The foregut of the Mysida (Crustacea, Peracarida) and its phylogenetic relevance

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CONTENTS

The foreguts of the mysids *Antarctomysis maxima*, *A. ohlinii*, *Hansenomysis antarctica*, *Heteromysis formosa*, *Mesopodopsis slabberi*, *Neomysis integer*, *Paramysis kessleri*, *Praunus flexuosus*, and *Siriella jaltensis* were examined by maceration methods, histological techniques, and scanning electron microscopy. Their morphology, their connection with the midgut glands, and probable function are described and summarized. Previous stomach investigations on mysids and the results of the present study are tabulated; a list of foregut characters, common to all Mysida, is presented. The phylogenetic relevance of these characters within the Malacostraca, especially within the Peracarida, is discussed. Most features are inherited from the ground pattern of the Malacostraca or Eumalacostraca. The bulbous cardia with its dorsal fold, the armature of the lateralia, and the construction of the funnel region are apomorphies for the Mysida. The results suggest that characters of mysidan and other peracaridan foreguts might also be useful in the elucidation of the phylogeny of the Mysida and Peracarida, respectively.

Keywords: foregut; Mysida; Malacostraca

1. INTRODUCTION

The study of crustacean stomachs has a long history. Since Aristotle described the teeth of a decapod foregut (in *Historia Animalium*, see translation, Aristotle (1911*b*)), numerous scientists have been fascinated by the complexity of the gastric armature of malacostracans. Based on seventeenth (Reaumur 1712; Herbst 1792) and eighteenth century (Cuvier 1805) work, Milne-Edwards (1834) published the first comprehensive and methodical study of a decapod foregut. His terminology is still used today. After Mocquard (1883), who contributed a basic work on decapod foreguts, most publications dealt with Decapoda too (see, for example, Huxley 1880; Yonge 1924; Patwardhan 1935*a*,*c*; Pike 1947; Fryer 1960, 1977; Schaefer 1970; Meiss & Norman 1977; Felgenhauer & Abele 1989;

King & Alexander 1994). Mocquard (1883) and Leuckart & Frey (1847) provided the first descriptions of mysid foreguts, unfortunately neglecting details of the gastric armature. In 1909, Gelderd published the first detailed comparison of several mysid stomachs; since then, compared with the numerous investigations on decapods, few publications have dealt with mysid foreguts (namely Haffer 1965; Nath & Pillai 1973; Mauchline 1980; Friesen *et al*. 1986; Storch 1989; Metillo & Ritz 1994). A comparative work on mysidan foreguts, analysing characters of phylogenetic importance is still lacking.

Initially, the fascinating complex morphology itself was the main impulse to work on crustacean stomachs. Today studies focus on foregut morphology in relation to ecological topics (Webb & Wooldridge 1989; Metillo & Ritz 1994) and phylogenetic analyses (for examples, see

559

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Wägele 1981, 1989; Felgenhauer & Abele 1983, 1989; Coleman 1992, 1994). Previous results of phylogenetic analyses based on decapod foregut anatomy were justified by the belief that the foregut anatomy is influenced not so much by diet, as by phylogeny (Meiss & Norman 1977; Felgenhauer & Abele 1985, 1989; Wallis 1995). Nevertheless, natural selection has an effect on all structures that have a function. The foregut is adapted to handle food and therefore reflects diet. This is clearly seen in parasitic Aegiidae (Isopoda) or in the Hyperiidae (Amphipoda) (see Wägele 1989; Coleman 1994). This does not mean that adaptive characters are of no use in phylogenetic analysis, what is essential is that characters must be homologies, regardless of the reasons causing the selection of these structures. The main problem is to discover convergent evolution of stomach structures caused by similar diets. In a phylogenetic analysis only their apomorphic, plesiomorphic or convergent status is of importance. Thus, those foreguts showing special adaptations to food and feeding (e.g. Aegiidae, Hyperiidae) are of great value for phylogenetic analyses, because their stomachs reveal the course of derivation as apomorphies.

The relations of the Mysida and Lophogastrida, unfortunately still called 'Mysidacea', remain contradictory (Siewing 1951, 1956; Watling 1981, 1983; Pires 1987; Gruner 1993). As in the Amphipoda (Coleman 1994), foregut features may be useful for phylogenetic research within the Mysida, whereas a basic pattern (Grundplan) of mysid stomach characteristics will help to elucidate peracaridan phylogeny. As already shown for the Decapoda, Isopoda, and Amphipoda, this study suggests that the mysid foregut is also of great phylogenetic value. It is not merely a single character, but an intricate complex of characters. This paper describes and compares the morphology of several mysid stomachs, incorporating previous investigations, and presenting an updated survey of these organs. Not only the ectodermal foregut, but also the termination of the stomodaeum and the beginning of the endodermal midgut glands (the transition of which is still unknown) are of special interest. A further aim is to work out a basic plan of foregut features common to all Mysida. This is an essential prerequisite for further phylogenetic analyses of peracaridan taxa.

2. MATERIALS AND METHODS

(a) *Material*

Specimens were fixed in 4% formalin (*Antarctomysis maxima, A. ohlinii*), 70% ethanol (*Hansenomysis antarctica, Mesopodopsis slabberi, Paramysis kessleri, Siriella jaltensis*) or in 1% glutaraldehyde in 4% formalin (McDowell & Trump 1976) (*Heteromysis formosa, Neomysis integer, Praunus flexuosus*).

(b) *Methods*

For serial sections of smaller specimens, the thorax of *Siriella, Praunus, Hansenomysis* and *Neomysis* was dehydrated with ethanol, embedded in Unicryl-Resin (British Bio Cell), cut at 1.5 µm with a Reichert–Jung microtome and stained with toluidine blue. Large *Antarctomysis* were stained with chlorazol black, embedded in gelatine, and sections prepared with a vibratome (Technical Products International).

More than 50 mysid stomachs were removed under a dissecting microscope and heated in concentrated potas-

sium hydroxide to remove tissue. The transparent foreguts were transferred into glycerol. They could be stabilized in the desired position within the glycerol drop by using small rods of glass. Drawings were prepared with the aid of a camera lucida.

For scanning electron microscopy (SEM) investigations the method of Nation (1983) was modified as follows: foreguts were macerated, dehydrated in ethanol and immersed in hexamethyldisilazane (HDMS), where they remained in a drop within a watch-glass until the fluid had evaporated. After sputtering (30 nm thickness) they were studied by SEM. Despite the use of HDMS, very thin chitinous cuticle shrinks slightly, e.g. the space between the pyloric stomach wall and the inferomedianum posterius (see figure 6c; SP) vanishes, so that the thin stomach wall directly lies on the inferomedianum and the strips of the filter cleaning setae stand out (figure 16b, below the letters PC).

(c) *Terminology*

Unfortunately, Milne-Edwards (1834) transferred the misleading terms 'cardia' and 'pylorus' from the vertebrate stomach to the terminology of decapod foreguts. Apart from Nicholls (1931), no one contradicted this, though inconsistently the main part of the vertebrate stomach, the 'fundus', was not transferred to decapod terminology. In classical terminology, the crustacean foregut consists of an opening (cardia) which is directly followed by the exit (pylorus). Despite the justified suggestions of Scheloske (1976a), the terms 'cardia' and 'pylorus' are retained here as a contribution to the history of zoology. One can simply use these expressions as 'cardiac' or 'anterior' and 'pyloric' or 'posterior' (for examples, see Storch 1989, Metillo & Ritz 1994). As stomach morphology becomes more important in malacostracan phylogeny, a uniform terminology would make comparisons easier. The author's terminology is derived from Scheloske (1976b), whose contributions are strictly logical and easily understood.

3. RESULTS

Relative size and location of the mysidan foregut seem to be uniform in all investigated species. The usual rule of thumb is the rough correspondence of the diameter of that of a normal-shaped mysid eye and the cardiac chamber. This cannot be applied to foreguts like that of *Mesopodopsis slabberi*, where the cardiac chamber (CC) is extremely slender (figure 13). However, the diameter of the cardia in most cases is one half to one third of the diameter of the anterior cephalothorax (figure 1).

In general the foregut of the Mysida can be divided into four parts: oesophagus, cardiac chamber, pyloric region, and funnel. Though no exact border can be defined, especially between cardia and pylorus, the superomedianum and the dorsal process, as well as the posterior tip of the inferomedianum anterius, delimit the anterior or cardiac region from the posterior or pyloric region (see figures 1, 4, 6, 10; DP, IMA, PT, SM).

(a) *Oesophagus*

The oesophagus (OE) runs from above the mandibles in an anterodorsal direction and opens into the cardiac chamber, the opening being guarded by the cardio-oesophagal valve (figures 1 and 13; OE, VDO). The length
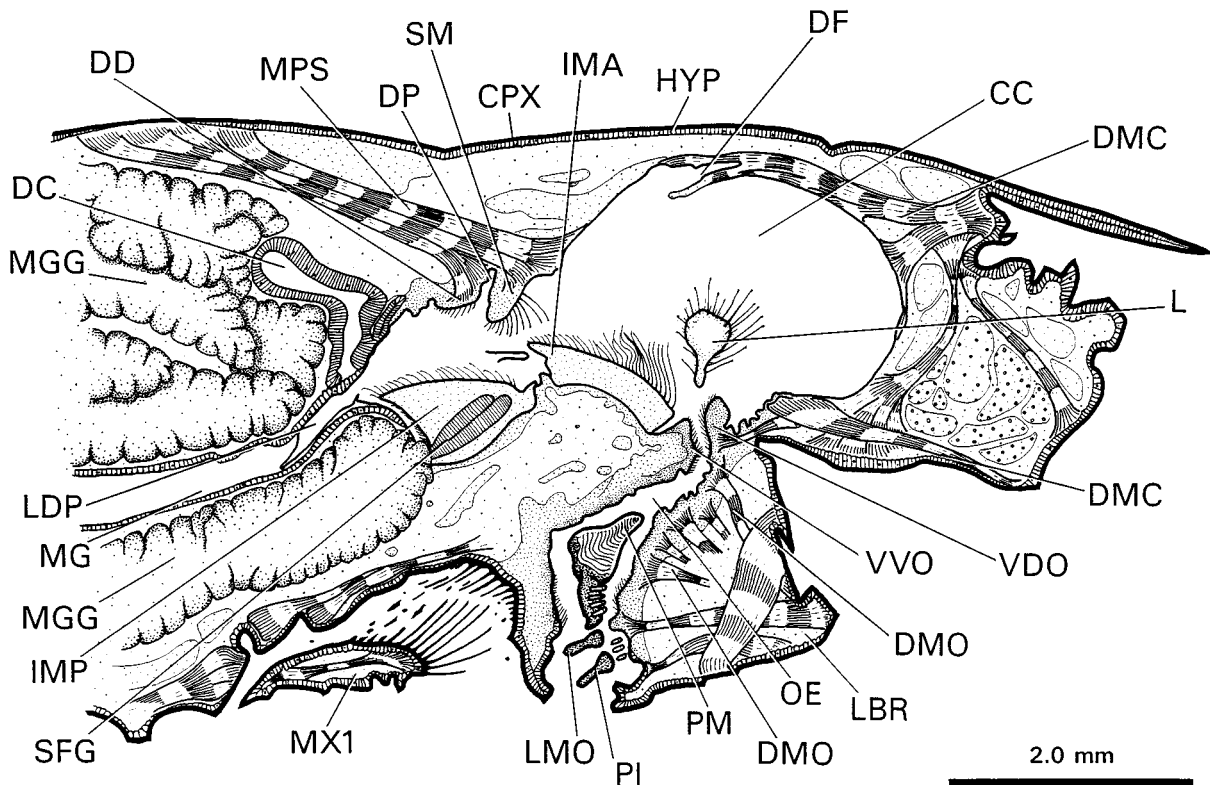
Figure 1. Mediosagittal gelatine section of the foregut of *Antarctomysis ohlinii*, semi-schematic. Abbreviations are listed in Appendix 1.

of the oesophagus is about half the height of the cardiac chamber, except in *Mesopodopsis slabberi* (see figures 1, 6, 10, 13). The 'valve', which can constrict the cardio-oesophagal passage, consists of four setose infoldings, protruding into the lumen of the oesophagus (figure 2; VLO, VDO, VVO). Spines on the valvulae oesophagi are orientated dorsocaudally, thus impeding loss of food particles. The oesophagus can be dilated by muscles (DMO), which help transport food into the cardiac chamber (see figures 1 and 2). In transverse sections of the cardio-oesophagal passage, the dorsal, ventral and lateral folds of the oesophagus are arranged in a typically x-shaped outline (figure 2c).

In lateral views of the mysid foregut, the roughly right-angled arrangement of the oesophagus, the base of the cardia below the inferomedianum anterior (IMA), and the base of the pylorus is obvious (figures 1, 4, 6 and 10). Again *Mesopodopsis slabberi* is an exception: its oesophagus runs dorsoventrally (figure 13; OE).

Between the oesophagus and inferomedianum anterius, a spine row running crosswise on a slight midventral pre-inferomedianum ridge was found in all investigated species, except *Siriella jaltensis* and *Mesopodopsis slabberi* (see figures 3a, 4, 6 and 12; SPR). These spines, like all the other foregut spines subsequently mentioned in the following text seem to be true spines with mechanical functions. In no case was a socket found, or a hollow centre of a spine seen in the semi-thin sections. Nevertheless, at least some true setae with sensory functions might be present, but the author did not explicitly search for them.

(b) *Cardia*

Despite some variations, the globe-shaped form and the relative size of the cardiac chamber are very similar within

investigated Mysida. Nevertheless, the dorsal and lateral outlines of the cardia change according to the degree of enlargement of the prominent dorsal fold (DF) or the smaller lateral folds (see figures 3 and 4). A circular outline can become egg shaped, simply by expanding the dorsal fold. In *Siriella*, the folds seem to be lacking in the macerated foregut (figure 10a), though in histological studies the dorsal fold is present and looks like any other mysid dorsal fold. In *Mesopodopsis slabberi*, the cardiac chamber is very slender, but is extended by a dorsal fold (figure 13; CC, DF). There are three main projections of the cardiac wall into the chamber: the unpaired inferomedianum anterius (IMA), the paired lateralia anteriorly (L), and the dorsolateral infoldings posteriorly (CDL) (for examples, see figures 4, 5a,b, 6, 12a and 16; IMA, L, CDL).

(i) *Inferomedianum anterius*

The inferomedianum anterius (IMA) is a prominent medial ridge, dividing the ventral part of the cardiac chamber longitudinally (figures 1 and 5b,c). The crest of its anterior region bears a row of posteriorly curved spines, the bases of which insert perpendicular to this ridge (figures 3b and 12b; SIA). On either side of the inferomedianum anterius, the primary filter grooves (PFG) run parallel to it; the grooves are roofed by mediodorsally running spines, called the clatri setarum anteriores (clathratus, latin: surrounded or covered with bars; CSA) (see figures 3b, 5b,c, 14i−k, 16d). These spines are regularly spaced, slightly upturned, and bear secondary spinules throughout their length: they arise on the inferolaterale anterius (ILA) (see figures 3b, 5c, 14j). Sometimes the clatri setarum anteriores touch the side of the inferomedianum or their tips meet on its ridge. The spacing of the spinules on the shaft differs from species to species. In *Antarctomysis maxima* and nearly all other species the spinelets
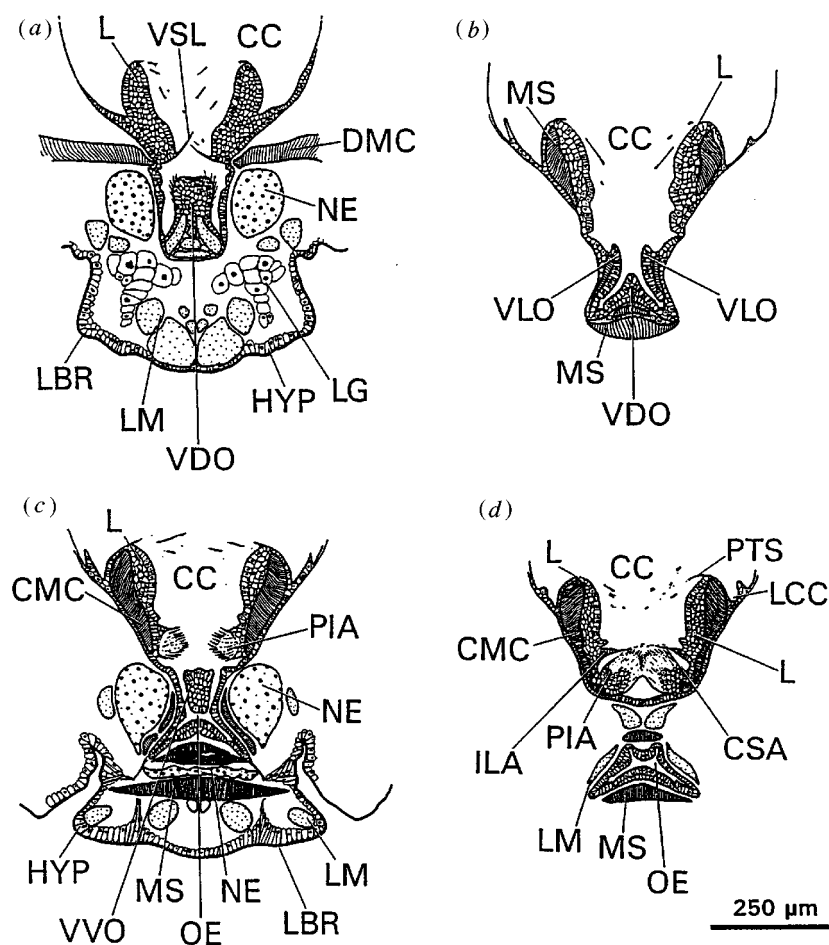
Figure 2. Aspects of ventral cardiac chamber: oesophageal valves and transition of oesophageal passage into cardia. Semi-thin sections of *Siriella jaltensis*; roof of cardia not shown. (*a*) Region ventral to lateralia showing anterior part of opening of oesophagus into cardia with prominent valvula dorsalis oesophagi (VDO). (*b*) Section posterior to *a*. Between the lateral valves (VLO) only base of VDO present. (*c*) Posterior to *b*, opening of oesophagus into cardia now nearly closed by valvula ventralis oesophagi (VVO). Outlines of oesophageal passage are x-shaped. (*d*) Lateral extensions of pre-inferomedianum ridge (PIA), anterior of inferomedianum anterius. This ridge bears very small but stiff spines, and is laterally connected with lateralia (see PIA in *c*). More posteriorly, lateral extensions fuse, thus forming anterior part of inferomedianum anterius, already bridged over by setae of primary filter (see PIA in *d*). Oesophagus runs posteroventrally (see figures 1 and 10*a*; OE), therefore in this section, posterior to *c*, the oesophageal passage is separated from the cardiac chamber. Abbreviations are listed in Appendix 1.

give a featherlike aspect to the CSA (figure 14*i*); *Siriella jaltensis* has only a few spinules at the base of the CSA (figure 14*j*). The clatri setarum anteriores and the ventrolateral grooves they cover, form the primary filters. Coarse food is filtered from the cardiac chamber into the ventral grooves via the clatri setarum anteriores (figure 5*b,c*).

At the anterior end, there is a slight upward slope to the inferomedianum anterius (figures 1 and 6; IMA); in the middle its outline varies in the different species, all have a triangular shape except *Siriella jaltensis*, where the outline is trapezoidal (figure 11*a,b*). In *Hansenomysis antarctica* the anterior region of the inferomedianum anterius shows lateral hollowings (figure 12*b*; HIM). However, in its centre its outline is triangular as in other species. The posterior end narrows and rises from the base of the stomach, so the posterior tip is like the end of an anvil directed towards the pylorus (figures 1, 4*b,c*, 6*a* and 13; PT).

(ii) *Lateralia*

The symmetrical lateralia (L) are the most outstanding features of the cardiac chamber. In most species their size is about one-third to one-half of the length of the cardiac chamber (figures 4, 6*a,b*, 12*a* and 17*a,b*). If the cardia is extremely expanded, the relative length of the lateralia is reduced to one-quarter of the cardiac length (figure 10*a*). The lateralia run longitudinally and have an ear-like outline. They reach their maximum extent in their anterior region, dorsal to the entrance of the oesophagus. Here, they nearly touch medially before turning and narrowing posteriorly (figure 4*a,b*, 5*a*, 6*b*; PPL).

Compared with other species, in *Hansenomysis antarctica* and *Mesopodopsis slabberi* for example, the lateralia and their armature are small (figures 12 and 13; L).

Because of its teeth (TPL), the posterior part of the lateralia is very different from the anterior region (figures 4*a*, 6*b* and 10*c*). The form of the posterior part differs between species and shows individual variation as well. Some species have two to four teeth on the PPL (*Heteromysis formosa*, *Neomysis integer*) (figure 4*a,b*), others have numerous teeth arranged in a group (e.g. in *Praunus flexuosus* and in *Antarctomysis*) (figures 3*b*, 10*c* and 15*c*). In *Paramysis kessleri*, the posterior part of the lateralia is like a single large tooth, bearing smaller teeth on its tip (figure 17*b*: parts 6.1, 6.2; PPL). The number of teeth on the PPL can sometimes be five on the left side and six on right, e.g. in *Antarctomysis ohlinii*. In *Hansenomysis antarctica*, there are only a few teeth on the PPL, in *Mesopodopsis slabberi* the lateralia lack any teeth on their posterior part (figures 12*a*, 13 and 15*i*). Nevertheless, all species bear armature on the posterior part of the lateralia, which is always separated from the anterior region by a more or less small furrow (figures 4*b* and 17*b*; PPL). In all species the teeth of the PPL bear smaller secondary teeth (or scales, in *Hansenomysis antarctica*) (figures 14*b,c* and 17*b*: parts 6.1, 6.2).

In nearly all species the spines on the anterior lateralia, dorsal of the oesophagus, are round-based, stiff, straight, and about twice as long as the teeth on the posterior part of the lateralia (figures 4*c*, 6*a* and 10*c*). In *Hansenomysis antarctica*, there is only a row of small spines on the anterior
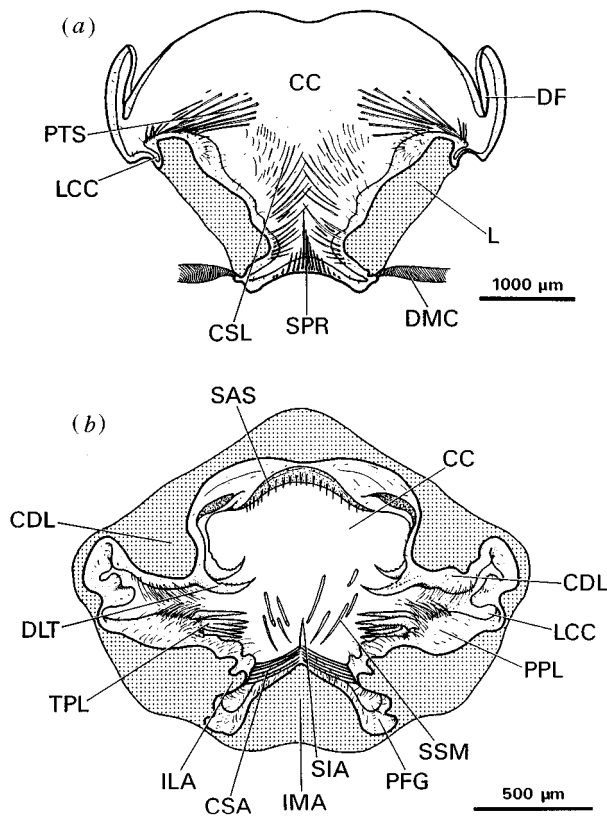
Figure 3. Thick transverse sections of gelatine embeddings of (*a*) *Antarctomysis maxima* and (*b*) *Antarctomysis ohlinii*. (*a*) Aspect of anterior region of cardiac chamber. The section is posterior of entrance of oesophagus, and anterior of beginning of inferomedianum anterius. (*b*) Aspect of posterior region of the cardiac chamber. The section is anterior to the superomedianum, the frontoventrally orientated setae of which (SSM) are already present above IMA. Abbreviations are listed in Appendix 1.

margin of the lateralia (figure 12*a*). In most investigated species there are two main types of stiff spines on the anterior lateralia: prong-tipped spines (PTS) with a crown-like tip mainly directed forward, and spinule-tip spines, with a tip formed by a bunch of fine spinelets, directed backwards (figures 3*a*, 4*a*,*c*, 6*b*, 10*b*, 14*a*–*f*,*h*, 17*b*, part 3). In *Siriella jaltensis*, only prong-tipped spines (figure 14*a*,*b*), and in *Hansenomysis antarctica*, only short triangular teeth, are present on the lateralia (figures 12*a* and 14*g*). In *Mesopodopsis slabberi*, there are soft spines on the margin of the lateralia (figure 13). In other species, bearing prong-tip spines, the number of apices of the crown-like tip varies. The exact form of the prong-tip seems to depend on the position of the spine on the lateralia and on the species. On a longer type of prong-tipped spine, spinules arise below the tip or the tip of the spine has one or two central prongs (see figure 14*c*–*e*; 17*b*, part 4). In *Paramysis kessleri*, apart from two types of long, round based spines, strong, short spines are present on the anterior margin of the lateralia. These spines resemble the teeth on the posterior part of the lateralia in other species (figure 17*b*, part 5).

In *Siriella jaltensis* the lateralia have mediofrontal extensions (MFE) and, apart from the clatri setarum anteriores (CSA), a second row of spines running parallel to the CSA (figures 10*a*–*d* and 15*g*). Transverse sections of the lateralia of all species showed small folds or grooves (LCC) where the dorsal surface of the lateralia fuses with the stomach wall (figures 3, 5*a*–*d* and 11*a*,*b*). These grooves may function as channels for the transport of digestive enzymes into the cardia. They are called lateral circulation channels.

(iii) *Dorsolateral infoldings*

The dorsolateral infoldings (CDL) are situated in the dorso-posterior region of the cardiac chamber, always anterior to the superomedianum and project into it. Their conspicuous features are their spinule-armed teeth (DLT). These are similar to those on the posterior part of the lateralia; they bear secondary teeth and are directed medially (figures 3*b*, 5*b*, 11*a*, 14*a*,*d*,*j*–*m*). In *Mesopodopsis slabberi*, the dorsolateral infoldings are present, but lack teeth (figure 13). The dorsolateral teeth are nearly always curved dorsally, whereas those inserting on the posterior part of the lateralia always bend ventrally (see figures 3*b*, 4*c*, 5*b*,*c*, 6*a*, 11*a*,*b*, 15*a*–*d*,*j*–*m*). With the exception of *Siriella jaltensis* and *Hansenomysis antarctica* all species studied have similar teeth: those of *S. jaltensis* are shaped like a fish-hook and have small secondary teeth on the inner side of curve (figure 15*k*,*l*). The teeth of *Hansenomysis antarctica* are unique. Those on the anterior margin and on the posterior parts of the lateralia, as well as the dorsolateral teeth are very simple and they line a reduced dorsolateral infolding (see figures 12*a* and 15*e*,*f*).

(iv) *Superomedianum*

The superomedianum (SM) is a prominent dorsal infolding located at the transition from the cardia to the pyloric chamber (figures 1, 4*a*,*c*, 6*a*,*b*, 12*a* and 13). Though paired anteriorly in some species, it becomes unpaired posteriorly (figures 5*c*,*d* and 15*j*). The cuticle becomes thicker anterior to the main part of this infolding, and sometimes bears tiny spinelets (SAS) (figures 3*b* and 5*b*). The main spines of the superomedianum are J-shaped, S-shaped or slightly curved. In none of the investigated species are there spines as solid as those of the superomedianum, except in *Mesopodopsis slabberi*, where the entire armature of the infoldings is reduced. The foreguts of *Neomysis integer* (figure 4) and *Heteromysis formosa* are very similar. Apart from slight differences (e.g. the crest of the IMP is more or less sharp in *H. formosa*, roundish in *N. integer*), the foreguts of these species can be distinguished only by the size of the superomedianum and the length of its spines. The superomedianum is larger, and its spines are relatively longer in *H. formosa* than in *Neomysis integer*.

The solid spines and some shorter, slender spines, are arranged in irregular rows, giving the superomedianum a pincushion-like appearance. It can be moved indirectly by the musculus promotor superomedianum (MPS) which originates on the dorsal exoskeleton, runs anteroventrally, and inserts anterior to the dorsal process (DP) (see figures 1 and 9*a*). A long, oval depression of the stomach roof (DD) is found posterior to the dorsal process in all investigated species (figure 16*a*–*c*). Lateral views of the macerated stomach show that the depression is spiniferous; the short spinules are always directed posteroventrally (figures 4*c*, 6*a* and 10*a*).

(c) *Pylorus*

The pylorus consists of three main units, the dorsal food channel (DFC), the paired dorsal circulation channels
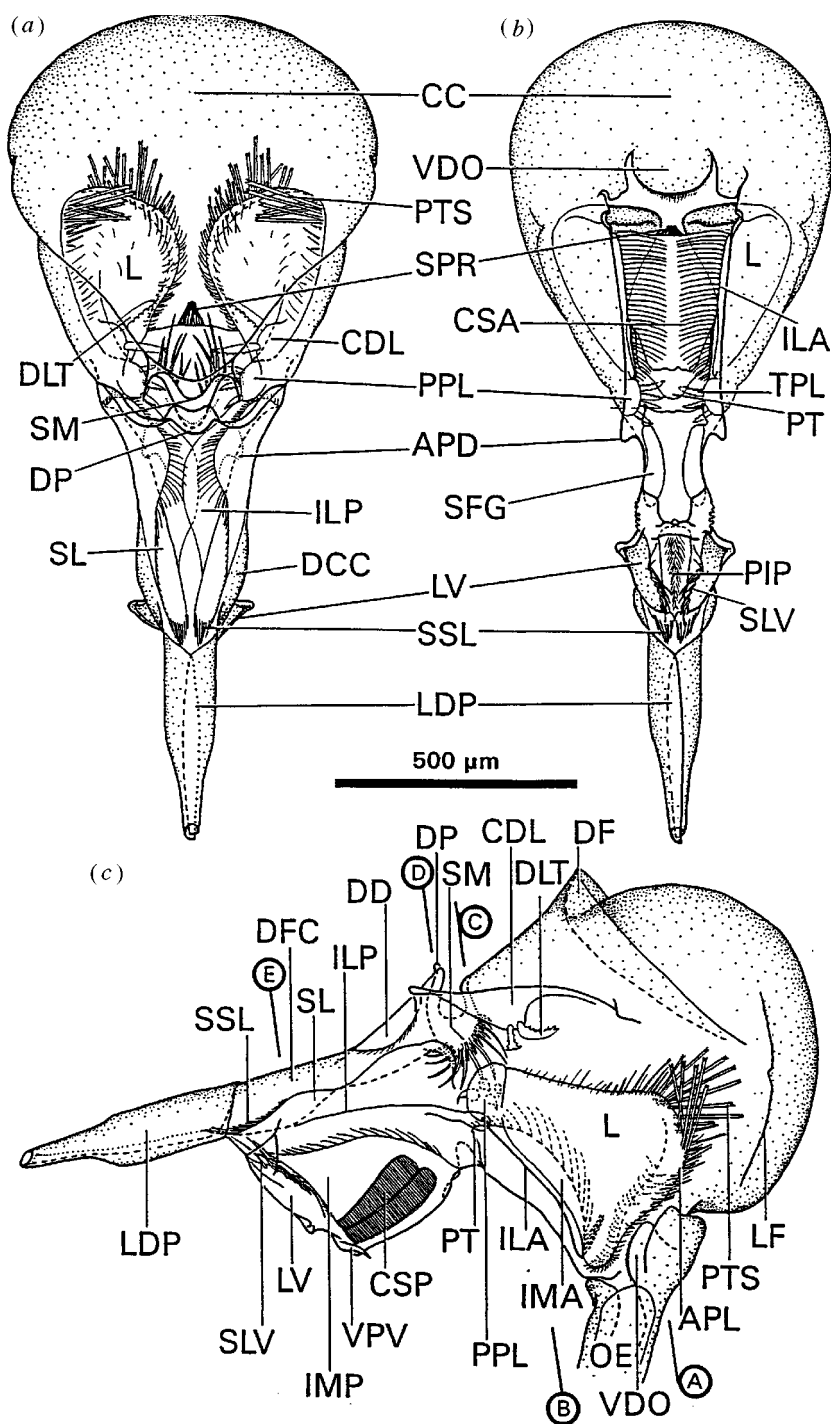
Figure 4. Foregut of *Neomysis integer*. Various views of the macerated stomach. (*a*) dorsal aspect; dorsal fold (DF) not shown. (*b*) Ventral view; oesophagus removed.(*c*) Lateral view; circled letters refer to sections shown in figure 5. Abbreviations are listed in Appendix 1.

(DCC), and the ventral filtration chamber (PC). The latter bears the inferomedianum posterius (IMP) as its prominent ventromedial ridge with filtration channels on each side (see figures 1, 4*c*, 9*b*–*d*, 11*c*, 16*b*). Posterior to the superomedianum, in the posterior region of the foregut, the inferolateralia posteriores (ILP) separate the dorsal food channel and the ventral filtration chamber. The anterior parts of the inferolateralia posteriores overlap distinctly, thus isolating the ventral filtration chamber from the dorsal food channel (figures 5*d*, 9*a*–*c*, 11*c*). Compared with the superolateralia and other infoldings, the chitinous cuticle of the inferolateralia posteriores is

very thin. The medial margins of these inferolateralia are so weak that they are often damaged, even by careful maceration.

The dorsal food channel and the adjacent funnel run exactly posteriorly, whereas the base of the ventral filtration chamber is orientated posteroventrally. In lateral views the outline of the ventral pyloric chamber is like a right-angled triangle, attached below the dorsal food channel by its hypotenuse (figures 1, 4*c*, 10*a*, 13 and 16*b*). On each side, the dorsal food channel is bordered dorsally and dorsolaterally by the superolateralia (SL). The slightly curved spines, insert on the margins of the superolateralia
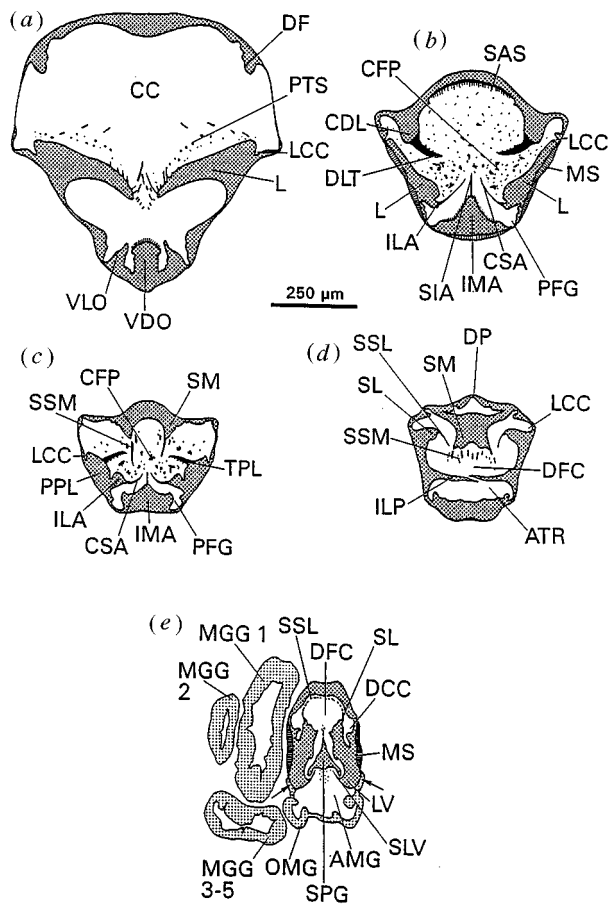
Figure 5. Transverse sections of foregut of *Neomysis integer*. Location of sections is shown in figure 4*c*. (*a*) Aspect of cardiac chamber with prominent lateralia. (*b*) Posterior region of cardiac chamber, showing strongly chitinous dorsolateral teeth (DLT), inserting on dorsolateral infoldings (CDL). The CSA prevent coarse food particles from entering the primary filter grooves (PFG). (*c*) Termination of cardiac region anterior to dorsal process. (*d*) Atrium region (ATR): the space between inferomedianum anterius (IMA) and inferomedianum posterius (IMP); beginning of dorsal food channel (DFC). (*e*) Connection of pyloric stomach with midgut glands (MGG). The outpocketings have fused with the foregut at the ventral parts of the lamellae ventrales (see arrows). Tip of inferomedianum posterius (spigot, SPG) prevents coarse food from entering antechamber of midgut glands. Latter shown only on one side. Abbreviations are listed in Appendix 1.

and meet medially, thus arching over the dorsal food channel. In the posterior region of this channel, the spines of the superolateralia (SSL) become more prominent, forming the main part of the channel (figures 4*a*, 9*b–e*). The superolateralia reach their maximum height at about one-third of their length, then narrow and turn medially until their terminal spines reach into the anterior funnel region (figures 4, 9*b–e*, 10, 11*c,d* and 13). So, above the inferolateralia posteriores, the superolateralia (SL) separate the laterally running dorsal circulation channels (DCC) from the dorsal food channel (DFC) (see figures 5*e*, 9*b–e*, 11*c*). In this posterior region of the pylorus, the dorsal circulation channels are flattened and drawn ventrally before opening into the midgut connection chamber at the ventroposterior end of the stomach (figures 5*e*, 9*d–e*, 11*c,d*).

(i) *Pyloric filtration chamber*

The ventral pyloric filtration chamber communicates with the cardiac filtration channels; the primary filter grooves. These cardiac and pyloric filtration units are connected by a small atrium (ATR) between inferomedianum anterius and inferomedianum posterius (figure 5*d*; see location of this section in figure 4*c*).

As the inferomedianum anterius (of the cardiac primary filter) divides the filtration chamber into channels at the sides of the stomach, so does the inferomedianum posterius of the pyloric secondary filter (figure 6*c*, arrows; figures 9*b,c*, 10*b* and 11*c*). These secondary filter grooves (SFG) run posteroventrally at the base of the inferomedianum posterius, merging into one single opening at the posterior end (OSF) (figures 6*c* and 10*a*). In lateral views of the macerated foregut one cannot see the filter grooves themselves, only their covering filter setae, the clatri setarum posteriores (CSP). These spines insert at the ventral margin of each groove, and run perpendicularly from its ventral to its dorsal margin (figures 4*c*, 6*d*, 9*b*, 10*a* and 11*c*). In all investigated species, the clatri setarum posteriores are similar to the spines of the primary filter (figure 14*i–k*). They are regularly spaced, with spinules inserting on the main spines; the spinules screen the space between the main spines, thus building a very fine sieve (figure 6*d*).

In all investigated species, lateral views of the foregut always reveal a triangular inferomedianum posterius which looks like a hood or a long pointed cap with the filter grooves along the length of its base. On its curved crest is a row of spines, beginning nearly at the base or at the middle of the slope and extending to the tip (figures 1, 4*c*, 6*a*, 10*a* and 13; spines on IMP). The posterior side of the inferomedianum posterius also bears spines, and its tip has more than one point in *Heteromysis formosa*, *Neomysis integer*, *Siriella jaltensis*, and in *Praunus flexuosus* (see figures 6*c*, 9*e* and 11*d*; DT, PIP).

Transverse sections series reveal that two (three in *Siriella jaltensis*) secondary filter grooves (SFC) are present in the Mysida. On the lateral walls of the stomach, opposite the filter grooves, filter cleaning spines (FCS) are directed diagonally towards the clatri setarum posteriores (figures 6*c*, 9*b*, 11*c* and 14*l*). In this foregut region, nearly the whole pylorus is embraced by constrictor muscles (MCP) which insert at the dorsal circulation channel and meet medially below the base of the inferomedianum (figure 9*b*).

In transverse sections of the posterior region of the inferomedianum posterius, where the secondary filter grooves have just terminated, the inferomedianum is no longer connected to the base of the pyloric filtration chamber (see figures 5*e* and 9*d,e*). More posteriorly, the tip region of the ridge forms a triangular spigot that functions as a valve. Protrusions of the base of this conus (SPG) are fitted between the stomach walls and the setae (SLV) of the lamella ventralis (LV), thus separating the dorsal food channel from the anteroom of the midgut glands (MGG) (see figures 5*e* and 9*d*). The lamellae ventrales (LV) are extensions of the posteroventral wall of the pylorus. They are of an irregular lance-oval shape, with strong, curved, relatively long spines (SLV) inserting onto their posterodorsal margins (figures 6*c*, 10*b* and 13). Transverse sections show that the tips of these lamellae
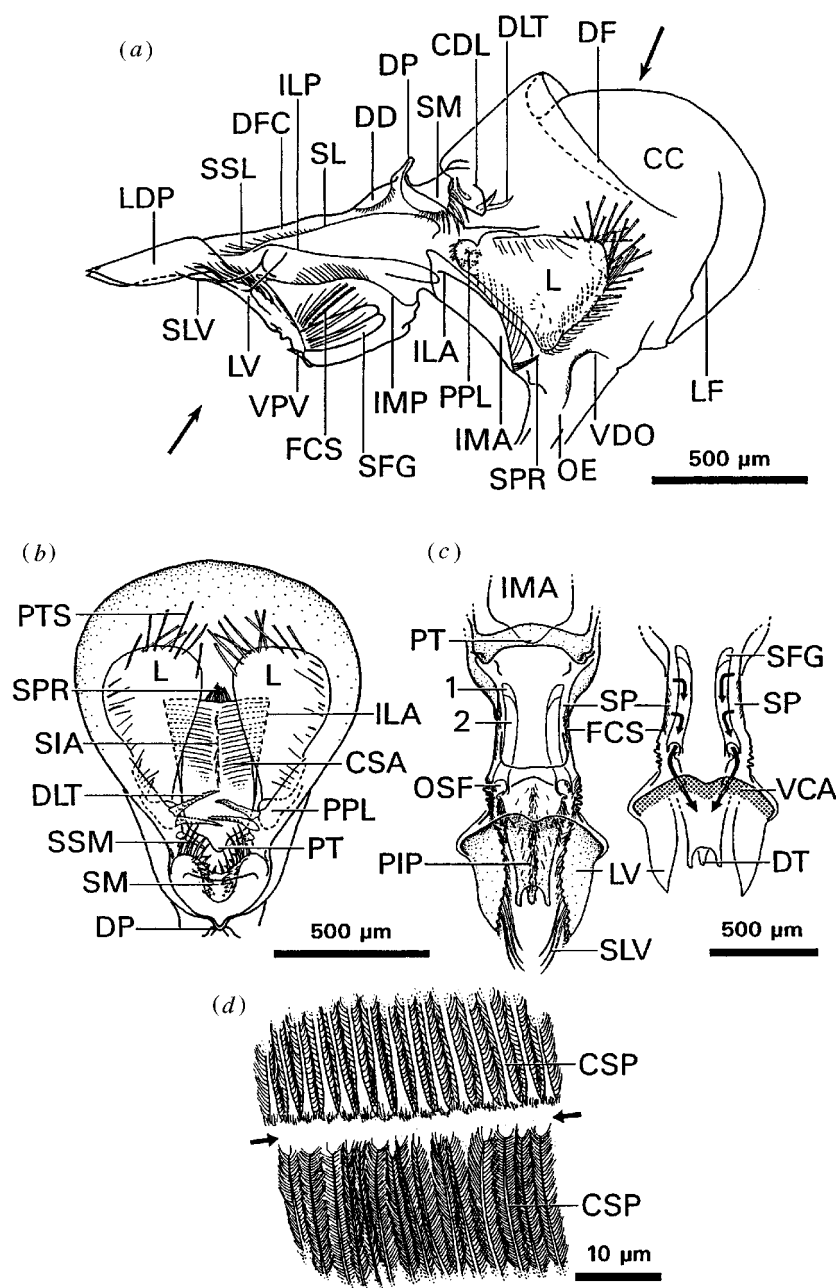
Figure 6. Foregut of *Praunus flexuosus*. (*a*) Lateral view. Arrows refer to the line of sight in *b* and *c*. (*b*) Dorsal view of cardiac region; dorsal fold not shown. (*c*) Ventral aspect of pyloric region. The right figure is a simplification of the left; it shows the passage of food particles, filtered by the setae of the secondary filter before entering the secondary filter grooves (SFG 1, 2). After leaving the secondary filter grooves at the posterior opening (OSF), the chyme can enter the endodermal antechamber, which is ventrally connected to the lamellae ventrales (VCA, dotted area); VPV not shown. (*d*) Clatri setarum posteriores (CSP), covering secondary filter grooves. Above: base and proximal half of the CSP. Below: distal half and tips of CSP covering ventral filter groove. Arrows: margin, separating filter grooves (see SFG in *a*). Abbreviations are listed in Appendix 1.

and their setae reach into a ventral slit of the anterior lamella dorsalis posterior, thus building a ventral part of the so called 'funnel'.

(ii) *Connection with the midgut glands*

In all investigated species the midgut glands (MGG) consist of five paired lobes, all converging to the postero-ventral pyloric stomach (figures 7, 9*e,f*; see 1–5). The posterior half of the pylorus is covered by the epithelia of the midgut glands (MGG) and the anterior midgut (MG) (figure 8). A connection of the midgut diverticula with the foregut is formed by two small outpocketings (OMG) of the medial sides of the anterior midgut lobes (figures 7*a*, 8, 9*c* and 11*c*). In transverse sections series (figures 8 and 9, sections *a–f*) these outpocketings are traceable from their first appearance lateral of the pyloric region (figures 9*c* and 11*c*), to their connection and opening (figures 5*e*, 9*d* and 11*d*). The medial coupling of the two outpocketings forms the midgut antechamber (AMG), which is attached

ventrally to the basal connection of the lamellae ventrales (VCA) (figures 6*c* and 16*d*; right arrowhead). This attachment is the ventral border between the ectoderm of the stomach and the endoderm of the midgut glands. From the base of the lamellae ventrales, this border runs dorsally; the anterior midgut (MG) and the midgut diverticula (OMG) are still separated (figure 9*d* and 11*d*; arrows). Not far caudally, the anterior midgut and the midgut glands totally enclose the posterior part of the pylorus (figure 9*d,e*). With the lamina dorsalis posterior (LDP), an ectodermal structure protrudes into the endodermal anterior midgut (MG) (see figures 1 and 9*f*).

(d) *Funnel, midgut, and dorsal caeca*

The lamina dorsalis posterior (funnel) (LDP) is a posterodorsal extension of the pyloric stomach, a continuation of the dorsal food channel (see figures 4, 6*a*, 10*a* and 12*a*). It has the form of a simple tube, narrowing posteriorly (figures 4, 10*a* and 13). The funnel originates
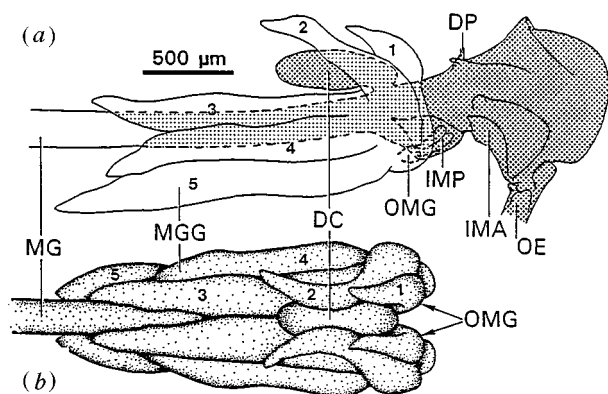
Figure 7. Midgut glands of *Neomysis integer* in relation to foregut. A total of five tubes are present on each side. (*a*) Lateral aspect of foregut and midgut glands of right side. (*b*) Dorsal view of *a*, foregut removed. The outpocketings of the midgut (OMG, broken line in *a* are located ventral to the small tube 1 on each side (OMG, arrows). Abbreviations are listed in Appendix 1.

above the ventral pyloric filtration chamber, where it is already completely enclosed by the anterior midgut (figures 8 and 9*f*). In section it is not simply circular: a midventral slit with rolled-up margins shows that it is not completely closed (figures 9*f* and 10*b*). When not rolled up, the margins overlap medially, thus closing the midventral slit. In the anterior part of the fissure, where the space is larger posteriorly, the distal parts and the spines of the lamellae ventralis reach into the lumen of the rolled-up funnel. The valvula posterior ventralis (VPV), is a small, thin tip. The maximum length of this valve roughly corresponds to the height of two secondary filter grooves (figures 4*c*, 6*a* and 10*a*). In all studied species a dorsal caecum (DC) is present (figures 1, 7, 9*c*–*f*). Anterior to it is a small fold, looking like a reduction of the dorsal caecum (figure 1). Unfortunately, in all prepared specimens of *Hansenomysis antarctica*, prepared for this study, the midgut glands and other soft tissues were already decomposed. Only one dorsal caecum could be found in one specimen.

4. DISCUSSION

Despite their complexity and irrespective of different diets and lifestyles, the foreguts of the Mysida studied here markedly resemble each other. Those of *Neomysis integer* and *Heteromysis formosa* are almost identical, so only figures of *N. integer* are shown. Because the stomachs of *Antarctomysis maxima* and *Antarctomysis ohlinii* are so similar, only pertinent details are shown; lateral views of the entire macerated foreguts would supply no additional information. For the same reason, the foreguts of *Hansenomysis antarctica* and *Mesopodopsis slabberi* are only shown in dorsal and lateral views, respectively.

A glance at the list of publications on mysid digestive tracts misleadingly suggests that the work on mysid foreguts has already been done (see table 1). In fact, though seemingly investigated in depth, detailed drawings of whole foreguts are still lacking for nearly all species, even for the common European *Neomysis integer*, whose foregut is typical of most Mysida (Mauchline 1980). Except for the excellent publications of Storch (1989), and Metillo & Ritz (1994),
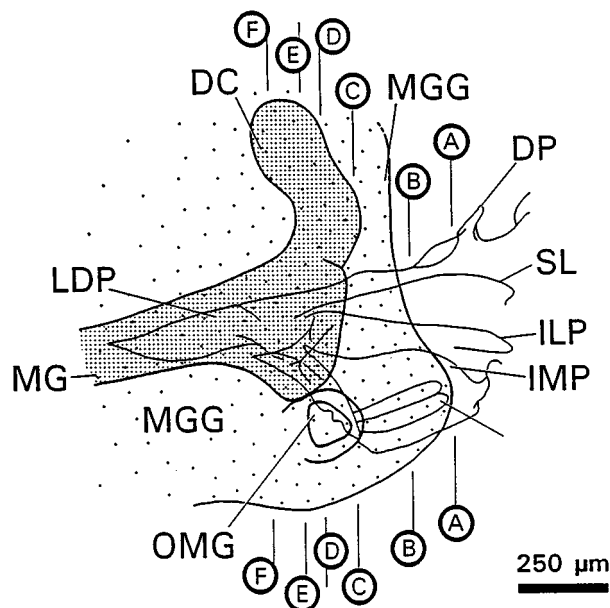

Figure 8. Anterior midgut, dorsal caecum, and anterior part of the midgut glands surrounding pyloric region of stomach of *Praunus flexuosus*; lateral. Circled letters refer to sections shown in figure 9. Abbreviations are listed in Appendix 1.

SEM investigations and a complete survey of mysid foregut armature (see table 2) are missing too.

Lack of confidence in the maceration technique is a possible reason for the absence of detailed drawings of mysid foreguts. The procedure allows unique views of this organ, although it sometimes causes a slight abnormal enlargement of the stomach (Coleman 1991). As a result, the folds of the cardiac chamber were sometimes extremely expanded and therefore could not be seen (figure 10*a*). Comparisons of macerated regions with the same regions studied by histological techniques suggest that this deviation from the normal condition may result from the weak cuticle in this region.

(a) *Some remarks on the diet of Mysids*

Mysida are generally regarded as omnivorous, feeding on algae, detritus, and zooplankton (for examples, see Tattersall & Tattersall 1951; Mauchline 1971*a*,*b*, 1980; Bowers & Grossnickle 1978; Fenton 1986; Gruner 1993). There seem to exist only tendencies towards pure carnivory, herbivory and/or detritivory (Webb & Wooldridge 1989; Modlin 1993; Metillo & Ritz 1994). The mysid diet changes according to distribution or depth range of species (Tchindonova 1959), according to the season (Jansen *et al.* 1983; Zagursky & Feller 1985), or even within 24 h, from benthic detritivore–herbivore during the day to a carnivorous diet at night, as in *Mysis relicta* (Lasenby & Langford 1973).

Therefore, the species prepared for the present study are regarded as omnivorous; in some species tendencies to special diets are reported. *Neomysis integer* and *Praunus flexuosus* are omnivorous with strong tendencies to carnivory (Mauchline 1971*a*,*b*, 1980; Jansen *et al.* 1983; Gruner 1993, Irvine *et al.* 1995), feeding on detritus, diatoms, algae, polychaetes (*P. flexuosus* only), amphipods, copepods and other crustaceans (Mauchline 1980), including carcasses of mysids (Molloy 1958). *Antarctomysis*
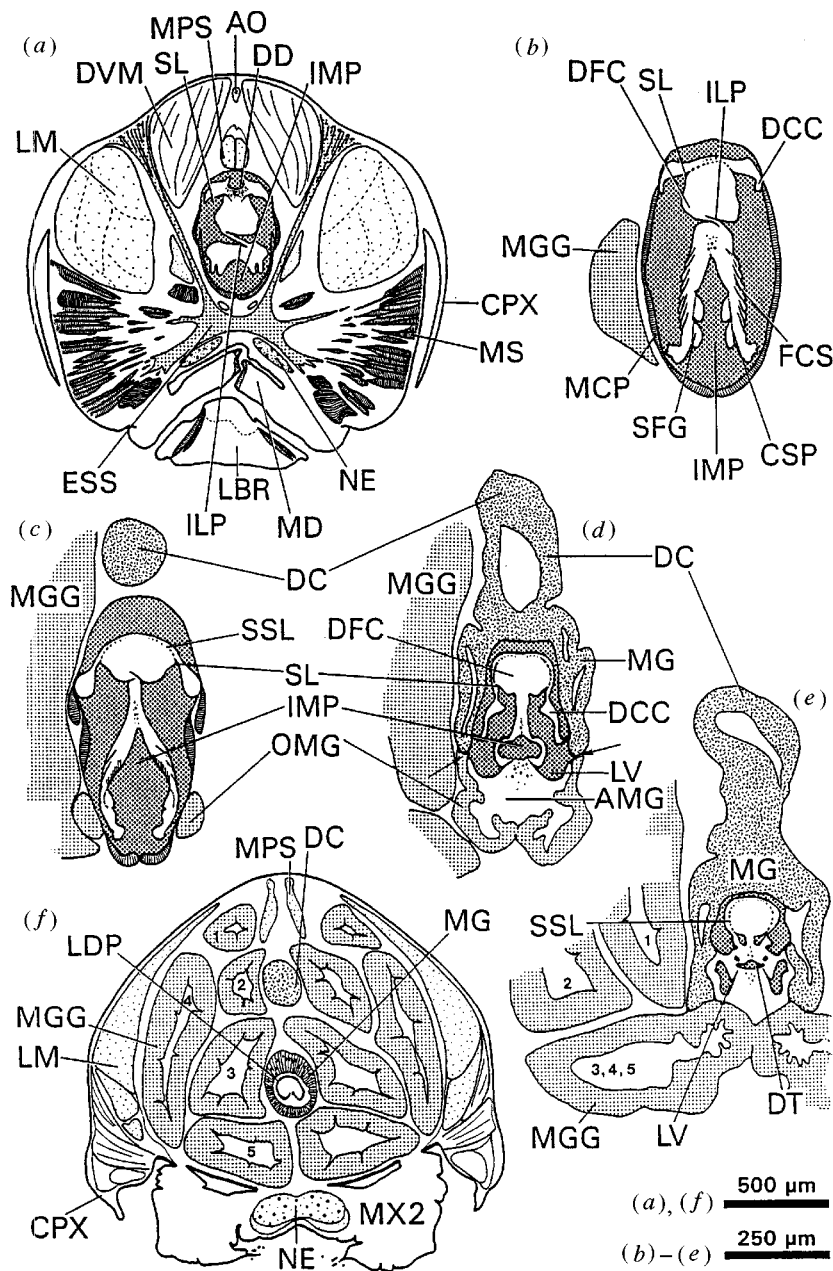
Figure 9. Semi-thin transverse sections of pyloric part of stomach of *Praunus flexuosus*. Location of sections *a–f* shown in figure 7. Only parts of the midgut glands are shown on right side of the pylorus, except in *f*. (*a*) Transverse section of cephalothorax. Beginning of pyloric region located dorsal to tentorium of head capsule (ESS). No midgut glands are present in this region. (*b*) Aspect of pylorus, half-way along length of inferomedianum posterius. (*c*) Posterior part of inferomedianum posterius; the secondary filter grooves have ended, and two outpocketings (OMG) of the midgut glands (MGG) occur lateral to the ventral part of the pylorus. (*d*) Tip of inferomedianum posterius (IMP) separating the dorsal food channel (DFC) from the antechamber of midgut glands (AMG). In this region, the pylorus is totally enclosed by the dorsal caecum (DC) and the anterior midgut (MG). Lateral to the lamellae ventrales the ectodermal foregut meets the endodermal midgut glands and the anterior midgut (arrows). (*e*) Beginning of funnel region of pylorus. Inferomedianum posterius terminates in three tips (DT; compare with DT in figure 5*c*). The endings of the superolateralia and their setae (SSL) are bridged over by the stomach roof, which forms the lamella dorsalis posterior (LDP). (*f*) Transverse section of whole cephalothorax, posterior of pyloric filtration chamber. The lamella dorsalis posterior reaches into the anterior midgut. All tubes of the midgut glands have separated from their common origin. The numbers of the tubes (1–5) refer to the comparable tubes in *Neomysis integer* (see figure 7). Abbreviations are listed in Appendix 1.

maxima is omnivorous, feeding on detritus, diatoms, copepods and amphipods (Mauchline 1980), and *Heteromysis formosa* seems to have an affinity to coarse textured sediments (Wigley & Burns 1971). If any stomach contents at all were found, the mysid foreguts (prepared for the present study) contained a very fine, particulate matter from which only a few coarse particles could be identified as sand grains (coarse grains in *Heteromysis formosa* and fine grains in *Hansenomysis antarctica*), or parts of other animals (in all other species except *Hansenomysis antarctica*). The omnivory of the species examined here seems to be reflected in the relative uniformity of their foregut morphology. Trophic differences of the mysids could be explained by the different foregut armatures, spines, filter sizes etc., which could be seen in the results.

(*b*) *General function of the structures of the chitinous foregut*

On the basis of this work and previous studies (for examples, see Storch 1989; Metillo & Ritz 1994), the probable function of the mysid foregut can be deduced as follows.

Food, entering the cardiac chamber from the oesophagus (OE), is retained by the oesophageal valves (VDO, VVO, VLO) (figures 1 and 2). Expansion of the cardiac chamber by musculature (DMC) (figure 1), the movement of the lateralia (figure 2*a*, *b*) and further intake of food, pushes the coarse food dorsally. In this region, the (prong-tipped) spines of the lateralia hold large particles of food and push them posteriorly. Ventrally, smaller pieces of food pass the sieve of the primary filter and enter the primary filter grooves (PFG) (figure 3*b*). Particles too large for this initial straining, can be pushed dorsally by the spines on the medial margin of the lateralia. Movement, mastication, and grinding of coarse food is done by the teeth of the posterior part of the lateralia (TPL on PPL) and the dorsolateral teeth (DLT) (figures 3*b*, 4*c*, 5*b*,*c* and 6*a*). Food masticated by this armature may still be filtered by the spines of the primary filter. There are just two
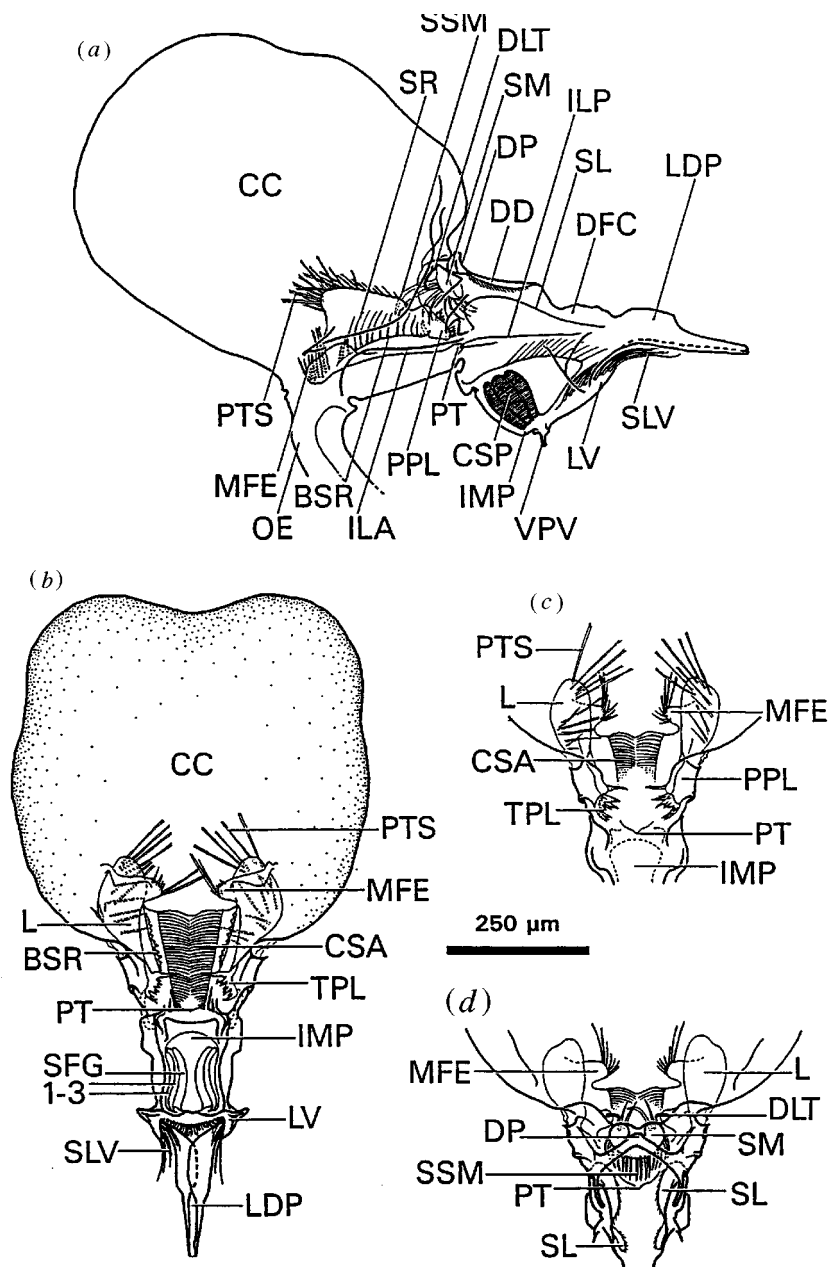
Figure 10. Aspects of the macerated foregut of *Siriella jaltensis*. (*a*) Lateral view (the cardiac chamber is extremely extended by the maceration procedure, the dorsal fold cannot be seen). (*b*) Ventral view of whole stomach; three secondary filter grooves (SFG 13) are present. (*c, d*) Dorsal views showing details of centre of foregut. The plane of focus in *c*, is ventral to that shown in *d*. Abbreviations are listed in Appendix 1.

ways of passing the cardia to finally reach the movable superomedianum: (i) as fine particles along the 'ventral fine-food route', where particles are sieved into the primary filter grooves; or (ii) along the 'dorsal coarse-food route', as large particles (SM) (figures 4, 6*a,b*, 12*a*, 13 and 17*a*).

(i) *Superomedianum and dorsal coarse-food route*

Lateral views of the foregut (figures 1, 4*a*, 6*a* and 10*a*) readily reveal the function of the dorsal process (DP) and dorsal depression (DD). The effect of the movement of the musculus promotor superomedianum (see figure 1; MPS) is enhanced by its insertion at the dorsal process, which functions as a pivot. There are two pairs of antagonistic muscles to the musculus promotor superomedianum: musculus retractor exterior and musculus retractor interior. These antagonists insert onto the bottom of the invagination which forms the superomedianum, and run longitudinally to the upper margin of the dorsal fold

(Haffer 1965). The contraction of the musculus promotor superomedianum pushes the dorsal process backwards, whose base, functioning as a pivot, extends the dorsal depression anteriorly. Depending on the direction of its movement, the superomedianum has two functions.

1. Moving up (by contraction of the musculus promotor superomedianum): in the dorsal region of the cardiac chamber, the base of the spines appear to prevent the passage of insufficiently triturated food particles into the pyloric chamber, by pushing larger clumps anteriorly.

2. Moving down (by relaxation of the superomedianum muscle and contraction of its antagonists): the sharp-edged tips of the spines can rake clumps of food posteriorly. Again it appears that the dorsal region of the cardia serves as a temporary store for coarse particles, e.g. insufficiently triturated food, which can either be masticated by the cardiac armature until it is small

Table 1. *Mysid foregut features*

(+: character is present; ?: character is probably present, but not documented; 0: character is not present, reduced.)

species	characters																	source
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
Anchialina agilis (G.O. Sars 1877)	+	+	+	+	+	+	1	+	+	?	+	+	+	?	+	3	+	Gelderd 1909; Molloy 1958
Anisomysis mixta australis Zimmer 1918	+	+	+	+	+	+	?	+	+	+	+	+	+	?	+	2	?	Metillo & Ritz 1994
Antarctomysis maxima Holt & Tattersall 1906	+	+	+	+	+	+	1	+	+	+	+	+	+	+	+	2	+	present study
Antarctomysis ohlinii Hansen 1908	+	+	+	+	+	+	1	+	+	+	+	+	+	+	+	2	+	present study
Bowmaniella floridana Holmquist 1975	?	+	+	+	+	+	?	+	+	+	+	+	+	+	+	+	?	Storch 1989
Echinomysis chuni Illig 1905	+	?	+	?	+	?	?	?	?	?	?	?	?	?	?	?	2	?	Illig 1930
Gastrosaccus simulans W. Tattersall 1951	+	+	+	+	+	+	1	+	+	+	+	+	+	+	+	3	?	Nath & Pillai 1973
Gastrosaccus spinifer (Goës 1864)	+	+	+	+	+	+	2	+	+	+	+	+	+	?	+	3	+	Gelderd 1909; Molloy 1958
Hansenomysis antarctica Holt & Tattersall 1906	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	2	+	present study
Hemimysis lamornae (Couch 1856)	+	+	+	+	+	+	1	+	+	+	+	+	+	+	+	+	?	Molloy 1958
Heteromysis formosa S. I. Smith 1874	+	+	+	+	+	+	1	+	+	+	+	+	+	+	+	2	+	present study
Leptomysis mediterranea G.O. Sars 1877	?	+	+	+	+	+	?	+	?	+	+	?	+	?	+	2	?	Molloy 1958
Mesopodopsis slabberi (P. J. van Beneden 1861)	+	+	+	+	+	+	2	+	+	+	0	+	?	0		2	+	Gelderd 1909; Molloy 1958; Mauchline 1980; present study
Mysidopsis bahia Molenock 1969	?	+	+	+	+	+	?	+	+	+	+	+	+	+	+	+	?	Storch 1989
Mysidopsis gibbosa G. O. Sars 1864	+	+	+	+	+	+	1	+	+	?	+	+	+	?	?	2	+	Gelderd 1909
Mysis sp.	?	?	?	+	?	+	?	?	?	?	?	+	?	?	?	?	?	Leuckardt 1848
Mysis stenolepis S.I. Smith 1873	+	+	+	+	+	+	1	+	+	+	+	+	+	?	+	2	+	Friesen *et al.* 1986
Neomysis integer (Leach 1814)	+	+	+	+	+	+	1	+	+	+	+	+	+	+	+	2	+	Gelderd 1909; Haffer 1965; Mauchline 1980; present study
Paramesopodopsis rufa Fenton 1985	+	+	+	+	+	+	?	+	+	+	+	+	+	?	+	+	?	Metillo & Ritz 1994
Paramysis kessleri (Grimm 1875)	+	+	+	+	+	+	1	+	+	+	+	+	+	+	+	2	+	present study
Praunus flexuosus (Müller 1776)	+	+	+	+	+	+	1	+	+	+	+	+	+	+	+	2	+	Frey 1846; Gelderd 1909; Storch 1989; present study
Schistomysis ornata (G.O. Sars 1864)	+	+	+	+	+	+	1	+	+	?	+	+	+	+	?	2	+	Gelderd 1909
Schistomysis spiritus (Norman 1860)	+	+	+	+	+	+	1	+	+	?	+	+	+	?	?	2	+	Gelderd 1909
Siriella sp.	+	+	+	+	+	+	1	+	+	+	+	+	+	+	+	3	+	Gelderd 1909
Siriella armata (M.-Edwards 1837)	?	+	+	+	+	+	?	+	?	+	+	?	+	?	+	2	?	Molloy 1958
Siriella jaltensis crassipes Czerniavsky 1868	+	+	+	+	+	+	1	+	+	+	+	+	+	+	+	3	+	present study
Spelaeomysis longipes (Pillai & Mariamma 1964)	?	+	+	+	+	+	1	+	?	+	+	0	?	?	?	3	?	Nath & Pillai 1972
Tenagomysis tasmaniae Fenton 1991	+	+	+	+	+	+	?	+	+	+	+	+	+	?	+	2	?	Metillo & Ritz 1994

enough to be sieved into the primary filter, or if the clumps cannot be broken by the gastric armature they can be discharged into the dorsal food channel (DFC) of the pylorus. So the dorsal coarse food route is continued in the pyloric chamber: coarse clumps proceed in the dorsal food channel (DFC), strictly separated from the ventral fine-food route by the inferolateralia posteriores (ILP) or by the ridge of the inferomedianum posterius (figures 5e, 9b–e, 11c; DFC, IMP). The posterior part of the inferomedianum posterius (spigot) functions as a cone, preventing coarse particles from entering the anteroom of the midgut glands (figure 5e; SPG). Finally, coarse particles are passed into the funnel and the anterior midgut.

(ii) *Ventral fine-food route*

The ventral fine-food route of the primary filter grooves is connected with the pyloric secondary filter grooves by a small atrium (ATR) (figure 5d), thus continuing this route into the pyloric chamber. Only pre-sieved particles pass ventrally to the secondary filter grooves, where they are sieved again by the clatri setarum posteriores of the pyloric filter (figure 6c,d). This is achieved by contractions of the constrictor muscles of the pylorus, which narrow the space (SP) between the outer pyloric wall and secondary filter spines, so that fine particles and the filter cleaning spines (FCS) are pressed against the secondary filter spines (CSP). This results in a pressure filtration of the fine food particles into the secondary filter grooves, and simultaneously a cleaning of the filter spines. Food items, too large to be squeezed through the filter are raked dorsally by the filter cleaning setae, preventing the sieve becoming blocked. The small spaces between the spinules of the secondary filter, imply that only particles about 1 μm in size or smaller, can enter the secondary filter grooves (figure 6d). Furthermore sections reveal that there

Table 2. *Spines of mysid foreguts*

(The entire set of spines presented here only occurs in 'typical' foreguts with a bulbous cardia, i.e. all species studied, except *Mesopodopsis slabberi*. The probable function of the spines is deduced from their location and morphology.)

spines	location	description	function
oesophageal spines (figures 1 and 13)	valvulae dorsales /laterales oesophagi (VDO, VVO)	thin, piliform, orientated in the direction of food movement	preventing loss of food from oesophageal passage
prong-tipped spines (PTS) (figures 24, 5b,c, 6, 10a, 14a–e, 15g, 17b, part 4)	anterior margin of the lateralia, sometimes only laterally (*Paramysis kessleri*) sometimes on the whole margin (e.g. *Praunus flexuosus*, *Neomysis integer*)	round based, straight, stiff; tip bearing a crown of 3–7 prongs, sometimes with central prong; shaft of longer type of PTS with sharp, triangular scales; arranged in clusters of spines; orientated dorsomedially	goring clumps of food, thus breaking up larger particles into smaller ones; keeping larger items of food in the dorsal region of the cardiac chamber, pushing them caudally by movement of the lateralia
spinule-tipped spines (figures 14f, h, and 17)	posterior, part of the anterior margin of the lateralia	round based, straight, stiff; tip bearing a cluster of spinelets, shaft with secondary spinules; orientated mediocaudally	similar function as prong-tipped spines; pushing clumps of food caudally
teeth of the anterior part of the lateralia (figures 14g, 17b, part 5)	lined up on the frontal part of the anterior margin of the lateralia	strong, short, nearly triangular teeth, bearing sharp spinelets as secondary teeth on their ventral side, curved distally; orientated lateroventrally	breaking up coarse food particles
teeth of the posterior part of the lateralia (TPL) (figures 3a, 6b, 10c, 12a, 15a–c, 17b, part 6)	cluster of spines on the posterior part of the lateralia (PPL)	straight spines as well as ventrally curved spines; dorsal side roundish, ventral side flat, with secondary teeth lined up; in *Hansenomysis antarctica*, the TPL spines are bearing scales	masticating and grinding larger particles of food, piled up in the posteriodorsal region of the cardiac chamber
spines on the mediofrontal part of the lateralia (VSL) (figures 2a, 15g, 17b, part 1)	margin of the mediofrontal part of the lateralia, dorso-caudal to the confluence of oesophageal passage and cardiac chamber; in *Siriella jaltensis* on the mediofrontal extensions (MFE)	strong, stout, curved; shaft with thin spinules; spinules become more abundant in the distal half of the shaft; orientated dorsomedially or ventrodorsally	preventing dropping of food back into the oesophageal passage; pushing particles dorsocaudally, simultaneously cutting and breaking up coarse food
spines of the medial margin of the lateralia (figure 17b, part 2)	medial margin of the lateralia	varying within the investigated species: in most cases slightly curved; the whole shaft with thin spinules	shearing already broken up particles, pushing them above the spines of the primary filter (CSA)
spines of the primary filter (CSA) (figures 5b,c and 14i–k)	lined up on the inferolateralia anterior (ILA), dorsolateral of the inferomedianum anterius	regularly spaced, curved distally; the spines are bearing thin, regularly spaced spinules on the whole shaft (feather-like spines)	sieving food particles
spines on the crest of the IMA (SIA) (figures 3b and 5b,c)	ridge of the inferomedianum anterius, (IMA)	irregularly curved, often bearing very fine spinules	preventing food items from avoiding the CSA
dorsolateral teeth (DLT) (figures 3b, 5a, 6a, 11a, 15a, d–f, k–m)	dorsolateral infolding (CDL)	acute-angled triangular shape, strong, short, often curved distally; dorsal side roundish, ventral side flat, bearing secondary teeth or scales	breaking up food particles, masticating, grinding

Table 2. *Continued*

spines	location	description	function
spines of the superomedianum (SSM) (figures 1, 4c, 15j)	superomedianum (SM = cardiac dorsal piece)	cluster of very stout and solid spines, nearly always curved in a J-like or S-like shape	preventing the passage of insufficiently triturated food particles into the pyloric chamber; raking smaller clumps of food posteriorly
spines of the superolateralia (SSL) (figures 4a, 5e, 9d)	lined up on the medial margin of the superolateralia (SL)	less stout, curved dorso-ventrally, often with fine spinules on the whole shaft	preventing food from entering the dorsal circulation channels; passing food into the anterior funnel region
spines of the secondary filter (CSP) (figures 4c and 9b)	lined up on the lower margin of the secondary filter groove (SFG)	similar to the CSA, the spines bearing very slender secondary spinules, so having a feather-like appearance; both spines and spinules are exactly and regularly spaced, thus building a very fine sieve, covering the SFG	sieving fine particles, pre-sieved by the primary filter
filter cleaning spinelets (FCS) (figures 6a, 11c, 14l, 16b; FCS, PC)	inner wall of pyloric chamber, opposite the secondary filter grooves	short, less stout, slightly bent towards the filter grooves; the spinules, orientated parallel to the triangular shaped roof of the IMP; often bearing secondary spinules on the medial side	food particles, too large to pass the secondary filter, would block the sieve; these food items are wiped off the CSP by the FCS
spines of the lamellae ventrales (figures 5d,e, and 11d)	lined up on the mediodorsal margin of the distal half of the lamellae ventrales (LV)	strong, but less stout; orientated mediocaudally, curved	preventing damage of anterior midgut and midgut glands: coarse particles are passed into the funnel region, and prevented from entering the anteroom of the midgut glands

are no particles in the secondary filter grooves, only chyme as a result of the final sieving at the secondary filter. After leaving these filter grooves at the posterior opening (OSF), the chyme can enter the antechamber of the midgut glands (see figures 5e, 6c, 9b–d).

One should not only consider the probable route of food items from anterior to posterior, but also the transport of enzymes in the opposite direction. The dorsal circulation channels (DCC) of the pylorus are connected with the atrium of the midgut glands (figures 9d,e and 11c,d); therefore transport of digestive enzymes, produced in the midgut glands, and secreted into the dorsal circulation channels, seems possible. This could be assisted by contractions of the constrictor muscles of the pylorus (figure 9b; MCP). Moving up-and-down the spigot (figure 5e), thus causing pressure changes in the pyloric chamber, the contractions of the MPS could facilitate the movement of enzymatic fluids as well as the transport of coarse food into the funnel. In the lateral circulation channels (LCC), continuing the DCC, transport of enzymes into the cardiac chamber also seems possible (figures 2d, 5a–d and 11a,b). As mentioned for other mysid foreguts (Storch 1989), transport of digestive enzymes in an opposite direction to the food, might have two functions: (i) in the opposite direction of the pressure filtration, particles

blocking the sieve are swept away, thus cleaning the secondary filter enzymatically; and (ii) chemical support of the breaking-up of food items in the dorsal part of the cardiac chamber, thus enhancing trituration and mastication.

These deductions are valid for species with a complete foregut armature, i.e. all studied species, except *Mesopodopsis slabberi*. In *M. slabberi*, and cave mysids like *Stygiomysis major* (W. Kobusch, unpublished data) with reduced cardiac chambers and reduced gastric armatures, in principle the foregut functions are the same, though the procedure described above must be simplified. However, descriptions of the function of the mysid foregut are supported by comparable findings in other Crustacea. Kanneworff & Nicolaisen (1969) and Icely & Nott (1984) report the transporting of enzymatic fluids from the midgut glands into the cardiac chamber of amphipods; their studies are based on observations in life, and histological and SEM investigations, respectively. King & Alexander (1994) found comparable, fully enclosed pathways in *Penaeus perguiensis* (Decapoda), whereas the excellent descriptions and SEM research of Storch (1989) and Metillo & Ritz (1994) on mysid foreguts, led to similar conclusions to those presented here. However, the precise mechanism of how the mysid foregut functions is
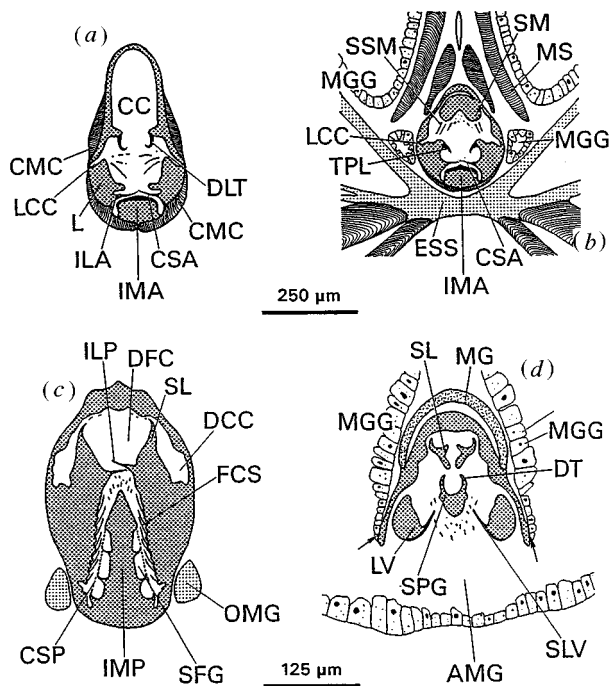
Figure 11. Transverse sections of foregut of *Siriella jaltensis*. (*a*) Posterior part of cardiac chamber. (*b*) Termination of cardiac region ventral to superomedianum (SM), dorsal to a tentorium (ESS). (*c*) Aspect of pyloric filtration chamber, half way along inferomedianum posterius. The two outpocketings of the midgut glands (OMG) fuse posterior to this region, thus forming the antechamber of the midgut glands. (*d*) Beginning of funnel region. The inferomedianum posterius ends with its tips (DT), and the anterior midgut is already arching over the stomach roof. Ventrally, the antechamber of the midgut glands is present. The endodermal midgut glands are laterally connected with the ectodermal foregut (arrows). Abbreviations are listed in Appendix 1.

still a hypothesis, but one that is now underpinned by more data.

(c) *Mysid foregut characters and their phylogenetic importance*

The Mysida investigated here show the following common set of foregut characters.

1. Valvulae oesophagi (i.e. dorsal, ventral, and two lateral valves).
2. Inferomedianum anterius (midventral cardiac ridge).
3. Inferomedianum posterius (midventral pyloric ridge).
4. Lateralia and inferolateralia anteriores in the cardiac chamber.
5. Superolateralia and inferolateralia posteriores in the pyloric chamber.
6. Superomedianum (unpaired).
7. At least one dorsal caecum.
8. Funnel region, leading into the anterior midgut; ventrally a connection to the midgut glands is realized.

These features are common to all peracaridan and eucaridan taxa. They also occur in the syncaridan *Anaspides tasmaniae* (Siewing 1956; Wallis 1995). In *Nebalia bipes* (Leptostraca), characters 1, 5, 6, and 8 are present, though there is only one dorsal oesophagal valve, and the

other features are considerably more simplified (Siewing 1956). A total of two more features (9–10) are probably typical for all higher taxa of the Eumalacostraca and therefore should be found in all peracarids. They are important for the function of the stomach (see, for example, Storch 1989), but until now it is unknown when and where they first occurred.

9. Atrium between the inferomediana connecting the cardiac primary filter grooves with the pyloric filter grooves, thus functioning as a link (atrium-filter unit) for the ventrolaterally moving fine food particles.
10. Dorsal circulation channels in the pylorus and lateral circulation channels in the cardia; both the channels support the transport of digestive fluids from the midgut glands into the cardiac chamber.

The atrium-filter unit (character 9) must have developed with the evolution of both the inferomedianum anterius and posterius; the latter is missing in *Nebalia bipes* (Rowett 1943; Siewing 1956). In *Anaspides tasmaniae*, Siewing (1956) thought the inferomedianum anterius to be continuous with the inferomedianum posterius, but one can also define it as a relatively long inferomedianum anterius (Wallis 1995). Conversely, in *Thermosbaena mirabilis* and *Monodella argentarii*, an inferomedianum posterius is present, but the inferomedianum anterius is missing (Siewing 1958; Fryer 1965). In the Stomatopoda, the foregut seems to be highly derived (Kunze 1983). Nevertheless, features 1–5 are modified but present in *Squilla mantis*: a reconstruction of whose foregut shows a dorsal oesophagal valve, the inferomediana (a primary as well as a secondary filter, linked by an atrium), and the superolateralia fusing with the inferolateralia posterior; the superomedianum is absent (Siewing 1956).

In the Euphausiacea an inferomedianum posterius is present in the genus *Bentheuphausia*, which is thought to be at the base of the phylogenetic tree (Casanova 1984). In other euphausiids a reduced inferomedianum posterius is also present (Ullrich *et al.* 1991), but the euphausiacean midventral pyloric ridge never bears filter grooves (Suh & Nemoto 1988; Ullrich *et al.* 1991). Despite the absence of the secondary filter, an atrium is present. According to the parsimony principle, the atrium-filter unit might first have been realized in the ground pattern of the Eumalacostraca. In *Anaspides tasmaniae* and in the small thermosbaenaceans it seems to be reduced. In the Euphausiacea its function is modified, whereas in the Decapoda and Peracarida it is well developed.

The transport of enzymes from the digestive glands into the cardiac region with the help of foregut structures (circulation channels) is known in the Decapoda, Mysida, Isopoda, and Amphipoda (Kanneworff & Nicolaisen 1969; Icely & Nott 1984; Storch 1989; Wägele 1992; Metillo & Ritz 1994; King & Alexander 1994). The first occurrence of circulation channels, which make the transport of digestive fluids easier, is still unclear. Transport of digestive enzymes into the anterior foregut may already have occurred at the base of the Malacostracan phylogenetic tree, in *Nebalia bipes* or in the near relatives of the Peracarida, the Thermosbaenacea, which are seen as a possible sister group of the Peracarida by some authors (Sieg 1984; Gruner 1993; Richter 1994). It is not known when a special groove, not merely a bend or crease of an infolding that was
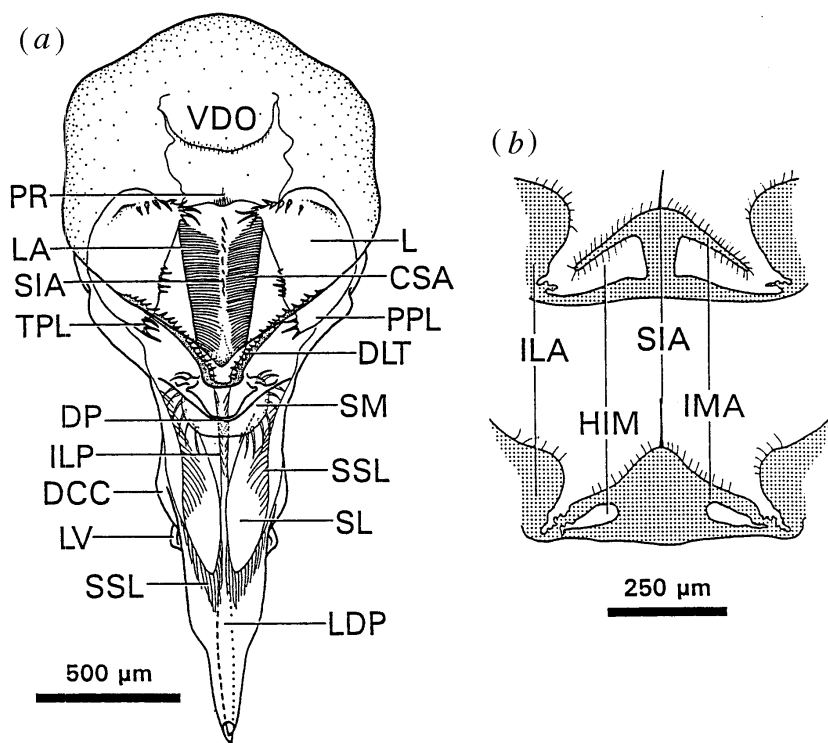
(a)

(b)

Figure 12. Foregut of *Hansenomysis antarctica*. (a) Dorsal view of whole macerated foregut; oesophagus removed, dorsal fold not shown. (b) Transverse sections of inferomedianum anterius (IMA), showing lateral hollows (HIM) of IMA, and setae (SIA) inserting on crest of inferomedianum. Abbreviations are listed in Appendix 1.

first used for transport, evolved for this function. Thus, the dorsal and lateral circulation channels in the Mysida may be involved in the transport of digestive fluids, but they are of no phylogenetic importance.

Further common characters of mysid foreguts include the following.

11. Armature of the prominent lateralia: strong spines on their anterior margins and teeth or spines on their posterior part.
12. Bulbous cardiac chamber, with a prominent dorsal fold and musculature inserting on the cardiac roof, forms a functional unit enabling further extension of the cardia.
13. Superomedianum placed dorsally to the posterior end of the inferomedianum anterius, nearly in the centre of the stomach, always armed with bristles, sometimes with very long and solid spines.
14. Dorsal process and dorsal depression posterior to the superomedianum.
15. Dorsolateral teeth (e.g. hooks, strong teeth with secondary denticles, rows of smaller teeth) inserting on the dorsolateral infoldings.
16. Either two or three secondary filter grooves in the inferomedianum posterius.
17. Special construction of the funnel region; funnel consisting of the lamina dorsalis posterior and the lamellae ventrales with a relative small valvula postero ventralis.

Unfortunately, not all of characters 11–17 are reported in published descriptions. They probably occur in other species, but as the drawings lack these details and the authors do not explicitly mention the characters, their existence is not proven (see ? in table 1).

The lateralia are well developed in all Peracarida, even in the Lophogastrida, where the existence of lateralia is controversial. According to Oshel & Steele (1988), lateralia are absent in *Gnathophausia ingens*, contrary to this, personal observations and the recent findings of De Jong and Casanova (unpublished data) prove their existence. Present knowledge suggests that the armature of the lateralia (typical prong-tipped spines in many mysids; teeth on the PPL, various other spines; see figure 17) is a unique mysid feature. At the genus or species level, the ultrastructure of these features is of taxonomical and ecological importance (Webb & Wooldridge 1989; Metillo & Ritz 1994).

Except in *Mesopodopsis slabberi*, the bulbous cardia is typical of all mysids in this study. Scheloske (1976a) believed a bulbous cardia ('Kropf') to have evolved independently three or four times: in the Stomatopoda, Mysida, and Eucarida. In the Mysida, however, the bulbous cardia has to be discussed in connection with the lateral and dorsal folds and the musculature which evolved to enlarge the cardia by pulling out these folds. Here we have a functional unit again, this time occurring only in the Mysida. Though a globular cardia allowing the storage of larger amounts of food evolved also in other taxa, e.g. in the Amphipoda (Coleman 1990, 1992); the combination of musculature, prominent dorsal fold and bulbous cardia, even in its non-enlarged form (see *Mesopodopsis slabberi*, figure 13) seems to be unique to the Mysida. As well as in the Isopoda and Amphipoda, the prominent dorsal and lateral folds are never found in the Lophogastrida, Cumacea, Tanaidacea (Siewing 1952, 1953, 1956; Haffer 1965; Wägele 1981, 1989; Coleman 1992). In the Euphausiacea, the Thysanopoda show prominent dorsal infoldings of the cardiac chamber, but their cardia is never described as being globular or bulbous as it is in the Mysida (Nemoto 1966, 1977; Suh & Nemoto 1988). Another consequence of the bulbous cardia has to be considered. Once pushed posteriorly, the dorsolateral
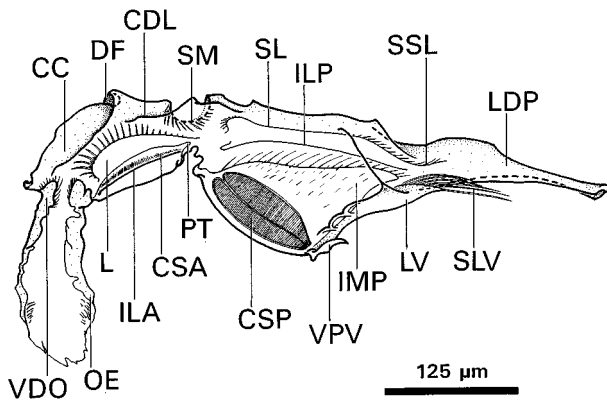
Figure 13. Lateral view of foregut of *Mesopodopsis slabberi*. The bulbous cardia, found in other mysid foreguts, is reduced. The proportions between the cardiac and pyloric regions are different from those of other mysids: the cardia appears to have shrunk, whereas the pyloric region has enlarged. Abbreviations are listed in Appendix 1.

infoldings (CDL) and the superomedianum (SM) with their outstanding armature are placed near the armed posterior parts of the lateralia (PPL, TPL), now in the centre of the stomach (figures 3*b*, 4, 5*c*, 6*b* and 10*c,d*). Parts of this concentration of armature around the superomedianum are considered to be homologous to the gastric mill of the Decapoda (Haffer 1965; Storch 1989). In the Decapoda, a well-developed gastric mill is only realized in taxa with a globular cardiac chamber. Obviously the construction of gastric a mill was enabled by the dilatation of the chamber, pushing the superomedianum and other armature in an optimal position in the middle of the foregut. A gastric mill immediately above the oesophagus could not work. So the mysid structures superomedianum, posterior part of the lateralia, and dorsolateral infoldings may be homologous to those structures which comprise the decapodan or euphausiacean gastric mill.

However, in previous works two mysids with a slender cardiac chamber were described: *Spelaeomysis longipes* and *Mesopodopsis slabberi* (Nath & Pillai 1973; Molloy 1958, respectively). The cardiae of these species resemble those of euphausiacean stomachs (see Nemoto 1977). The foregut of *Spelaeomysis longipes* was thought to be similar to the lophogastridan stomach; the authors therefore called *S. longipes* a 'missing link' between Mysida and Lophogastrida (Nath & Pillai 1973). It was overlooked that in the lophogastrid stomach, not only is the cardia slender (Scheloske 1976*a*), but the position of the superomedianum within is different (Haffer 1965; W. Kobusch, unpublished data). Haffer thought that its position and the globular mysid cardia have developed from the lophogastrid condition by enlargement of a cardiac area, anterior of the superomedianum, which was pushed posteriorly by 'blowing up' the cardia. The dorsolateral infoldings are also pushed posteriorly by this enlargement. So in the Mysida, these infoldings are still near the superomedianum, but the position of both superomedianum and infoldings is now in the centre of the foregut (Haffer 1965). Even in *Mesopodopsis slabberi*, possessing a slender cardia, the dorsal fold is present, and the superomedianum and the dorsolateral infoldings retain their
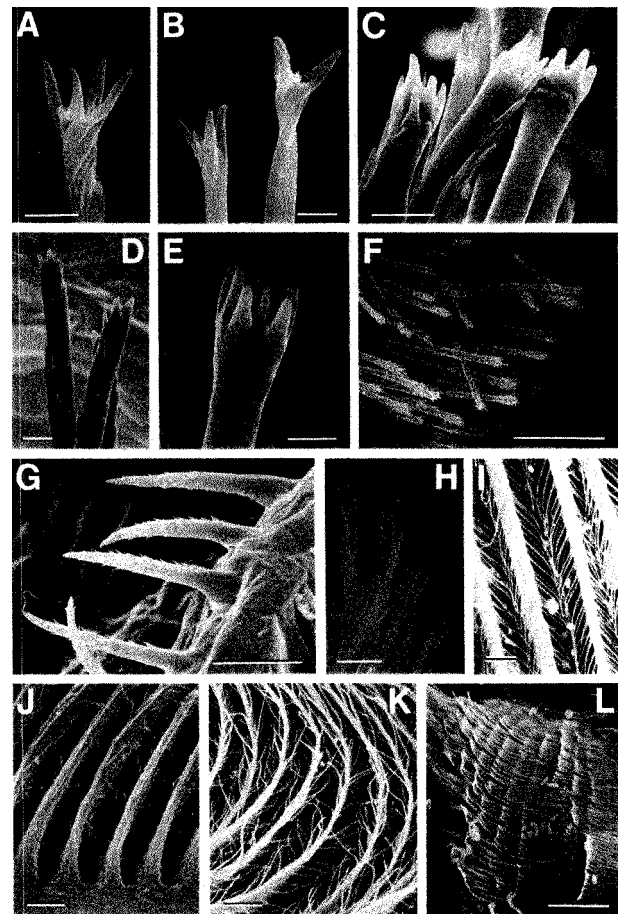

Figure 14. Spines of mysid foreguts. (*a, b*) Prong-tipped spines inserting on the lateralia of *Siriella jaltensis*. (*c*) Prong-tipped spines in *Neomysis integer*. (*d*) Prong-tipped spines in *Antarctomysis maxima*. (*e*) Lateralian spine with a crown-like tip and a central prong of *Neomysis integer*. (*f*) Caudally orientated spinule-tip spine inserting on anterior margin of lateralia of *Antarctomysis maxima*. (*g*) Spines inserting on anterior margin of lateralia in *Hansenomysis antarctica*. (*h*) Spinule-tip spines inserting on lateralia in *Neomysis integer*. (*i*) Clatri setarum anteriores in *Antarctomysis maxima*. (*j, k*) Spines of primary filter (clatri setarum anteriores) in *Siriella jaltensis*. (*j*) Base of spines, inserting on inferolaterale anterius, shown at the lower margin of figure. (*k*) Curved endings of spines, where they touch inferomedianum anterius. (*l*) *Praunus flexuosus*, inner side of pyloric stomach wall (lower margin of the figure frontal, upper margin caudal, left margin dorsal) bearing rows of filter-cleaning spinules. Scale bars (*a, b*) 5 μm; (*c, d*) 10 μm; (*e*) 5 μm; (*f*) 50 μm; (*g*) 25 μm; (*h*) 10μm; (*i*) 5 μm; (*j, k*) 5 μm; (*l*) 50 μm.

position in the middle of the stomach (see figure 13; Molloy 1958). In *Spelaeomysis longipes*, the position of the superomedianum seems to be more anterior, although dorsal to the inferomedianum anterius (Nath & Pillai 1972). Therefore the slender form of the cardia seems to be a reduction in *M. slabberi* and in *S. longipes*.

Considering their function, the dorsal process (DD) and the anterior dorsal depression (DP) (see figures 1, 4*a*, 6*a*, 10*a* and 13), as expected, occur in those mysids which have to deal with coarse food particles. In *M. slabberi*, the dorsal process is reduced, therefore the musculus promotor superomedianum simply inserts on the surface of the stomach roof. In this case the superomedianum cannot be moved as effectively as in other species, which
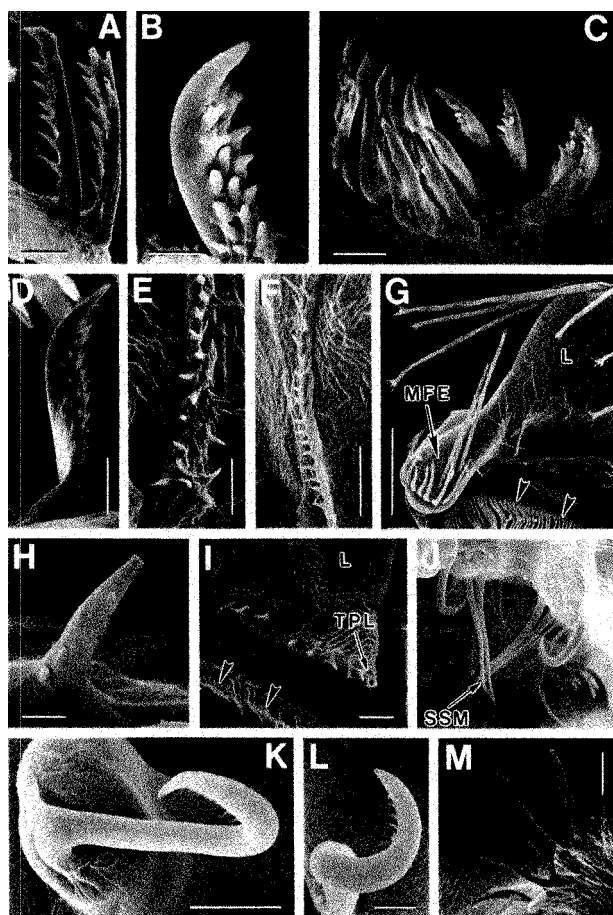
Figure 15. Chitinous teeth of mysid foreguts. (*a*, *b*) *Neomysis integer*, left margin of figures is dorsal. (*a*) Dorsolateral teeth. (*b*) Tooth on posterior part of lateralia. (*c*) Teeth on posterior part of lateralia in *Antarctomysis ohlinii* (upper margin of figure is ventral). (*d*) *Antarctomysis ohlinii*, one of five dorsolateral teeth shown in figure 14*m*, (left side of figure ventral). (*e*,*f*) *Hanseno-mysis antarctica*, lined up dorsolateral teeth inserting on strip-like dorsolateral infoldings. (*g*) Right laterale (L) of *Siriella jaltensis* (left margin of figure is frontal). The laterale shows a spine-bearing mediofrontal extension (MFE). Ventral to this extension the setae (CSA) of the primary filter can be seen (arrowheads). Parallel to the CSA (above the arrowheads) a second row of spines (BSR) is present. In the upper left edge long prong-tipped spines reach to the MFE (see figure 13*a*,*b*). (*h*, *i*) *Hansenomysis antarctica*: (*h*) single tooth from strip of teeth shown in *e*,*f*; (*i*) posterior part of lateralia (L), mediocaudal margin of which bears spines (TPL). Lower left, setae (CSA) of primary filter can be seen (arrowhead). (*j*) Region of supero-medianum in *Siriella jaltensis* (upper side of figure is dorsal). Between the hook-like dorsolateral teeth, very strong setae (SSM) of the superomedianum are orientated mediofrontally. (*k*, *l*) Hook-like dorsolateral teeth of *Siriella jaltensis*; inner margin of curve bears small secondary spinules. (*m*) Complete group of dorsolateral teeth in *Antarctomysis ohlinii* (left margin of figure is dorsal). Scale bars (*a*) 25 µm; (*b*) 10 µm; (*c*, *d*, *e*) 50 µm; (*f*) 100 µm; (*g*) 50 µm; (*h*) 5 µm; (*i*) 50 µm; (*j*) 25 µm; (*k*) 15 µm; (*l*) 5 µm; (*m*) 100 µm. Abbreviations are listed in Appendix 1.

bear a dorsal process. This simplified movement of the superomedianum, the slender form of the cardiac chamber, and the reduction of the stomach armature support arguments that the foregut of *M. slabberi* probably has to deal only with small food particles. By analogy
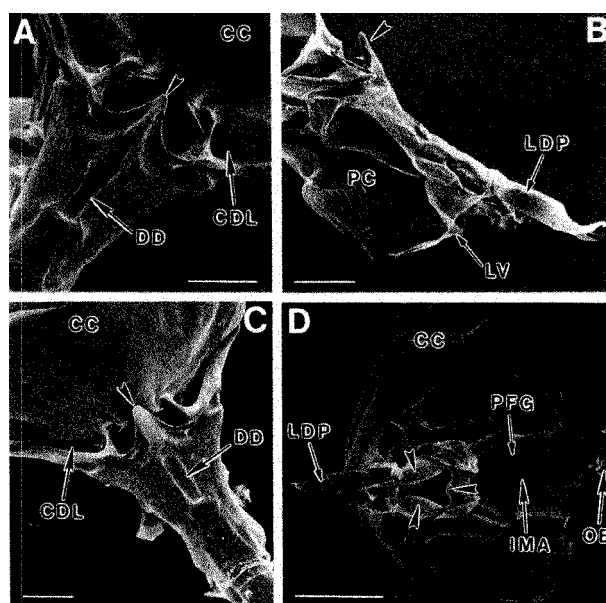
Figure 16. Views of mysid foreguts. (*a*, *b*) *Antarctomysis maxima*. (*a*) Dorsal view of centre of stomach showing dorsal process (arrowhead), dorsal depression (DD), and dorsolateral infold-ings (CDL). At upper right, roof of cardiac chamber (CC). (*b*) Lateral view of left side of pyloric stomach. Arrowhead: dorsal process. PC: pyloric filtration chamber. Below letters PC, strips of filter cleaning setae can be seen. (*c*, *d*) *Antarctomysis ohlinii*. (*c*) Dorsal view of centre of stomach. Arrowhead: dorsal process. (*d*) View of ventral pyloric stomach (line of sight from ventro-caudal to dorsofrontal; left side of figure is dorsal). From outside, inferomedianum anterius (IMA) seen as invagination of base of foregut. Upper and lower arrowheads refer to medial margins of lamellae ventrales, which nearly enclose back side of bristled inferomedianum posterius (see PIP in figure 5*c*); right arrowhead refers to base of lamellae ventrales (see VCA in figure 5*c*). All arrowheads mark areas where pyloric foregut is connected with midgut glands. Scale bars (*a*, *b*, *c*) 500 µm; (*d*) 1000 µm. Abbreviations are listed in Appendix 1.

with adaptations to fine food in some amphipods (Coleman 1990), in *M. slabberi* the secondary filter is enlarged in relation to the cardiac primary filter. It seems probable that the slender form of the cardiac chamber and the reduction of the dorsal process of *S. longipes* are also adaptations to fine food.

It is not known if the dorsal process is a plesiomorphic character which is present in other eumalacostracan taxa, because in many cases the dorsal depression, and even the dorsal process, are not shown in illustrations of foregut morphology. Gelderd (1909) showed this process and the inserting muscle in *Anchialina agilis*, Chun (1896) only mentioned the muscles inserting on this structure (Chun 1896, plate XII, fig. 2; Gelderd 1909, plate III, fig. 33), and in Metillo & Ritz (1994) the dorsal depression is partly shown (see upper margin of figure 3*a*).

Compared with the Lophogastrida, the location and the prominence of the superomedianum seems to have changed in other peracarids. In the Mysida it is in the centre of the foregut and is more prominent than in Cumacea and Tanaidacea, where the it is reduced (Siewing 1956); in Amphipoda and Isopoda it is absent (for examples, see Scheloske 1976*a*; Wägele 1989, 1992; Coleman 1990, 1991, 1992). In this study, the location of the superomedianum in the middle of the stomach is
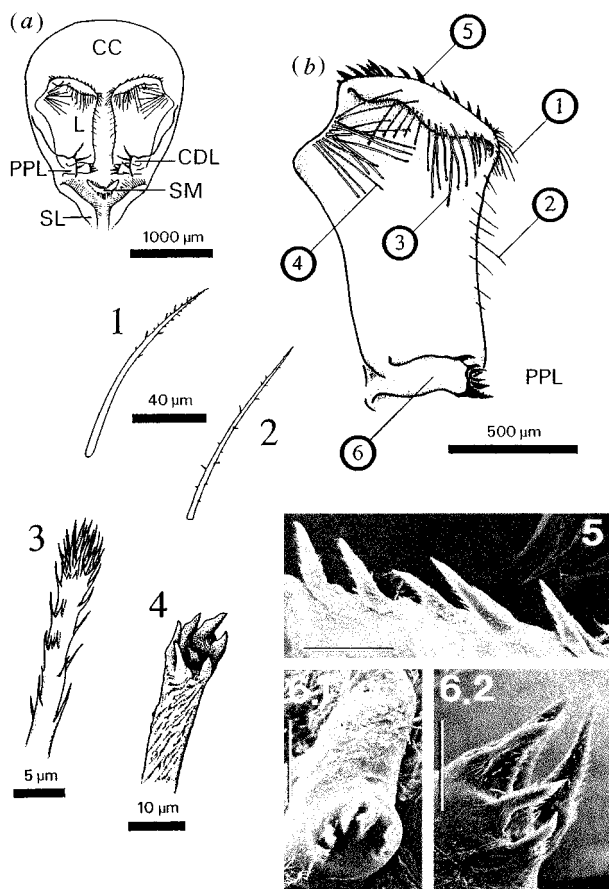
Figure 17. Lateralia and its armature in *Paramysis kessleri*. The number of the spines (types 1–4) slightly reduced in this drawing. (*a*) Dorsal view of cardiac region of stomach showing position of lateralia (L), dorsolateral infoldings (CDL) and superomedianum (SM). (*b*) Enlargement of left lateral infolding from *a*. Right side medial, upper side frontal. Circled numbers refer to six types of lateralian spines; single spines are shown in enlargements B 16. (1) Simple spine, located at edge of anterior margin and mediolateral margin of lateralia, dorsal to entry of oesophageal passage into cardiac chamber. (2) Spine type similar to (1), lined up on mediolateral margin of lateralia. (3) Caudally orientated spinule-tip spine on posterior side of anterior margin of lateralia. (4) Prong-tipped spine inserting on outer lateral margin of lateralia. (5) Spines on anterior side of anterior margin of lateralia. (6) Arrangement of teeth of posterior part of lateralia (TPL) on tip of nearly cylindrical, distinctly separated PPL. (6.1) TPL on PPL, viewed medially; lower side medial, upper side lateral. (6.2) Enlargement of TPL in (6.1), seen in caudal view; lower side ventral, left side lateral, right side medial. Scale bars (5, 6.2) 50 μm; (6.1) 100 μm. Abbreviations are listed in Appendix 1.

considered to be a feature of the Mysida, and for the Cumacea and Tanaidacea, where it is present in a similar location (Siewing 1952, 1953, 1956).

In *Mysis stenolepis* the superomedianum is continuous with a dorsal infolding (Friesen *et al.* 1986). This structure is called the 'dorsal plate' (in the figures designated as 'dorsal process'). It bears the stout prong-tipped spines found on the anterior part of the lateralia in other mysid species. In *M. stenolepis* these additional prong-tipped spines are directed downward. The conspicuous dorsal plate fuses with the superomedianum, in its posterior region called 'median process' by Friesen *et al.* (1986). A

dorsal process, as defined by this study (as an insertion of the musculus promotor superomedianum), is not shown (Friesen *et al.* 1986). Despite these peculiar features, the gross anatomy of the foregut in *M. stenolepis* resembles that of the foreguts studied here.

Within the Peracarida, strong chitinous dorsolateral teeth (DLT, figures 5*b*, 6*b*, 11*a*, 14*a,d,j–m*) only occur in the Mysida. These teeth may be one of the features that can be used for a phylogenetic analysis within the Mysida, e.g. in the genus *Siriella* dorsolateral teeth with a hook-like shape seem to be unique (figures 11*a*, 14*k,l*; see Molloy 1958, fig. 30). Dorsolateral teeth are missing in the Lophogastrida (Oshel & Steele 1989; W. Kobusch, unpublished data), Cumacea (Stappers 1909; Siewing 1952), Tanaidacea (Siewing 1953), Amphipoda (Storch 1989; Coleman 1992, 1994), and Isopoda (see Flasarová 1967, 1968; Scheloske 1976*b*; Wägele 1989, 1992; Storch 1989). In addition to the dorsal fold, there is a further similarity of mysid and euphausiacean foreguts, in that dorsolateral teeth also become part of the gastric mill (Suh & Nemoto 1988; Suh 1990). Apart from the dorsal fold and the dorsolateral teeth, a Mysida–Euphausiacea lineage is supported by the anatomy of the blood system of these taxa (Watling 1983). Haffer (1965) has already pointed out conspicious similarities between the mysid *Neomysis integer* and the euphausiacean *Thysanoëssa spinifer*, and Ullrich *et al.* (1991) found a resemblance between *Euphausia superba* and the Mysida. Despite the suggestions of Ullrich *et al.* (1991), the funnel region of *E. superba* is not the funnel region of a mysid; it is nearly identical with the lophogastridan funnel of *Eucopia sculpticauda* (see Siewing 1956) and *Gnathophausia ingens* (W. Kobusch, unpublished data). Recent findings show evidence that the Euphausiacea are more related to the Lophogastrida and the Mysida than to the Decapoda. A monophyletic origin of Syncarida, Euphausiacea, Peracarida, and Pancarida is considered, based on unifying characters of the eyes of the taxon 'Xenommacarida' (Richter 1993, 1994). If this interpretation of eumalacostracan phylogeny is accepted, the Euphausiacea is no longer at the base of the eucaridan phylogenetic tree, and the taxon Eucarida is invalid.

Compared with the Stomatopoda, Lophogastrida and Decapoda, the secondary filter grooves are reduced in the Mysida. In the Stomatopoda there are numerous secondary filter grooves (Petricevic 1916; Reddy 1935; Siewing 1956; Kunze 1983), in the Lophogastrida the inferomedianum posterius bears six to eight filter grooves (Siewing 1956; Oshel & Steele 1988) and in the Decapoda there are numerous secondary filter grooves as well (see, for example, Meiss & Norman 1977; Ngoc-Ho 1984; Felgenhauer & Abele 1985). Within the Peracarida, the Amphipoda possess two secondary filter grooves (see, for example, Agrawal 1965; Coleman 1990; Schmitz 1992), whereas the Cumacea, Tanaidacea, and Isopoda as well as the Thermosbaenacea have reduced the number of filter grooves to one single groove (Stappers 1909; Siewing 1952, 1956 1958; Fryer 1965; Wägele 1992). In the spelaeogriphacean species *Potiicoara brasiliensis* there is also only one single filter groove (W. Kobusch, unpublished data). In the Mysida there are two secondary filter grooves, except in *Spelaeomysis longipes*, *Gastrosaccus simulans* (Nath & Pillai 1972, 1973) and *Siriella jaltensis* (Gelderd 1909) which are bearing three pyloric filter grooves.

The lamina dorsalis posterior (LDP) is the outstanding feature in the funnel region (figures 4, 6*a*, 10*b*, 12*a*, 16*b*,*d*). The function of this lamina is to pass coarse material from the dorsal food channel into the anterior midgut without damaging the stomach–midgut connection (Siewing 1956; Storch 1989) (figure 11*e*–*g*). Unfortunately, many authors are misled by the morphology of the lamina dorsalis posterior. Very often the term 'funnel' is only applied to the dorsal extension of the pylorus reaching into the anterior midgut (figures 7 and 10; LDP). However, the lamellae ventrales also extend into the anterior midgut. Food particles too large for the pyloric secondary filter have to be prevented from entering the midgut glands. These semi-coarse particles can be passed dorsoposteriorly into the 'funnel' by the lamellae ventrales and the up and down movement of the inferomedianum posterius, which can close the ventral triangular opening of the lamella dorsalis posterior with its tip. So the term 'funnel' has to be extended to include the lamellae ventrales. Consequently in the Mysida the 'real' funnel consists of the lamina dorsalis posterior and the lamellae, which both pass coarse food into the midgut. Though its function is still not known, the valvula postero ventralis (see figures 2 and 12; VPV) probably should also be mentioned along with the funnel region. Again a complex of foregut features probably form a functional unit to pass on or stop food particles. The manifestation of the three homologous structures, lamellae ventrales, lamina dorsalis posterior, and valvula postero ventralis seems to be different in the peracaridan orders.

The lamina dorsalis posterior and the lamellae ventrales are fused in Amphipoda. Compared with the Mysida, the relative size of the valvula postero ventralis is larger in Amphipoda (Scheloske 1976*a*; Coleman 1991, 1992). In Isopoda, the funnel region is different from that in mysids and in amphipods. The lamellae dorsales protrude into the anterior midgut ventrally of the reduced lamina dorsalis posterior (Siewing 1951, 1956; Haffer 1965; Wägele 1992). The funnel region seems to be reduced in the Cumacea and Tanaidacea (Siewing 1951, 1952, 1953; Haffer 1965). The inferolateralia posteriores, and the setae of the super-olateralia, function as a funnel in Lophogastrida (Siewing 1951, 1953; W. Kobusch, unpublished data). In the Cumacea there seems to be another type of 'funnel region' (Stappers 1909).

Thus the stomachs of the peracaridan taxa, which all show eumalacostracan foregut features, seem to be specialized in their funnel regions. There are at least four different types of peracarid funnels (Lophogastrida, Amphipoda, Isopoda, and Mysida), and these seem to be important in the phylogenetic analysis of peracaridan taxa.

The following conclusions can be drawn from the data presented here.

1. The mysid foregut is a complex structure with a coop-erating set of spines and teeth, adapted to processing food. Despite different mysid food preferences, causing differences in foregut shape (volume) or in details of armature, all studied species display a uniform set of homologous characters.
2. Numbers 1–8 are inherited from the ground pattern of the malacostracan foregut. The atrium filter-unit (9) and the dorsal circulation channels (10) seem to be present principally in the Eumalacostraca. Conse-quently, characters 1–10 are plesiomorphic characters of the Mysida.
3. The specialized armature of the lateralia (11), the bulbous cardia with its dorsal fold (12), and the special construction of the funnel region (17), seem to be apomorphies for the Mysida.
4. The central position of the superomedianum (13) seems to be typical of Mysida, Cumacea, and Tanaidacea.
5. The characters of their foreguts not only reflect trophic differences, but can be useful in the elucidation of mysid phylogeny.

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APPENDIX 1. ABBREVIATIONS USED IN THE FIGURES

AMG, antechamber of the midgut glands

AO, aorta

APL, anterior part of the lateralia

ATR, atrium between end of IMA and beginning of IMP

BSR, basic spine row of the VSL, dorsally of the CSA, runs parallel to the CSA

CC, cardiac chamber

CDL, dorsolateral infolding of the cardia

CFP, coarse food particles

CMC, constrictor muscle of the cardia

CPX, carapace

CSA, clatri setarum anteriores, spines of the cardiac primary filter

CSP, clatri setarum posteriores, spines of the pyloric secondary filter

DC, dorsal caecum

DCC, dorsal circulation channel

DD, dorsal depression of the foregut, posterior of DP

DF, transversely running dorsal fold of the cardia

DFC, dorsal food channel of the pylorus

DLT, dorsolateral tooth, inserting on CDL

DMC, dilator muscle of the cardia
DMO, dilator muscle of the oesophagus
DP, dorsal process, near SM, place of insertion of MPS
DT, dorsocaudal point(s) of the hood-like IMP
DVM, dorsoventral musculature
ESS, tentorium, endoskeletal structure
FCS, filter cleaning setae of the secondary filter
HIM, lateral hollow of the anterior part of IMA
HYP, hypodermis
ILA, inferolaterale anterius
ILP, inferolaterale posterius
IMA, inferomedianum anterius, midventral cardiac ridge
IMP, inferomedianum posterius, midventral pyloric ridge
L, lateralia
LBR, labrum
LCC, lateral circulation channel of the cardiac chamber
LDP, lamina dorsalis posterior, funnel
LF, lateral, vertically running fold of the cardia
LG, labral glands
LM, longitudinal musculature
LMO, lacinia mobilis of the mandible
LV, lamella ventralis
MCP, musculus constrictor pylori
MD, mandible
MFE, mediofrontal extension of the lateralia
MG, midgut
MGG, midgut glands
MPS, musculus promotor superomedianum
MS, musculature
NE, nerves
OE, oesophagus
OMG, outpocketings of the MGG, forming the AMG

OSF, opening of the secondary filter groove
PC, pyloric filtration chamber
PFG, primary filter groove besides IMA
PI, pars incisiva of the mandible
PIA, pre-ridge of IMA
PIP, posterior side of IMP, back side of SPG
PM, pars molaris of the mandible
PPL, posterior part of the lateralia
PT, posterior tip of IMA
PTS, prong-tipped spines
SAS, spinelets anterior of the superomedianum (SM)
SFG, secondary filter groove, lateral channel within IMP
SIA, spines on the crest of IMA
SL, superolaterale
SLV, spines of the lamella ventralis (LV)
SM, superomedianum, cardiac dorsal piece
SP, space between outer wall of the pyloric chamber and IMP
SPG, spigot, the point of the hood-like posterior part of IMP
SPR, crosswise running spine row, anterior of IMA
SSL, spines of the superolateralia (SL)
SSM, spines of the superomedianum (SM)
TPL, chitinous teeth on the PPL
VCA, ventral connection of AMG with the foregut
VDO, valvula dorsalis oesophagi
VLO, valvula lateralis oesophagi
VPV, valvula postero-ventralis
VSL, ventral, mediodorsally orientated spines of the anterior part of the lateralia
VVO, valvula ventralis oesophagi