 minutes each with phosphate buffer followed by post-fixation in 2% osmium tetroxide in 1.25% sodium bicarbonate (pH = 7.2) for two hours. Tissues were washed as before, and rinsed with distilled water. Specimens were then dehydrated by placing them in an ascending series of ethanol concentrations (10 min in each from 10%-100% alcohol).

In contrast to foreguts (Metillo and Ritz, 1994), mouthparts had to be critical point dried as tissue shrinkage occurred with hexamethyldisilazane (HMDS) treatment. Prior to examination, tissues were mounted on aluminium stubs, sputter coated with gold, and examined at an accelerating voltage of 15 kV in a Philips 501 SEM.

Mouthparts for line drawing were dissected from individuals which were fixed in 5% neutral formalin in seawater. Dissected mouthparts were mounted on glass slides with cover slips using polyvinyl lactophenol as mountant, and drawn using a camera lucida attached to a an Olympus microscope. Four pairs of mandibles from adult individuals of each species were examined to detect morphological differences among the three species. The edge index expressed as a ratio of the *pars molaris* longest length to the *pars incisiva* length (Nemoto, 1977) was calculated for each species. Intersetal and intersetular distances of the mouthparts were measured from scanning electron micrographs.

Intersetal gap measurements were made from the five most anterior thoracic endopods of formalin preserved (5% v/v) individuals. The sixth or most posterior endopod was excluded because it mainly functions in grooming reproductive structures. After measuring the total lengths of four specimens from each species, the intact right side endopods were dissected out and mounted in between glass slides and cover slips with polyvinyl lactophenol. Soon after mounting, the gaps were measured using a phase contrast compound microscope with an ocular micrometer. All intersetal gap measurements from the five endopods were pooled, and frequency and cumulative frequency distribution plots were constructed.

Results

The Structure of the Cephalothoracic Feeding Appendages

Basic Structure of the Thoracic Endopods and Mouthparts

The terminology used here is based on Mauchline's (1980) review. The description is from posterior to anterior feeding appendages.

Similar in gross form, the endopods show the basic set of podomeres or segments from proximal to distal: basis, pre-ischium, ischium, merus, carpus, propodus and dactylus (Figure 1). Terminating in an enlarged nail, the three distal segments possess structures associated with the cleaning mechanism (Figure 7E). The majority of setae project from the medial surface of these endopods (Figures 1, 6B).

Although maxilliped II has a similar disposition and curvature (it overlies the ventral face of maxilliped I), the relatively longer length of the merus gives the fused carpo-propodus, and dactylus a more anterior position than the equivalent segments of maxilliped I (Figures 2, 6A, 8A). Maxilliped I shows a similar gross form and is also composed of the basic podomeres (Figure 3). Unlike in the thoracic endopods, these segments are wider and flatter due to the presence of lobes and flat endites. Along with the other mouthparts the pair of maxillipeds I form acute angles with the underside of the thorax (Figures 3; 6A,D; 7A; 8A). The first maxillipeds form a ventral cover of the paired maxillae and maxillules.

The gross form of the paired maxillae is similar (Figures. 4, 7A, 8B). The maxillae are composed of concave thin plates which are in direct contact with the anterior surfaces of the first maxillipeds. Their setae-fringed exite projects out towards the thorax. The maxillary palps touch the ventro-posterior surface of the mandibular body. The setae arming the maxillary palp are different in the three species. Immediately lateral to the maxillary palp are three concave plates or endites, two distal and one proximal. The rows of serrated setae fringing the distal endites lie on the same plane as those of the maxillary palps while the setae on the proximal endite are curved towards the median food groove and lie on the same plane as those of the basal endite.

The maxillule is relatively simple, comprising ventral proximal and dorsal distal endites (Figures 5, 6M) and is similar in the three species. The

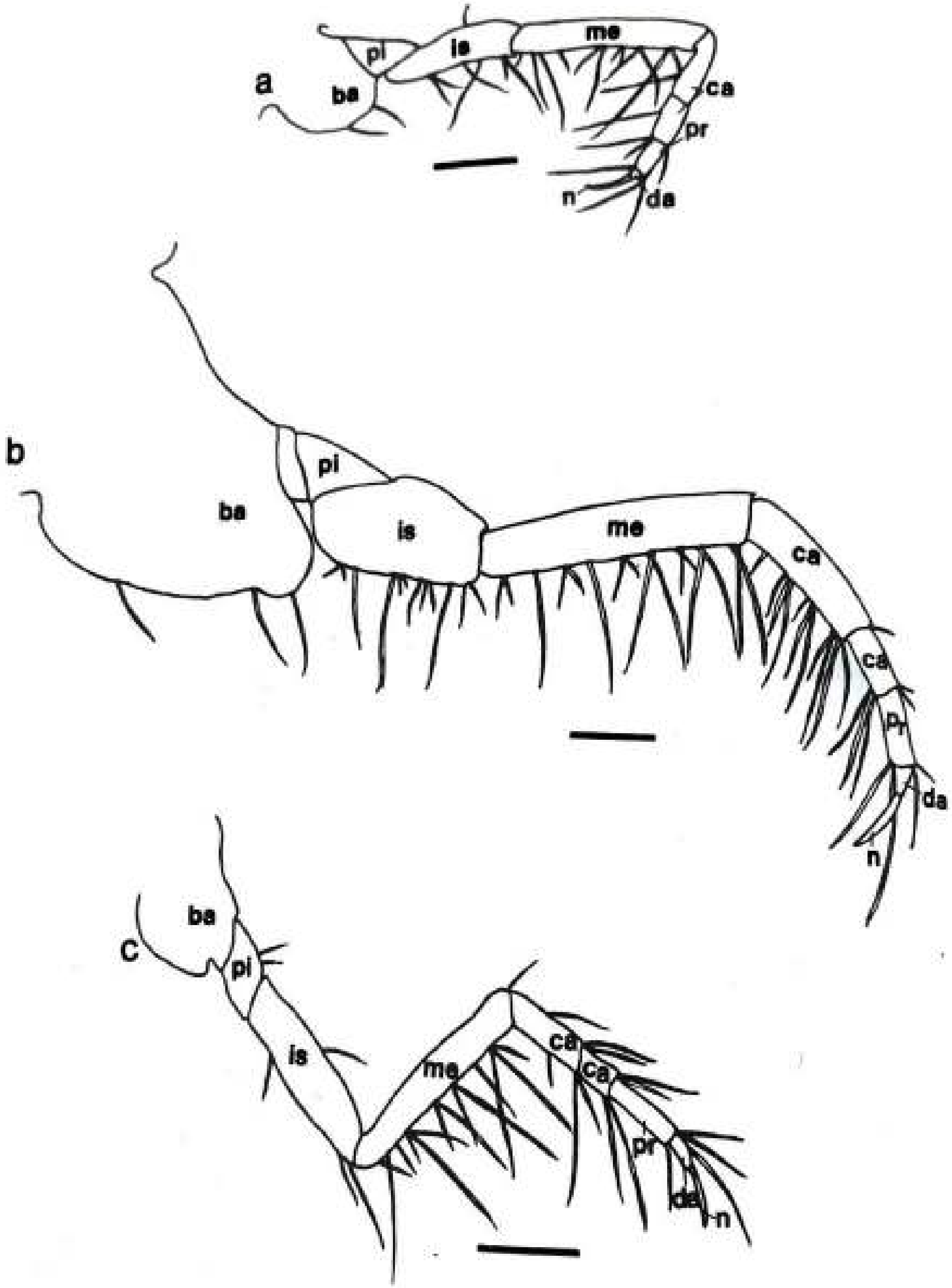


Figure 1. The second thoracic endopods of the three mysid species. a. *Anisomysis mixta australis*: ba-basis, pi-pre-ischium, is-ischium, me-merus, ca-carpus, pr-propodus, da-dactylus, n-nail. b. *Paramesopodopsis rufa* (abbreviations as in a).c. *Tenagomysis tasmaniae* (abbreviations as in a). Scale bars = 0.2 mm.

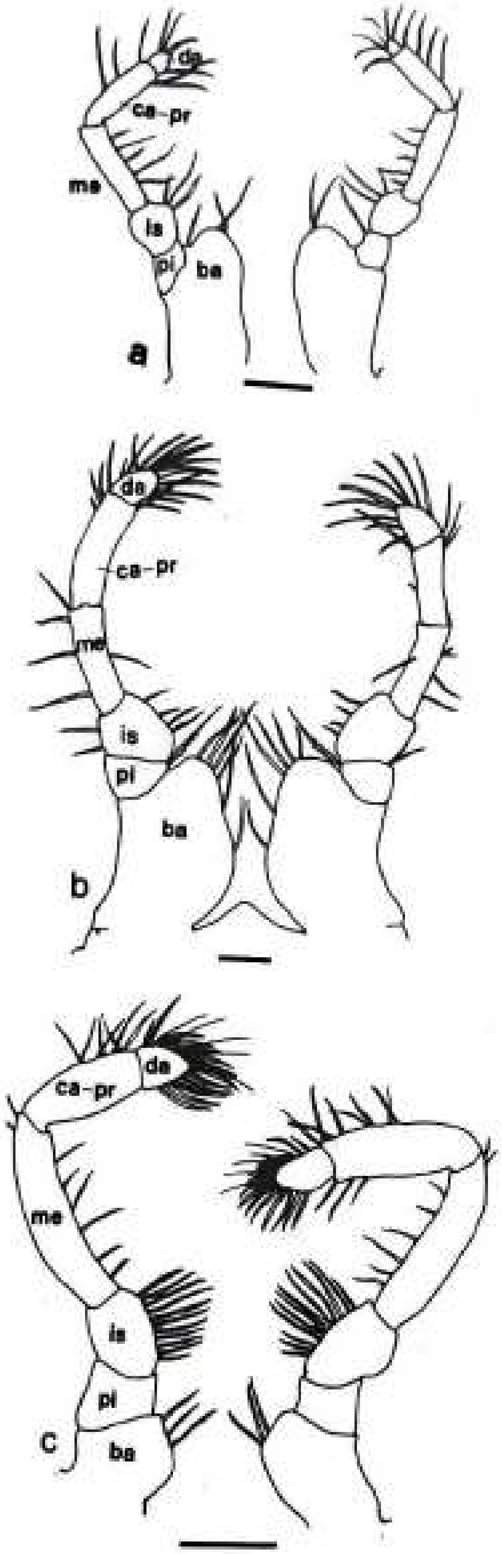


Figure 2. The maxilliped II of the three mysid species. a *Anisomysis mixta australis:* ba-basis, pi-ischium, is-ischium, me-merus, ca-pr-carpo-propodus, da-dactylus, n-nail. b. *Paramesopodipsis rufa:* (abbreviations as in a). c. *Tenagomysis tasmaniae* (abbreviations as in a). Scale bars = 0.2mm.

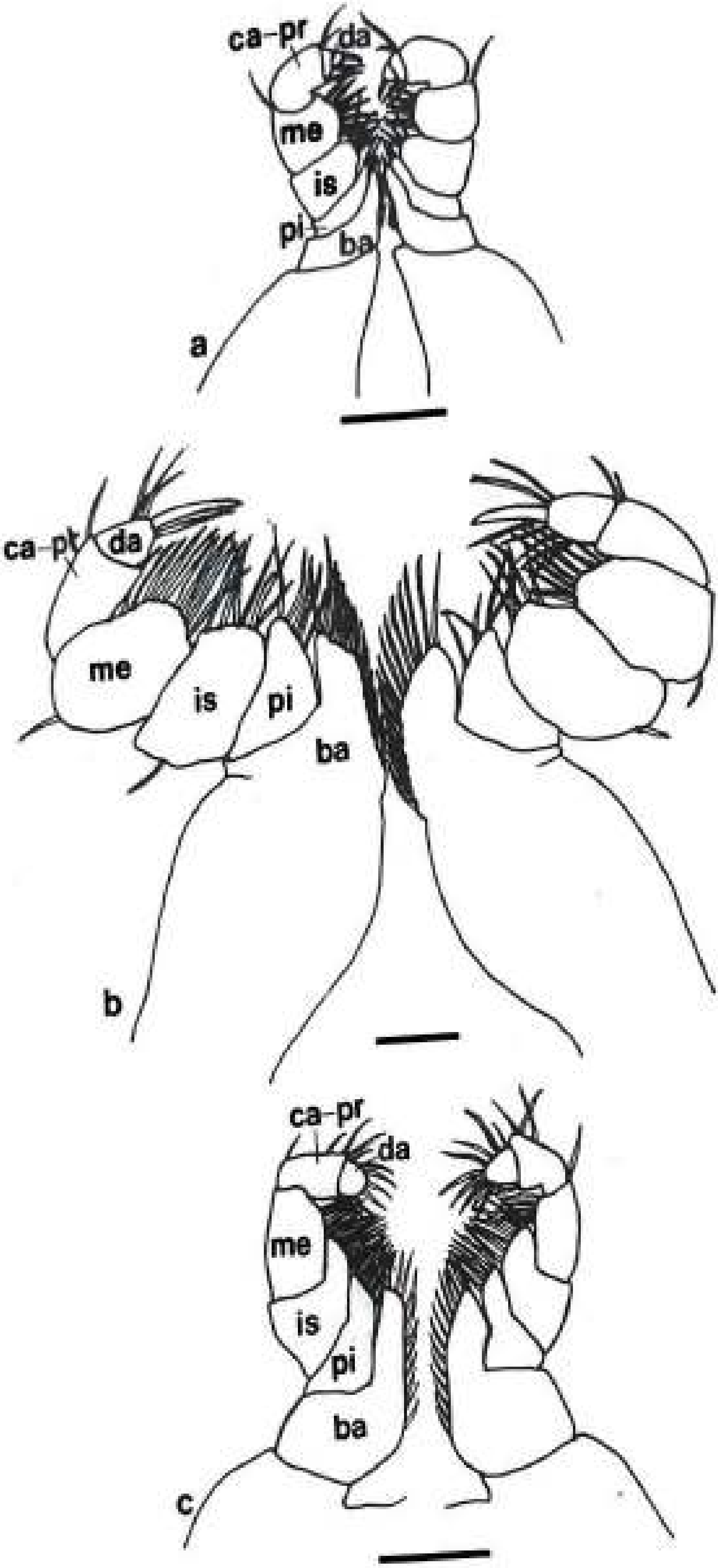


Figure 3. The maxilliped I of the three mysid species. a. *Anisomysis mixta australis;* ba-basis, pi-pre-ischium, is-ischium, me-merus, ca-pr-carpo-propodus, da-dactylus, n-nail. b. *Paramesopodopsis rufa:* (abbreviations as in a). b. *Tenagomysis tasmanie* (abbreviations as in a). Scale bars = 0.2mm.

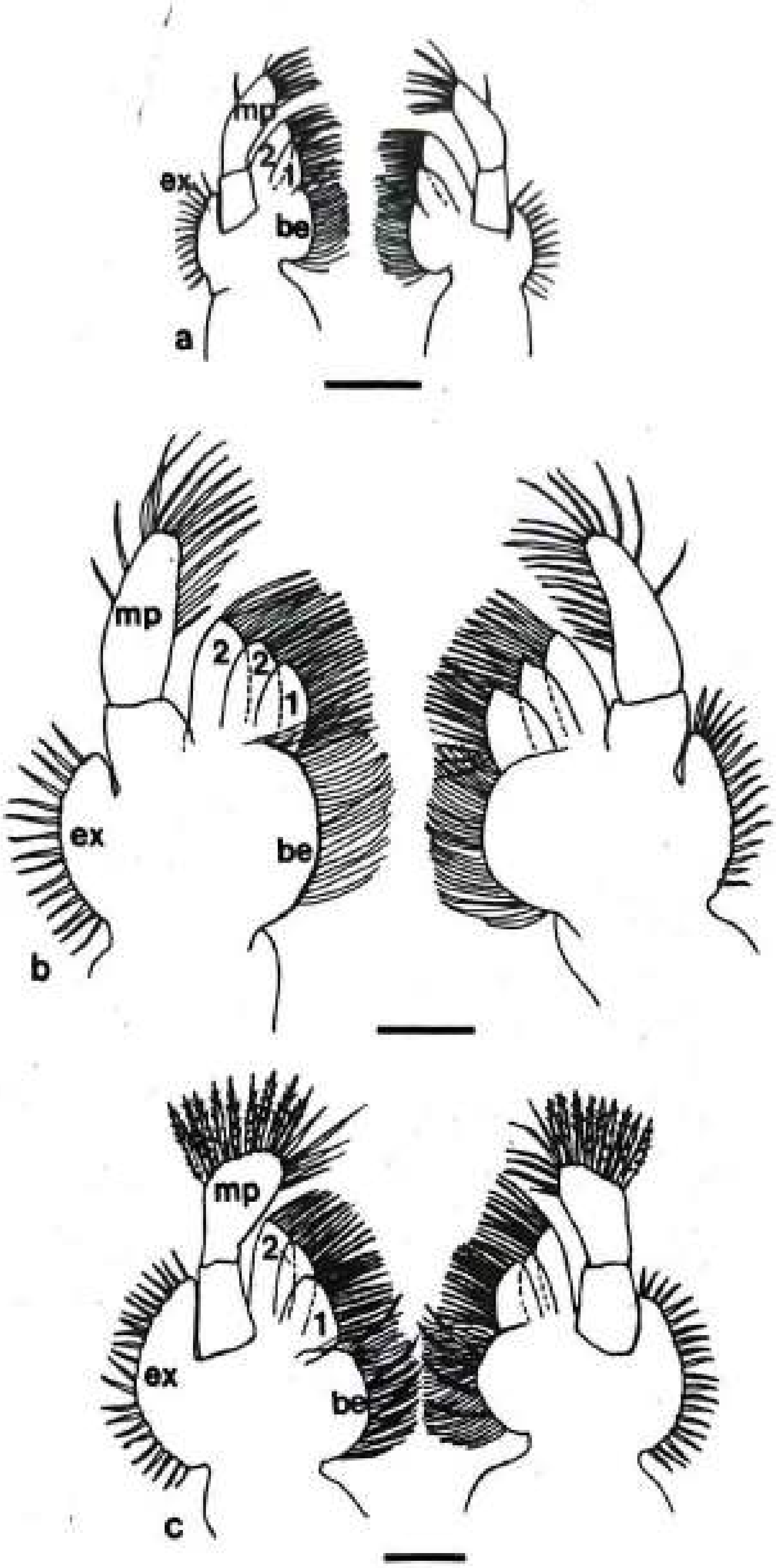


Figure 4. The maxilla of the three mysid species. a. *Anisomysis mixta australis*: mp-maxillary palps, ex-exite, be-basal endite, 1-proximal endite, 2-distal endites, b. *Paramesopodopsis rufa*: (abbreviations as in a). c. *Tenagomysis tasmaniae* (abbreviations as in a). Scale bars = 0.2mm.

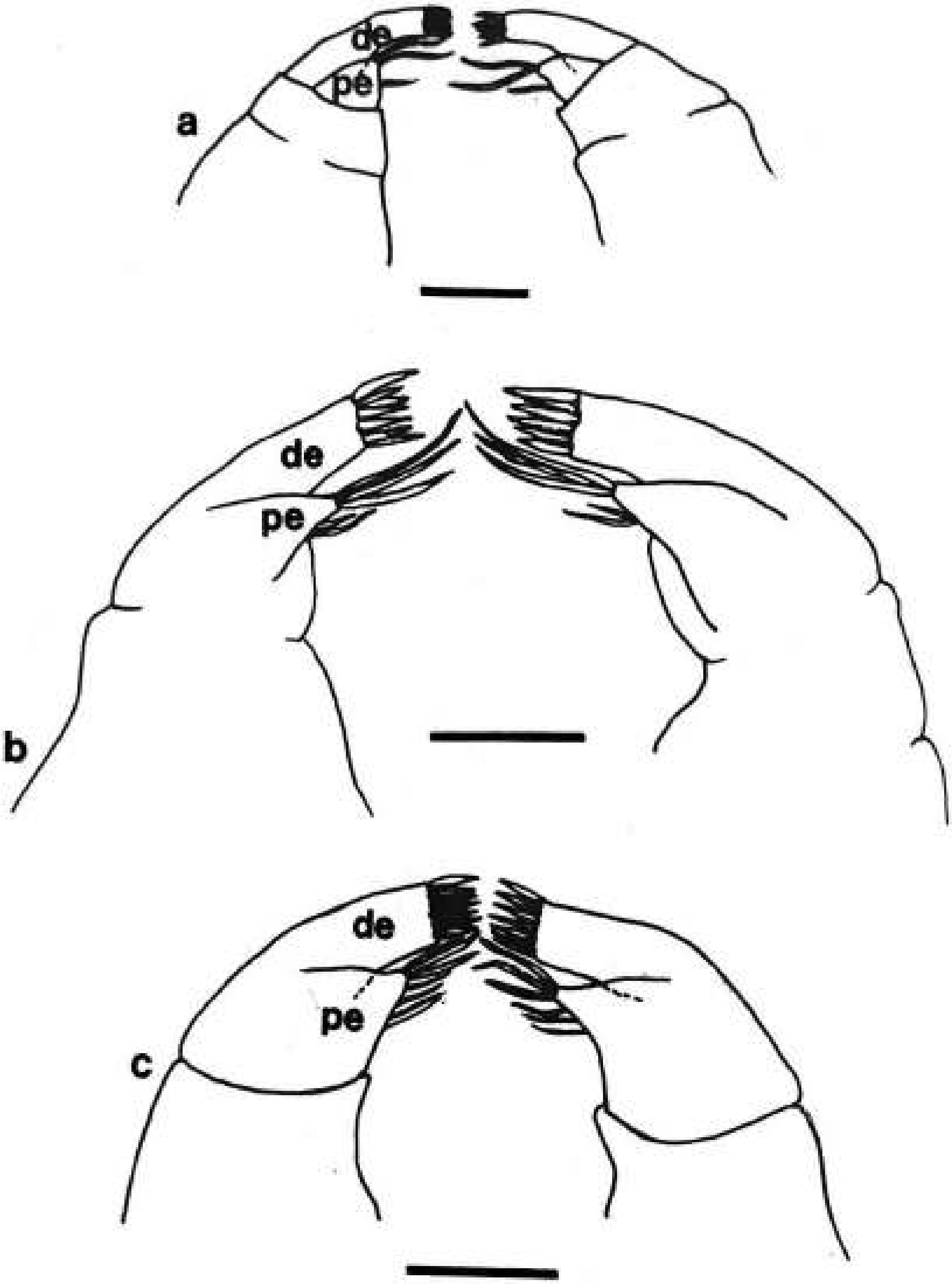


Figure 5. The maxillules of the three mysid species. a. *Anisomysis mixta australis:* pe-proximal endite, de-distal endite. b. *Paramesopodopsis rufa:* (abbreviations as in a). c. *Tenagomysis tasmaniae* (abbreviations as in a), Scale bars=0.2mm.

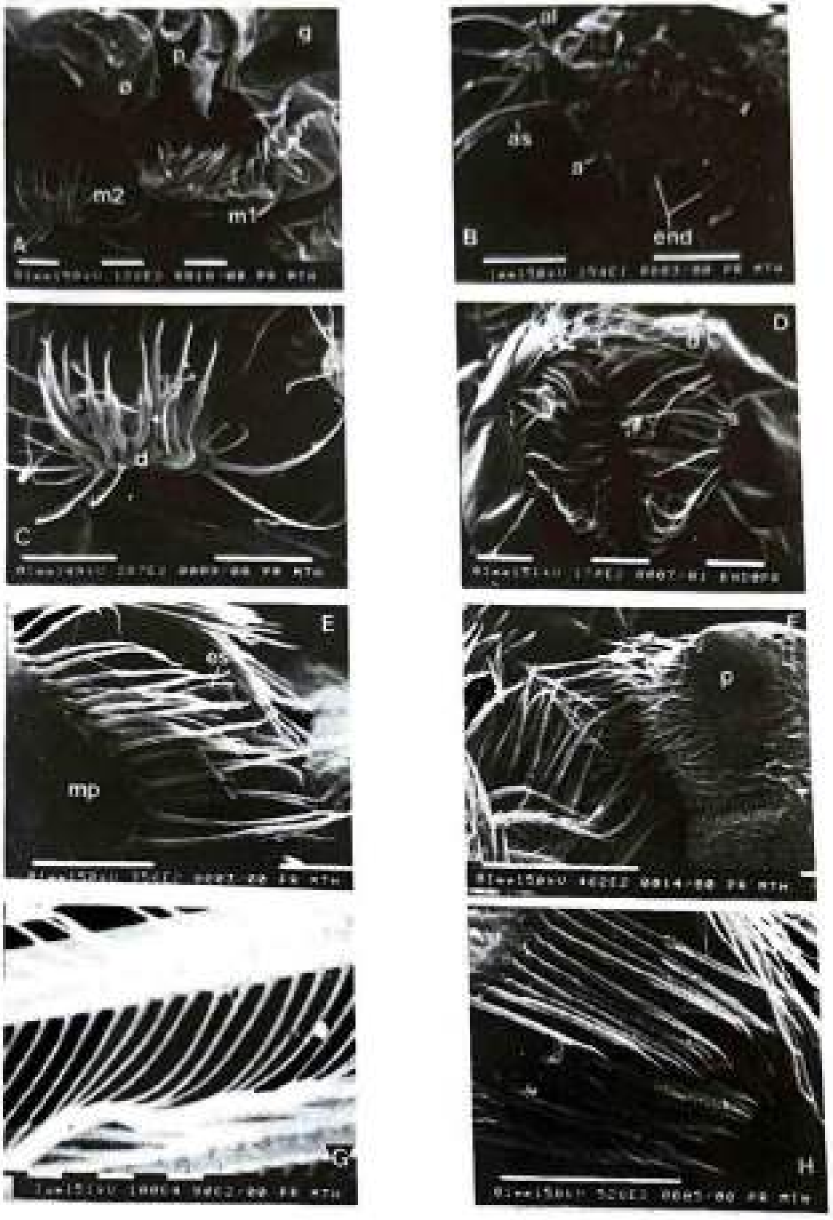
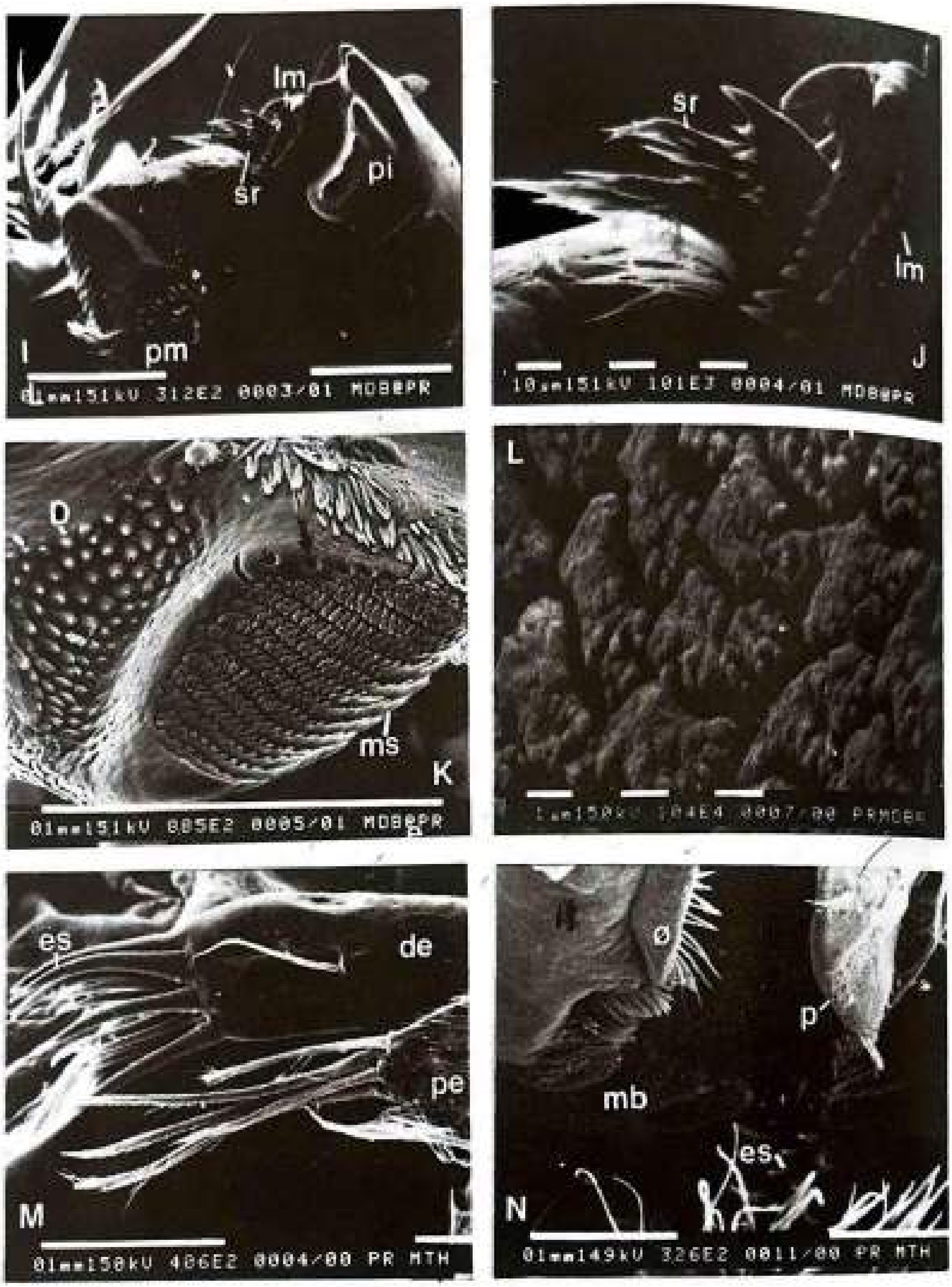


Figure 6. SEM micrographs of *Paramesopodopsis rufa* mouthparts. A. Median lateral view of right side mouthparts: g-median groove of labium, ml-maxilliped I, m2-maxilliped II, p-labial paragnaths, 0-labrum. B. Median sagittal of anterior half of the animal showing cephlothoracic appendages; a - antenna, al - antennule, as - antennal scale, end - right endopods. C. Close-up of maxilliped II dacytylus (d): + - stout sharp spines. D. Ventral view of Maxillipeds I: d-dactylus, + stout sharp spines - plumose setae E. Close-up of labial paragnaths (p). G. Fine structure of setules on setae of maxillary proximal endite. H. Serrated setae on distal endites of maxilla. I. Left mandible armed edge: lm-*lacinia mobili*, pi-*pars incisiva*, om-*pars molaris*, sr-spine row. J. Close up of *lacinia mobilis* (lm) and spine row (sr). K. Close of *pars molaris*: D-region, ms-marginal spines, arrow points pore on the margin of grinding region. L. Fine structure of the grinding region teeth. M. Appendages of the left maxillule: de-distal endite, es-spines of the dorsal endite, pe-proximal endite. N. Close up of right mouthparts: es-spines of the maxillular distal endites, mb- right mandible, p-labial paragnaths, 0 - labrum.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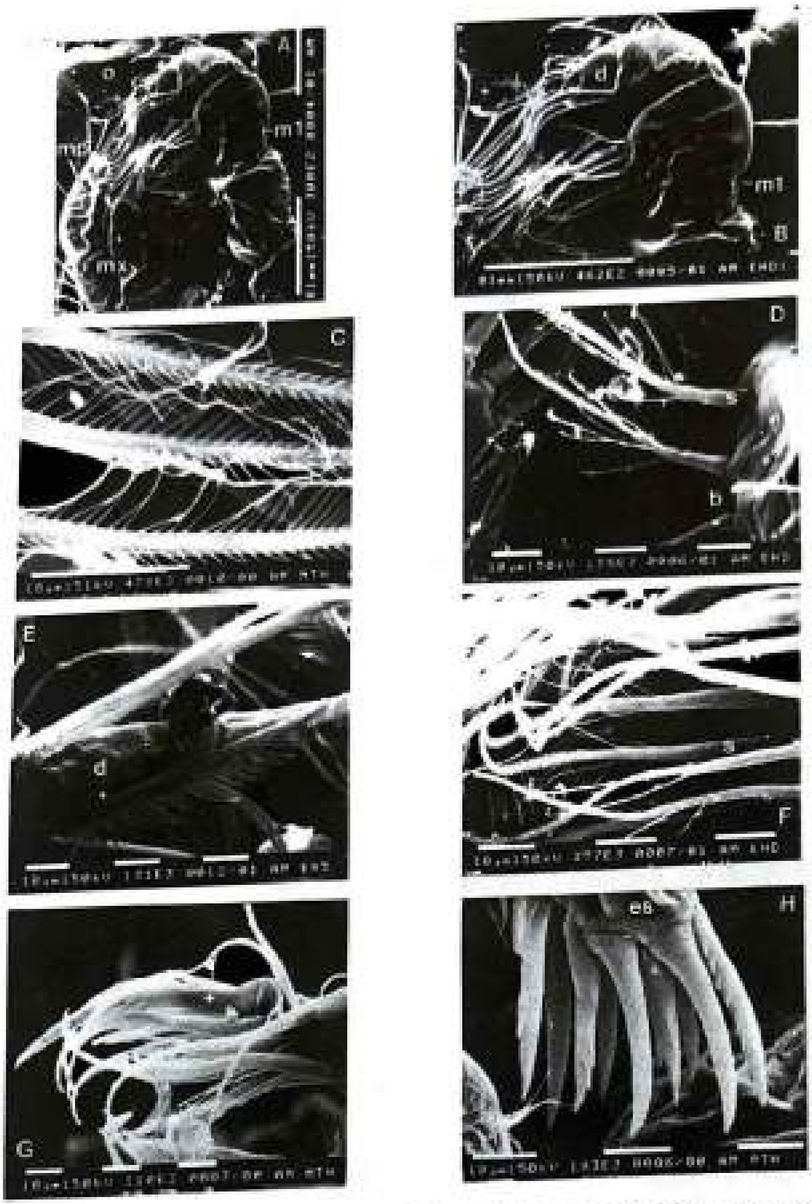
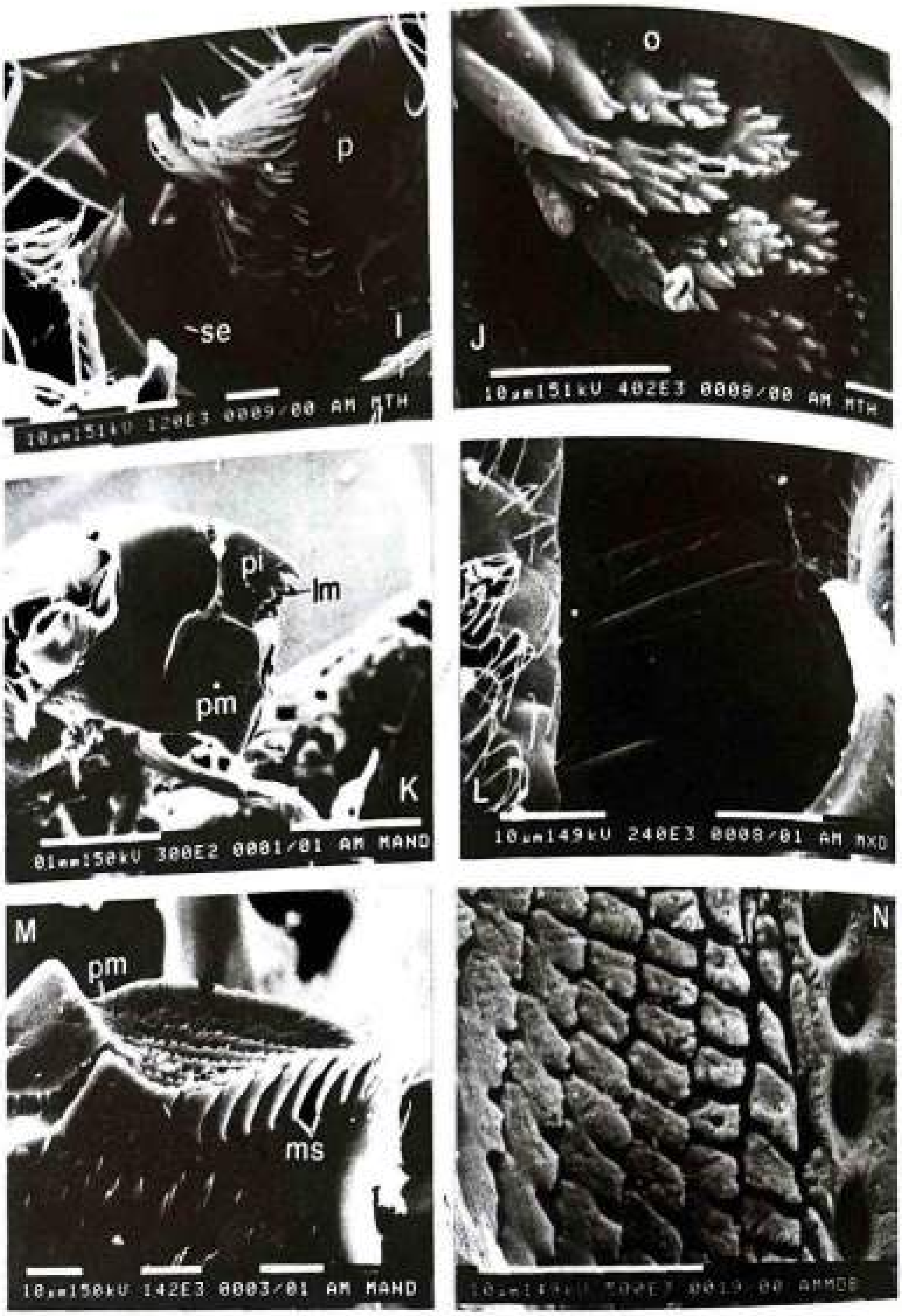


Figure 7. SEM micrographs of *Anisomysis mixta australis* mouthparts. A. ventral view or right maxilla (mx) and left maxilliped I (ml): 0-labrum. B. Close up of left maxilliped I: d - dactylus. C. Fine structure of setules on setae of maxillary exite. D. Setae (s) on the basal endite of left maxilliped I. E. Close up of the dactylus of theoracic endopod showing comb setae. F. Setae (s) on the merus of left maxilliped I. G. Dactylus of left maxilliped I: + - stout sharp spine. H. Close-up of the spines on the maxillular dorsal endite. I. Close up of left labial paragnaths (p): se-serrated setae of the maxillular proximal endite. K. Close up of cluster spines on the dge of labrum (0). K. Posterior view of left mandible: lm-*lacinia mobilis*, pi - *pars incisiva*, pm-*pars molaris*. L. Fine structure of setules on setae or right maxilla proximal endite. M. Close-up of *pars molaris* (pm): ms-marginal spines, arrow points pore on the margin of grinding region.N. Fine structure of the *pars molaris* grinding surface: arrow as in M.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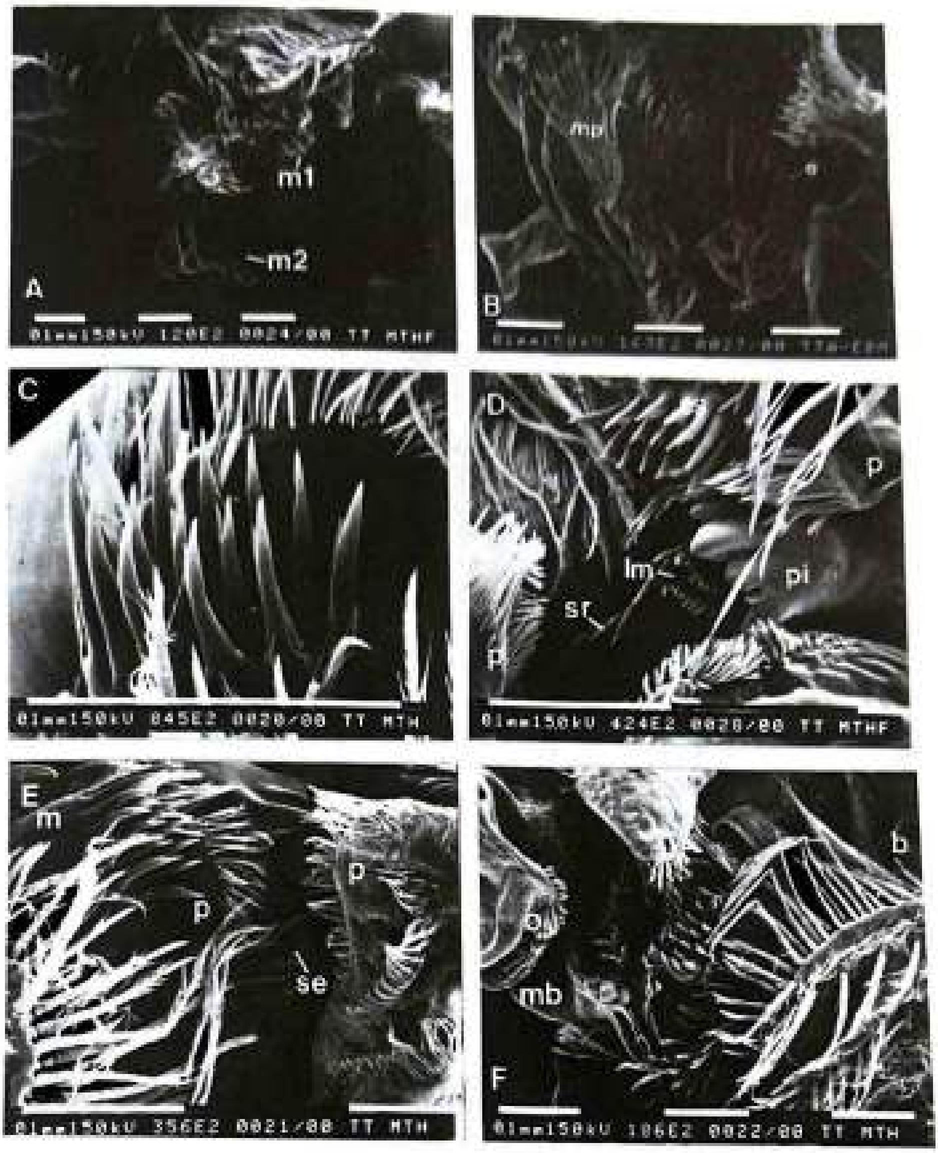
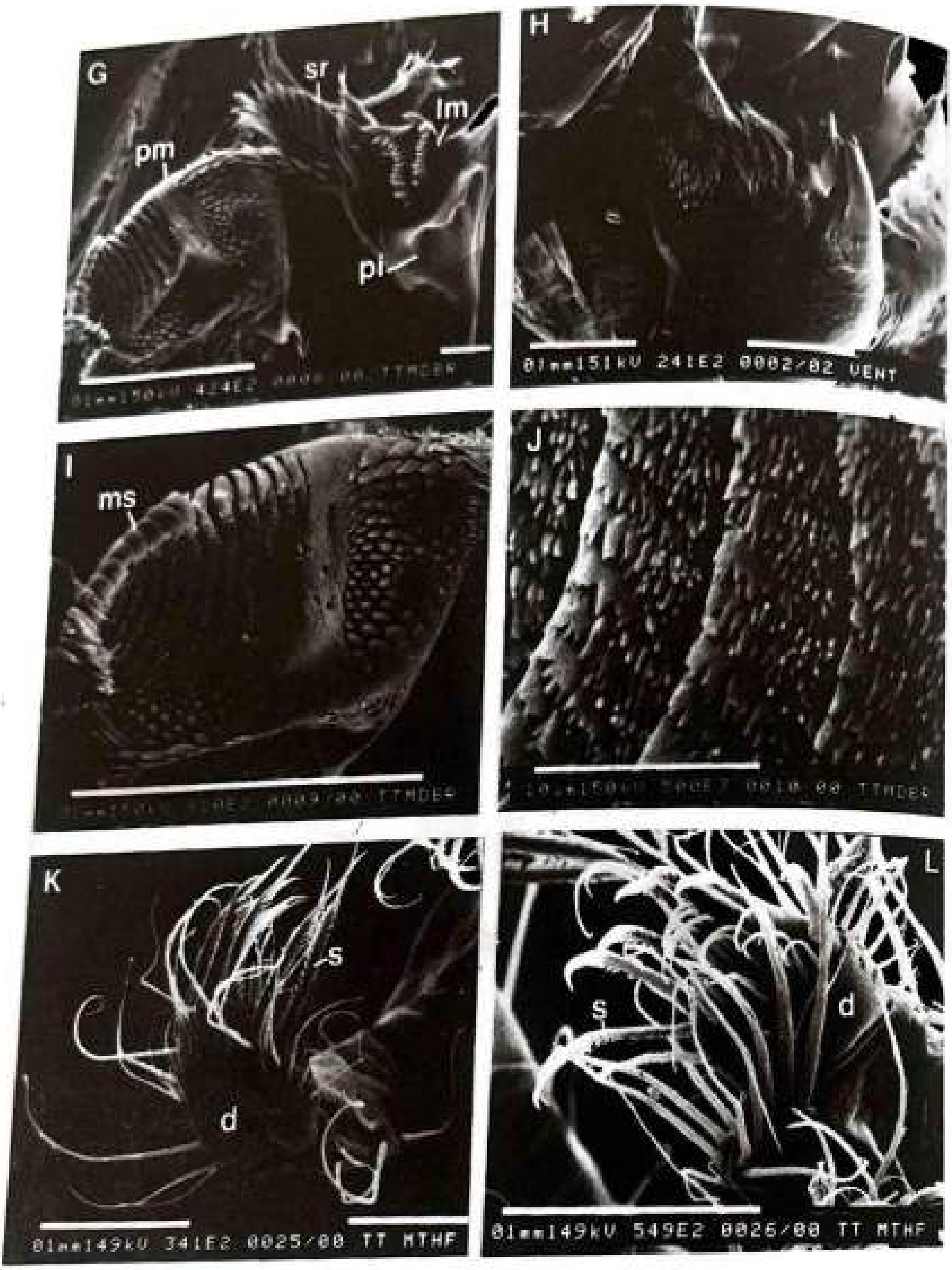


Figure 8. SEM micrographs of *Tenagomysis tasmaniae* mouthparts. A. Median lateral view of right side mouthparts: g - median groove of labium, ml - maxilliped I, m2 - maxilliped II. B. Ventral view of maxillae: e - setae on proximal endite, mp - maxillary palp. C. Close-up of spine on the maxillular distal endite. D. Close up of ventral view of mouthparts: es - spines on the right maxillular distal endite, lm-*lacinia mobilis* of right mandible, p - labial paragnaths, pi - *pars incisiva* of right mandible, sr - spine row of right mandibel, E. Close-up of labial paragnaths (p); m-distal endite of right maxillule, se-serrated setae of the maxillular proximal endite. F. Median lateral view of right mouthparts: b - basal endite of maxilliped I, mb - right mabdible, o - labrum. G. Left mandible: lm-*lacinia mobilis*, pi-*pars incisiva*, pm-*pars molaris*, sr-spine row. H. Right mandible. I. Close up of *pars molaris* of left mandible ms-marginal spines, arrow points pore on the margin of grinding region. J. Fine structure of *pars molaris* grinding region. K. Close-up of maxilliped II dactylus (d): s - serrated seta on apical edge of dactylus. L. Close-up of maxilliped I dactylus (d): s - as in K.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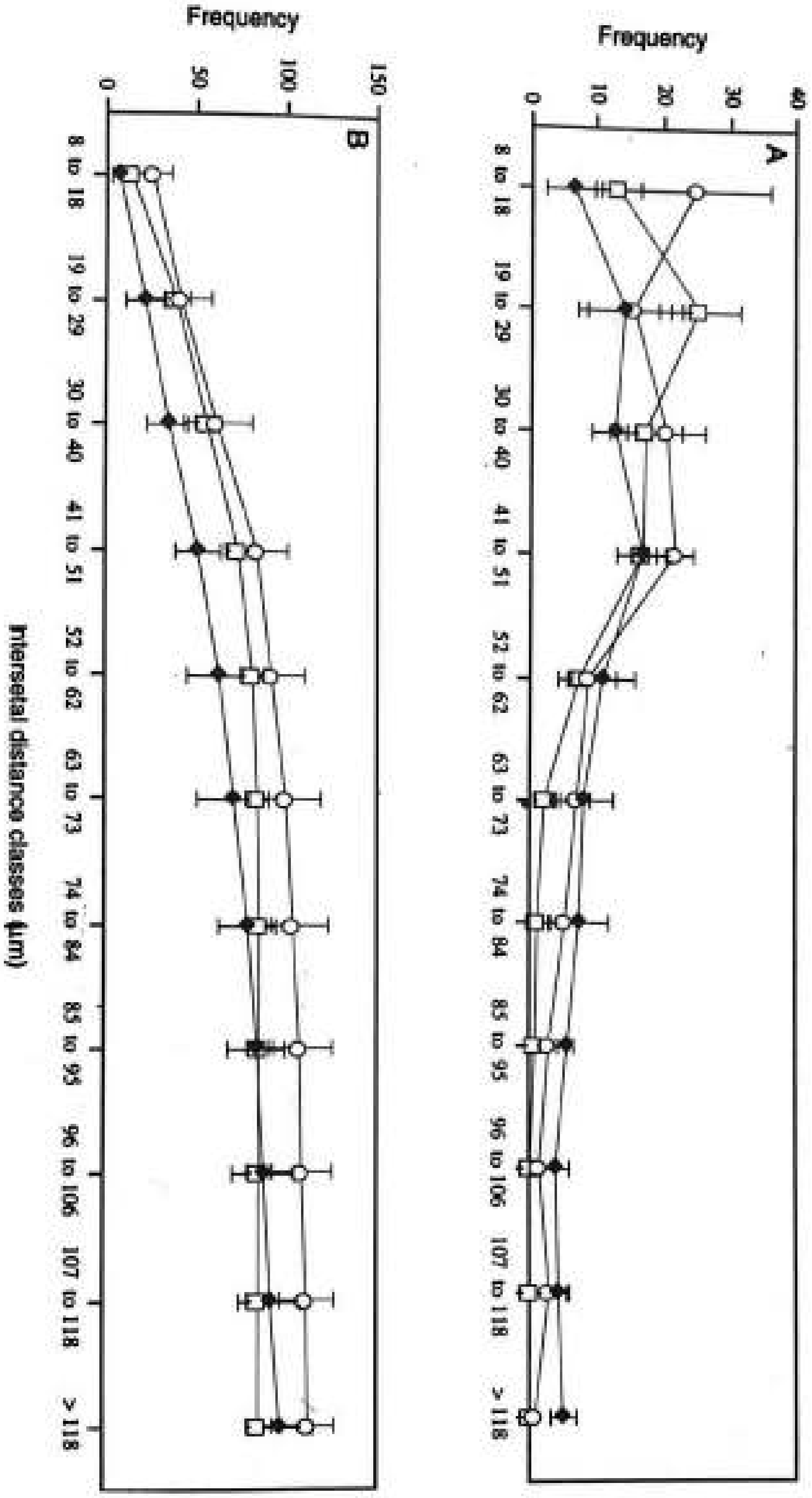

Figure 9. Mean intersetal distances on the thoracic endopods in the three mysid species. A. Frequency distribution B. Cumulative frequency distribution. Squares - *Anisomysis mixta australis*, solid diamond - *Paramesopodopsis rufa*, circl- *Tenagomysis tasmaniae*.

ventral endite bears bristled long setae which are in contact with the posterior face of the paragnath. The distal endite bears a bunch of slender and biting spines with a row of broad-based spinules on its inner shaft. These spines are ventral to the ventral edge of the paragnaths, and almost touch the base of the *pars incisiva* of the mandibles. Disposition and number of spines on the distal endite vary between the three mysid species.

No marked specialization is shown in the labia of the three species (Figures 6F, 7I, 8E). The paired paragnaths of the labium border the posterior oral cavity with their concave anterior surfaces. The median edge of their anterior lobes are densely covered with thin, stiff, and bristled setae. These dense setae intermesh with each other forming a screen that fills up the space between the medial edges of both paragnaths. Small and fine setae are found on the ventral convex surface of the paragnaths. The labium becomes fused on its medial base forming a cleft or a median narrow groove.

The basic form of the mandibular palps is similar in the three species (Figures 6I; 7K; 8G,H). All possess a pair of mandibles whose food-processing surfaces are asymmetric, dovetailing in the middle. The mandibular cutting edge of a typical mysid consists of four main elements which are all present on the left mandible. These edge structures are the *pars incisiva*, *lacinia mobilis*, spine row, and the *pars molaris*. The *lacinia mobilis* usually is reduced, if not lost among the edge structures in the right mandible. The anterior aspect of the *pars molaris* wall bears patches of flat serrated spines occurring in groups of 3 or 4.

The labrum is thick and disc-shaped and forms the anterior border of the oral cavity (Figures 6A,N; 7A; 8F). Flat, robust and setulose spines border the edge directly adjacent to the oral cavity. These features are shared by the three mysid species.

Differences in the Structure of Endopods and Mouthparts

Endopod Intersetal Gap

The intersetal spaces in the three mysid species ranged from 8 to > 118 um, and their average relative frequency and the cumulative frequency are plotted in Figure 9. All three species showed a significant variation in their frequencies of intersetal distances (two factor analysis of variance: $F = 3.713$, $df = 2$, $p < 0.05$). Differences between species for a particular class intersetal distance were also highly significant (interaction: $F = 14.84$, $df = 20$, $p < 0.001$). It is interesting to note that average values of intersetal gaps in the three species intersect in the 52 to 62 um intersetal gap class. Similar frequency values were shown by *Tenagomysis tasmaniae* and *Anisomysis mixta australis* for the lowest gap class, while *Paramesopodopsis rufa* had fewer values of this gap class. Highest frequency in *A. mixta australis* was in the 19 to 29 um gap class. *T. tasmaniae* showed a peak at 41 to 51 um. Peak in intersetal gap frequency in *P. rufa* occurred in the 74 to 84 um gap class. In the same class, *T. tasmaniae* showed half the frequency, while very few of this size were recorded in *A. mixta australis*. No intersetal gaps > 96 um occurred in *A. mixta australis*. *P. rufa* showed a higher frequency > 118 um than in the other two species. The three species showed similar frequencies for the rest of the intersetal gap classes.

Mouthparts

Paramesopodopsis rufa

Maxilliped II

The median edge of both the ischium and merus bears a row of widely spaced short setae. The transversely positioned carpus bears few long setae. The distal anterior edge of the propodus is lined by a row of long setae which form a rake-like structure with those lining the medial edge of the dactylus. Eight comb-like setae are present on the same edge of the dactylus, and parallel to these setae is the bristle-free stout spine very similar to that in the dactylus of maxilliped I (Figure 6C).

Table 1. Intersetal and intersetular distances of the maxilla and maxilliped I in the three mysid species. (numbers in um)

	Paramesopodopsis rufa	*Anisomysis mixta australis*	*Tenagomysis tasmaniae*
Maxilla			
Endite intersetal gap (range)	3.4 - 6.2	3.9 - 9.4	6.9 - 9.0
Endite setae intersetular gap (range)	0.35 - 0.74	0.5 - 0.8	0.38 - 0.55
Maxilliped I			
Endite intersetal gap (range)	8.1 - 13.3	4.3 - 10.4	3.2 - 6.9
Endite setae intersetular gap (range)	5.0 - 11.6	2.5 - 6.9	9.0 - 14.8

Maxilliped I

The basis bears a plate-like endite, the edge of which is fringed with a row of long and plumose setae (Figure 6A,D). The tips of these setae touch portions of the median groove of the labium. The tips of the longer setae touch the posterior surface of the labial paragnaths. The anterior edge of the ischium is fringed with stout and setulose setae. The merus, like the ischium bears similar types of setae on its anterior edge. Lying horizontally and pointing anteriorly is the carpus which bears rows of stout bristled setae on its medial surface. The propodus curves medially and bears a few bristled setae which form a mesh with those on the carpus. Pointing medially, the dactylus has thin and stout setae on the edge of its tip (Figure 6D). These setae are coplanar with those found on the ischium, merus, carpus and propodus and form a screen. Intersetal gaps of these podomeres ranged from 8.1-13.3 um and intersetular gaps of these setae ranged from 5.0-11.6 um (Table 1). The dactylus of maxilliped I bears a stout and sharp spine.

Maxilla

The maxillary palp of this species is fringed with comb setae which are of a similar type to those in *A. mixta australis* (Figure 6E). However, these setae appear more dense in *P. rufa* than in *A. mixta australis*. Gaps between these setae ranged from 3.4 - 6.2 um. The setae fringing the basal endite have setules forming a mesh (Figure 6G). In P. rufa, the intersetular distance of the mesh ranged from 0.35-0.74 um (Table 2).

Table 2. Edge Index and other feature of the right mandible of the three mysid species. (numbers in um).

	Paramesopodopis rufa	*Anisomysis mixta australis*	*Tenagomysis tasmaniae*
Edge Index *pars molaris/ pars incisiva)*	1.14±0.06	1.24±0.00	1.63±0.20
*pars incisiva*5.7 - 31.7 teeth gap (range)	2.2 - 9.3	7.7 - 20.9	
pars molaris teeth groove gap (range)	13.9 - 6.4	1.3 - 2.4	3.5 - 4.8
*pars molaris*8 number of teeth rows	12	13	

Maxillule

The distal endite of the maxillules possess 12 spines which have blunt tips and few broad based spinules (Figure 6M,N).

Mandible

The 1.14 ± 0.06 mandibular edge index for *P. rufa* is the smallest of all three species (Table 1). The left mandible of *P. rufa* bears the *pars incisiva* with seven blunt peaks (Fig. 6I) 5.7 - 31.7 um apart (Table 1). Bearing two rows of stout sharp spines, the *lacinia mobilis* is dorsal to the *pars incisiva* and its ventral convex surface fits the concavity of the *pars incisiva* (Figure 6I,J). Fourteen spines arm the dorsal row while the ventral row has 11. The largest spine on each row is the most anterior. These spines become shorter towards the middle spine, while the lengths increase towards the posterior end. The mandibular spine row is composed of three powerful stout spines each of which bears on its posterior aspect very sharp, broad and thin-based spinules (Figure 6I,J). The three spines are fused at their bases. A patch of setae is found adjacent to the third spine of the spine row. The region between the spine row and the base of the *pars molaris* is devoid of any cuticular projections.

The gross shape of the *pars molaris* is cylindrical with its elevated heavily armed surface at the level of the *pars incisiva* (Figure 6I,K). The *pars molaris* consists of a squeezing or crushing D-region where round based and blunt projections are found, and a grinding region composed of 12 rows of teeth with groove gaps ranging from 3.9-6.4 um (Table 1). The dorsal margins of these rows of teeth are knife-like (Figure 6K). Five to six large pores are present on the anterior margin of the grinding region (Figure 6K). The dorsal corner of the grinding region has a tuft of flat spines, and long stiff setae. The teeth in the grinding region are blunt (Figure 6L).

Anisomysis mixta australis

Maxilliped II

The fewer setae on the second maxillipeds distinguishes A. *mixta australis* from the other two species (Figure 2A). A few of the serrated setae are found on the dactylus, and as in *P. rufa*, a stout spine is present on this podomere.

Maxilliped I

The distinctive feature of the maxillipeds I in *A. mixta australis* is the reduced number of setae on the different podomeres (Figure 7A,B). Few serrulate setae are found on the merus. Only two plumose setae which lie on the same plane as the meral setae are found on the carpus (Figure 7F). Few setae are also found on the fused carpo-propodus. Gaps between these setae ranged from 4.3 ± 10.4 um (Table 2). A terminal stout spine is present of the dactylus of maxilliped I (Figure 7G). The basal endite of this mouthpart only bears three of the plumose type of setae (Figure 7D) with widely spaced setules ranging from 2.5 - 6.9 um.

Maxilla

The proximal endite bears finely setulated setae (Figure 7C) and the inter-setular distances range from 0.5 - 0.8 um (Table 2). The two plates of the distal endites bear plain plumose setae, and few of the sharply serrated setae (Figure 7A). The most distal portion of the maxillary palp is fringed with few simple plumose setae which, like those in the distal endite plates, form a single row (Figure 7A). Intersetal gaps of the endites ranged from 3.9 - 4.9 um (Table 2).

Maxillule

The distal endites of the paired maxillules bear 9 sharp spines with few broad based spinules (Figure 7H).

Mandible

The cutting edges of the *pars incisiva* are at the same level as those on the *pars molaris* (Figure 7K). Six triangular teeth (gap range = 2.2 - 9.3 um (Table 2)) are present in the ***pars incisiva*** while four teeth are present in the *lacinia mobilis*. The three barbed spines which comprise the spine row are fused at their bases. A small patch of flat spines arises from the base of the *pars incisiva*. The right mandible has no spine row, and its *pars molaris* bears no squeezing or D region.. However, the *pars molaris* of the left mandible has seven rows of teeth which terminate as sharp marginal spines (Figure 7M). A bunch of long and stiff setae are present on the dorsal part of the *pars molaris*., and like in *P. rufa*, this structure consists of the squeezing or crushing D-shaped region on which dome-shaped thickenings are found, and the grinding region with rows of teeth. The gaps between these rows ranged from 1.3 - 2.4 um (Table 1). A row of pores lies on the posterior margin of the grinding region; four of these are large and one small (Figure 7N). The small pore lies closer to the D region of the *pars molaris*. The mandibular edge index for *A. mixta australis* is 1.24 which is between those of the other two species (Table 1).

Tenagomysis tasmaniae

Maxilliped II

The maxillipeds II in *T. tasmaniae* differ from those in the other two species by the presence of closely spaced setae on their ischia (Figure 2C). The other segments contain few setae except the dactylus which ventrally has long and slender setae. The edge of the dactylus bears 7 setae which are robust, serrated, and with pointed and curved tips (Figure 8K). The dactylus of the maxilliped II lacks the sharp spine characteristic of those in the other two species.

Maxilliped I

The basal endite comprises two sets of setulated setae arranged in a single row (Figure 8F). Six of these long and finely setulated setae are found on the most distal portion of the endite interspersed with fifteen other long but strongly serrated stout setae. These setae are in contact with the row of setae on the basal endite of the maxilla. The tips of the long setae extend up to the base of the medial cleft of the paragnaths (Figure 8E). Measurements of intersetal gaps ranged from 3.2-6.9 um and intersetular gaps 9.0 - 14.8 um (Table 2). With the exception of the dactylus, the remaining segments of maxilliped I bear rows of long plumose setae. The dactylus lacks the spine present in the other two species. Short and thin setae form a patch on the dorsal aspect of this segment. Interspersed among these setae are 7 stout and strongly serrated setae with curved tips (Figure 8L).

Maxilla

In *T. tasmaniae*, each of the 13 to 14 double serrated setae on the apical edge of the maxillary palp is characterized by sharper and stouter setules projecting from the distal half of the shaft (Figure 8E). Intersetal distances ranged from 6.9 - 9.0 um while the intersetular distance from the setae of the basal endite ranged from 0.38 - 0.55 um (Table 2).

Maxillules

The spinous distal endite of the maxillules in *T. tasmaniae* is wider and bears 14 biting spines sharper than those in the other two species (Figuure 8C,D,E).

Mandible

T. tasmaniae showed the highest (1.63 ± 0.20) mandibular edge index indicating a much larger *pars molaris* compared to those in the other two species (Table 1). The *pars incisiva* possesses five cutting teeth (Figure 8G) 7.7 - 20.9 um apart (Table 1). The form of the *lacinia mobilis* is similar to that in *P. rufa* (Figure 8G). However, fewer spines are present on its ventral row (10) and on the dorsal row (12). Projecting perpendicular to the *lacinia mobilis* is the spine row which is flanked on its ventral and dorsal side by a bunch of flat, long and stiff setae. The spine row consists of six blade-like spines with 3-4 anterior broad-based spinules (Figure 8.8G). These spines share a common base on which flat and long spines originate. The area between the spine row and the *pars molaris* bears a dense projection of these spines.

The *pars molaris* region includes a grinding surface which comprises 13 slightly overlapping rows of wider and larger teeth (Figure 8I; Table 1) with very sharp cusps (Figure 8J). The gap between these rows of teeth ranged from 3.5 - 4.8 um (Table 1). On the margins where each row terminates, the teeth become stout spines which are curved towards the surface of the grinding region. The dorsal marginal teeth become a bunch of sharp and flat spines. Adjacent to these structures is a tuft of long flat setae. The ventral ridge of the grinding region reveals a row of three small pores, while the anterior ridge bears two large pores (Figure 8I). The ventral ridge separates the grinding region from the squeezing and shearing region. The shearing region is armed with large, flat, and sharp spines as well as round-based and blunt tipped spines.

All the different structures of the left mandible except the spine row are present in the right mandible (Figure 8H). The *lacinia mobilis* possesses three blunt teeth which are slightly above the teeth of the *pars incisiva*. The spine row of the right mandible is composed of four rows of long and short soft setae which are curved towards the ventral aspect of the *pars molaris*. A patch of of dome-shaped spines is found below the anterior ridge of the grinding region. Pores are also present on the ridges bordering the grinding region. The marginal teeth of each row are not curved and spine-like, but are similar in dentition to the rest of the teeth. The most dorsal margin of the grinding region also bears a tuft of flat, long and stiff setae.

Discussion

The Endopods

The endopods of the three mysid are similar, and are consistent with those described in the majority of mysid species (Tattersall and Tattersall, 1951; Mauchline, 1980). All three have a terminal sharp spine or nail and serrated setae, which contribute to grasping large food particles. In oceanic genera such as Eucopia and *Hansenomysis*, the terminal nail and one or more setae on some endopods form a pseudochela which increases grasping efficiency (Mauchline, 1980).

Setal types found on the endopods of the three species are similar to the types of setae in *Antromysis juberthiei* (Crouau, 1989) and those in *Mysis relicta* (Sierszen *et al.* 1982). The setae possess setules on the proximal regions of their shafts and sharp tips which may function both for capturing small and large particles (Gauld, 1966 cited in Tiselius and Jonsson, 1990). Crouau (1989) has identified chemosensory, mechanosensory, and chemo-mechanosensory types. Serrated types of setae may be associated with grooming function (Acosta and Poirrier, 1990). These cuticular projections may also be involved in increasing the efficiency of capturing microscopic and macroscopic potential food particles (Mauchline, 1980; Webb and Wooldridge, 1989; Sierszen *et al.*, 1982). The cleaning mechanism structures on the endopods may have a role in crustacean feeding (Robertson and Man,, 1980).

Although the mechanical sieve hypothesis for the feeding appendages in suspension feeding crustaceans has been discredited as a poor predictor of the size range of food particles by several studies (Donaghay and Small, 1979; Vanderploeg, 1981; Vanderploeg & Ondricek-Falscheer, 1986; Donaghay; 1988), data from mesh size ranges could not be entirely considered useless nor the hypothesis entirely rejected (McClatchie & Boyd, 1983). Aside from Boyd (1976), several more recent studies performed on calanoid copepods and in other crustaceans, support the hypothesis but only within a modified conceptual framework. Intersetal or intersetular gap measurements are usually made on the assumption that setules and setae are stiff and immovable structures. This is absolutely not the case as feeding appendages from which these bristles arise are movable, therefore intersetal gaps depend on the orientation and overall behaviour of these limbs (Vanderploeg, 1990). Movements and orientation in space of the different feeding limbs affect the actual efficiency of the different setal and setular projections (Strickler, 1984; Vanderploeg, 1990). Nevertheless, the data presented here would still provide relevant information on the potential sizes of food particles suspension feeding crustaceans may be capable of capturing. From micro-videographic observations (Metillo, 1995), outstretched endopods have their component segments twisted close to 90° posteriorly resulting in the tips of their setae touching the setae-free shaft of the next more posterior endopod. This orientation of the setae could capture a range of particle sizes of potential food not necessarily reflected by the intersetal gaps.

The intersetal gap range of 8-118 um reported here does not necessarily suggest capture of food particles which fall within this range. The three mysid species are, indeed, capable of capturing food particles larger than 118 um through the raptorial mode. Capture of large size particles may be limited by the maximum allowable span of the endopods. The intersetal gaps reported may be best related to capture of finer food particle. Body size appears to be related to intersetular gap measurement. The smallest species, *A. mixta australis* showed no intersetal gaps > 96 um indicating that this species may be efficient in capturing much finer sizes of food particles. The medium size species, *T. tasmaniae*, also seems better equipped for capturing finer particles as indicated by comparable frequency of smaller intersetal gaps to those in *A. mixta australis*. However, the comparable frequency of the much wider gaps to those in *P. rufa* also suggests probable efficiency for large sized particles. The largest species, *P. rufa* may show reduced efficiency in capturing very small particles, but seems to be well suited to capturing larger particles.

The Mouthparts

The basic form of the mouthparts of the three mysid species is similar to those described in the majority of mysid species by Mauchline (1980). The most anterior, the upper lip or the labrum, does not show distinct modification in the three mysid species. In addition to swinging forward allowing the mandibles to perform their latero-ventral food-processing movements, the labrum in mysids also acts as an anterior boundary of the buccal cavity and prevents ingested food from falling ventrally (Hassal, 1977; Mauchline, 1980; 1989). The flap in contact with the paragnaths of the labium is fringed with spines which may serve to fix food in place. These spinous structures are similar in form and disposition and may not indicate specialized function or a particular feeding habit.

The symmetrical labium or lower lip and its ventrally projecting paragnaths is similar in the three mysid species and those in other species (Mauchline, 1980). The fact that these structures can move laterally to a limited degree as noted in euphausiids (Mauchline, 1989), they may also aid in holding particles being ingested or for large particles chewed by the *pars incisiva* of the mandibles. During mandibular chewing, the meshing on the paragnaths may also prevent loss of colloidal and particulate organic carbon as indicated in *Mysis relicta* (Sierszen and Brooks, 1982). In euphausiids, this meshing can actually remove food from the filtering setae and spines on the lobes of the maxillules and maxillae (Mauchline, 1989).

The mandibular palps, joined at the anterior aspect of the body of the mandibles, are directed anteriorly and adpressed against the ventral base of the antennae. The palps of the three mysid species are similar to those of *Schistomysis ornata* described by Mauchline (1980). The palps remove food from the posterior mouthparts and push it into the mouth (Mauchline, 1980). The mandibular palps in Euphausiacea are very similar in disposition and form to those in Mysidacea, and Mauchline (1989) noted that in euphausiids, the palps aid in transferring food from the mouthparts to the oral cavity. Palps with elaborate setation have been associated with herbivorous feeding in euphausiids (Mauchline, 1980; 1989) and in caprellid amphipods (Caine, 1974). This structure may be reduced or absent in predatory amphipod and euphausiid species.

Itohs (1970) edge index is not directly applicable in Euphausiacea and Mysidacea because copepod mandibles differ from those in the two groups (Mauchline, 1980). Nemoto (1977) developed an edge index for euphausiids which, according to Mauchline (1980), is also applicable in mysids. McClatchie and Boyd (1983) have shown that in the primarily herbivorous species, *Euphausia superba*, apart from having a large *pars molaris*, it is also endowed with specialized surfaces that can split diatom chains, cut or fracture hard tests, and grind particles smaller than 10 um. Mauchline (1980) noted that the deep sea lophogastrid mysids possess large *pars molaris* suggesting herbivory; their habit of vertically migrating to shallower regions at night to forage on diatomaceous phytoplankton may explain the use of a large grinding region in their mandibles.

The mandibular edge index measurements suggest differences in the feeding habits of the three mysid species. The smallest *pars molaris* was shown by *P. rufa*, and *T. tasmaniae* had the largest. The mandibular edge indices shown by the three mysid species agree with the predominant dietary items (Fenton, 1986). *P. rufa*, with the lowest mandibular edge index, fed more on crustaceans while *T. tasmaniae*, with the largest index fed largely on algal detritus. It is interesting to note that *A. mixta australis* with a median edge index fed mostly on finer particulate food materials. Its higher edge index value than that in *P. rufa* suggests feeding habits similar to that in *T. tasmaniae*. However, it is too simplistic to interpret feeding habits from features of the mandibles alone. For instance, the mandibular edge index of the euphausiid *Nyctiphanes australis* suggested a carnivorous feeding habit, however mandibular palp length suggest herbivory (Dalley and McClatchie, 1989). This euphausiid species has been regarded as an opportunistic omnivore from morphological and gut content evidence. The orientation and disposition of the *lacinia mobilis* and spines rows of the mysids in the present study are similar in the two large species indicating similar masticating function. However, in *A. mixta australis*, blunt spines on the *lacinia* and thin spines comprising the spine row may function best for softer and finer food particles. The functions of the *lacinia mobilis* in Peracaridan mandibles include biting, cutting, guiding the *pars incisiva* into right planes and position, and holding food particles during the bite (Dahl and Hessler, 1982; Watling, 1993). The three mysid species possess pores on the edges of their *pars molaris*. These pores may function in contact chemoreception as noted in copepods (Friedman, 1980) and in *Artemia* (Mura and del Caldo, 1992).

The maxillules are considered the most constant mouthpart in form and probably in function, however differences were found between the three species. The number of stout and barbed spines on the distal lobe or endite varies considerably. The smallest species, *A. mixta australis* bears the lowest number of these spines, while *T. tasmaniae* has the highest number. Another difference is in the shape of these biting spines: *T. tasmaniae* has sharp tips suggesting greater efficiency in containing or holding food particles. In contrast, *P. rufa* and *A. mixta australis* have more blunt spines similar to those shown in *Antromysis juberthei* (Crouau, 1989). The differences in the spine shape may be a function of the size of the species and the quality of food the three species process. *A. mixta australis* could manipulate smaller food than the two larger species.

The maxilla of the three species is similar to the phyllopodan type of crustacean appendage (McLaughlin, 1982). Features which differ markedly between the three species include the number and type of setae on the inner margin of the proximal and distal endites, and the margin of the maxillary palps. In terms of number and type of setae, the two larger species, *P. rufa* and *T. tasmaniae* show close resemblance in that they possess denser plumose and strongly serrated types than in *A. mixta australis*. This may be because *A. mixta australis* is small in size and prefers small or softer types of food (perhaps from scavenging) which do not require powerful setation. In contrast, the two larger species feed on a much broader range of food particles, with particular emphasis on large size. These larger species could be differentiated by the type of setae on the apical margin of the maxillary palp. *T. tasmaniae* bears strongly serrated and sharp-tipped setae which may help push and contain coarse and tough food materials to the entrance of the mouth. These setae are unusual in the genus although all *Tasmanian Tenagomysis* have them (Fenton, 1992). This type of setae, in conjunction with similar types of setae found on the dactyli of the first and second maxillipeds, may explain the observed habit of rolling sand grains against these mouthparts as a method of removing organic materials that coat these particles. This may not be shown in the other two species which bear simple plumose and lightly serrated setae on their maxillary palps.

The first and second endopods are not strictly defined as maxillipeds because of the presence of exopods (Mauchline, 1980; Crouau, 1989). However, morphological and functional evidence shown in this study strongly supports naming the first two thoracic endopods as maxillipeds. The disposition and arrangements of the two limbs agrees with the description by Cannon and Manton (1927). Observations from suspension and predatory feeding mechanisms in the three species have revealed the food handling and manipulating function of the maxillipeds or first and second endopods (E1 and E2). Variable density of setae distributed on the medial surfaces of the different podomeres of the maxillipeds I is shown in the three mysid species. *A. mixta australis* has fewer and less powerful setae than the other two larger species. This may be related to its preference for small sized and softer food particles. However, *A. mixta australis* possesses a very sharp spine on the dactylus of its first maxilliped, a feature present in *P. rufa* but absent in *T. tasmaniae*. By virtue of this robust spine, *A. mixta australis* and *P. rufa* may show a greater efficiency than T. tasmaniae in immobilizing and restraining animal prey. The strongly serrated, curved and sharp setae of the latter species are efficient in dealing with food materials such as algal detritus and in scraping from hard surfaces.

The maxillipeds II are similar in the three species, but specializations were also observed. Only *T. tasmaniae* showed closely gapped serrated setae on the maxilliped dactylus and extensive and closely-spaced setae on the medial surface of the pre-ischium of maxillipeds II. This further supports the idea that this species is more capable of processing and manipulating tough and coarse food particles. The dactyli of the maxillipeds II of both *A. mixta australis* and *P. rufa* have a robust spine suggesting that they are more efficient manipulators of animal prey. The pre-ischia of these two latter species bear widely-spaced setae.

Species with similar trophic ecologies may coexist by partitioning of feeding niche as indicated by differences in feeding structures (Schoener, 1974). Webb and Wooldridge (1989) noted that the differences in mouthparts morphology allow two co-occurring mysid species to utilize overlapping portions of the food resource. Aside from habitat and food resource partitioning (Fenton, 1986), the morphological evidence presented here may also help to explain the co-occurrence of these three mysid species.

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