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Evidence for filter-feeding by the wood-boring isopod, *Sphaeroma terebrans* (Crustacea: Peracarida)

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Abstract

The morphology of the mouthparts and proventriculus of the wood-boring isopod *Sphaeroma terebrans* has been described, with particular reference to its possible filter-feeding abilities. Scanning electron microscopy revealed that while the mandibles might be designed to scrape pieces of wood from the cavity wall during boring, the rest of the mouthparts are better suited for microphagous feeding. Video observations of the mouthparts demonstrated the ability of *S. terebrans* to filter out particulate material from the water column, by means of the filtering setae on the first three pairs of pereiopods. The morphology of the gut was found to be largely similar to that of terrestrial herbivorous isopods; primary and secondary filter apparatuses were present, but the masticatory apparatus present in terrestrial herbivores was missing. The morphology of both the gut and mouthparts provides additional support for the assumption that wood is an unlikely food source for *S. terebrans*.

INTRODUCTION

Sphaeroma terebrans (Bate 1866) (Fam: Sphaeromatidae) is often regarded as the most common and destructive wood-boring isopod crustacean in brackish tropical waters, and has been held responsible for causing extensive damage to both living mangrove trees and wooden structures in locations as far apart as the Florida Everglades in the United States (Rehm & Humm, 1973) and the west coast of India (Lakshmana Rao, 1986). This species also has a widespread distribution ranging from Africa to South East Asia and Australia, and from South America to the Mediterranean Sea (Kensley & Schotte, 1989). While the literature on other wood-boring organisms such as the temperate water isopods *Limnoria* spp. and the bivalves *Teredo* spp. and *Bankia* spp. is abundant (see Turner, 1984), relatively little is known about the biology and ecology of the wood-boring Sphaeromatidae.

Information on the feeding structures of *S. terebrans* and its congenerics is sparse. Little is known of the structure and function of the sphaeromatid digestive system, while studies on the mouthparts are restricted to only a few species. These include brief descriptions of mouthpart function in *S. quoyanum* (Rotramel, 1975) and *S. terebrans* (Messana *et al.*, 1994). Filter-feeding, however, has never been directly observed in any member of the Sphaeromatidae, although it has been suggested to be possible in several species (Rotramel, 1975).

This study aims to investigate the functional morphology of the mouthparts and digestive system of *S. terebrans*. As past studies have suggested their possible filter-feeding capability (Rotramel, 1975), the present study will investigate the validity of this hypothesis.

MATERIALS AND METHODS

Scanning electron microscopy

Live animals were collected from driftwood along the banks of Stuart Creek, northern Queensland (Australia) at low tide. Whole animals were fixed in 10% formalin-acetic acid-calcium chloride (FAACC) and dehydrated by passing them through a graded ethanol series of 70%, 80%, 90% and 100%. Dehydrated specimens were dried in a Pelco CPD2 critical point dryer, coated in gold or platinum in a JEOL JUC-5000 sputter-coater, and observed under a Philips XL-20 scanning electron microscope. The mouthparts of larger specimens were removed from the animal and processed as described above. Intact guts were dissected from freshly killed animals, fixed in FAACC solution for at least 48 h, dehydrated and embedded in paraffin wax. Transverse

and longitudinal sections (7 μm thick) were cut and every fourth or fifth section examined under a compound microscope to determine how much tissue had been removed, as well as the location of gut structures. The specimen, still embedded in wax was then immersed in xylene for 24 h to dissolve away the wax. The dewaxed specimens of gut were then transferred to 100% ethanol before critical point drying, coating and observing with the scanning electron microscope.

Video observations

Live animals were starved for 2–3 days and narcotized by placing them in small vials of seawater, immersed in an ice bath for approximately 15 min. Narcotized animals were blotted dry and secured with a dissecting pin attached to the dorsum of the animals (see Fig. 3a). Observations were made using a JVC TK-870E colour video camera mounted on a Carl Zeiss Tessovar, illuminated by a Volpi 6000 fibre optic lamp. Mouthpart movements were initiated by placing a few drops of a suspension of the live marine alga *Pavlova salina* (Prymnesiophyta: Pavlovales) into the water above the animal.

RESULTS

Morphology of feeding appendages

A detailed description of individual appendages, from the posterior, and using some of the terms employed by Harrison & Holdich (1984), is given below.

Pereiopods

A marked dimorphism exists between the first three pairs of pereiopods and the remaining four pairs of pereiopods (Fig. 1a). The first three pairs are slender, and bear long rigid setae along the dorsal margin of the ischium and merus. The setae on pereiopods 1–3 are arranged in two parallel rows, with a separation of ≈ 20 μm between two adjacent setae in the same row. The remaining posterior four pairs, and especially the fourth are more robust, and lack the long dorsal setae. Each seta on pereiopods 1–3 bears two rows of fine setules arranged in a pinnate manner. The distance between two adjacent setules is approximately 5 μm.

Maxillipeds

The maxillipeds consist of a maxillipedal palp of five segments, and a medially placed, flattened maxilliped endite. The inferior margins of segments 2–4 of the maxilliped palp bear dense fringes of long (≈ 400 μm) setae (Figs 1b & c), while the maxilliped endites possess a row of stout, plumed setae on their inner (dorsal)

margins (Fig. 1c). The fringes along the maxillipedal palp consist of two types of setae, with (1) stiff and needle-like pinnately arranged setules, and with (2) curved, limp, pinnately arranged setules further bearing tertiary setules ≈ 2 μm in length.

Second maxillae

The three lobes are held close to the interior surface of the maxilliped palp, and *in situ* is completely hidden behind it (Fig. 1b). The two outer lobes bear long (> 250 μm), slender setae along their medial margins, while the inner lobe bears a dense fringe of finer, plumose setae (Fig. 1d). The setae on the outer lobes bear pinnately arranged flattened teeth ≈ 5 μm in length. The setae are arranged so that they are just long enough to skim over the distal ends of the setae on the maxillipedal palps as the second maxillae move medially.

First maxillae

The first maxilla consists of an inner and outer lobe (Fig. 1e) – the inner lobe with three medially curving spines bearing simple setae, and the outer lobe with several stout incisiform spines along the medial margin of the distal one-fourth of its length. The distal most spines are simple, but become progressively more serrated proximally and medially. The largest spines are > 100 μm in length, and all spines in the living animal have an amber coloration, from sclerotization of the cuticle.

Paragnaths

The paragnaths consists of a large outer lobe and a much smaller inner lobe – both lobes are covered on their outer surface, as well as on their distal and medial margins by fine dense setae, some > 200 μm in length. The paragnaths guard the space below the molar processes of the mandibles, which leads to the oesophagus.

Mandible

Each mandible (Fig. 1f) has an incisor process distally, a molar process medially, a much-reduced lacinia mobilis in between, and a lateral three-segment palp. The incisor processes are asymmetric, with the right process having two distinctly subequal teeth, and the left process bearing only one uneven tooth (Fig. 1f). The incisor processes in the living animal are a dark amber colour, indicating a high degree of sclerotization. The molar processes are almost square in shape, and form effective grinding surfaces with shallow grooves running diagonally across them.
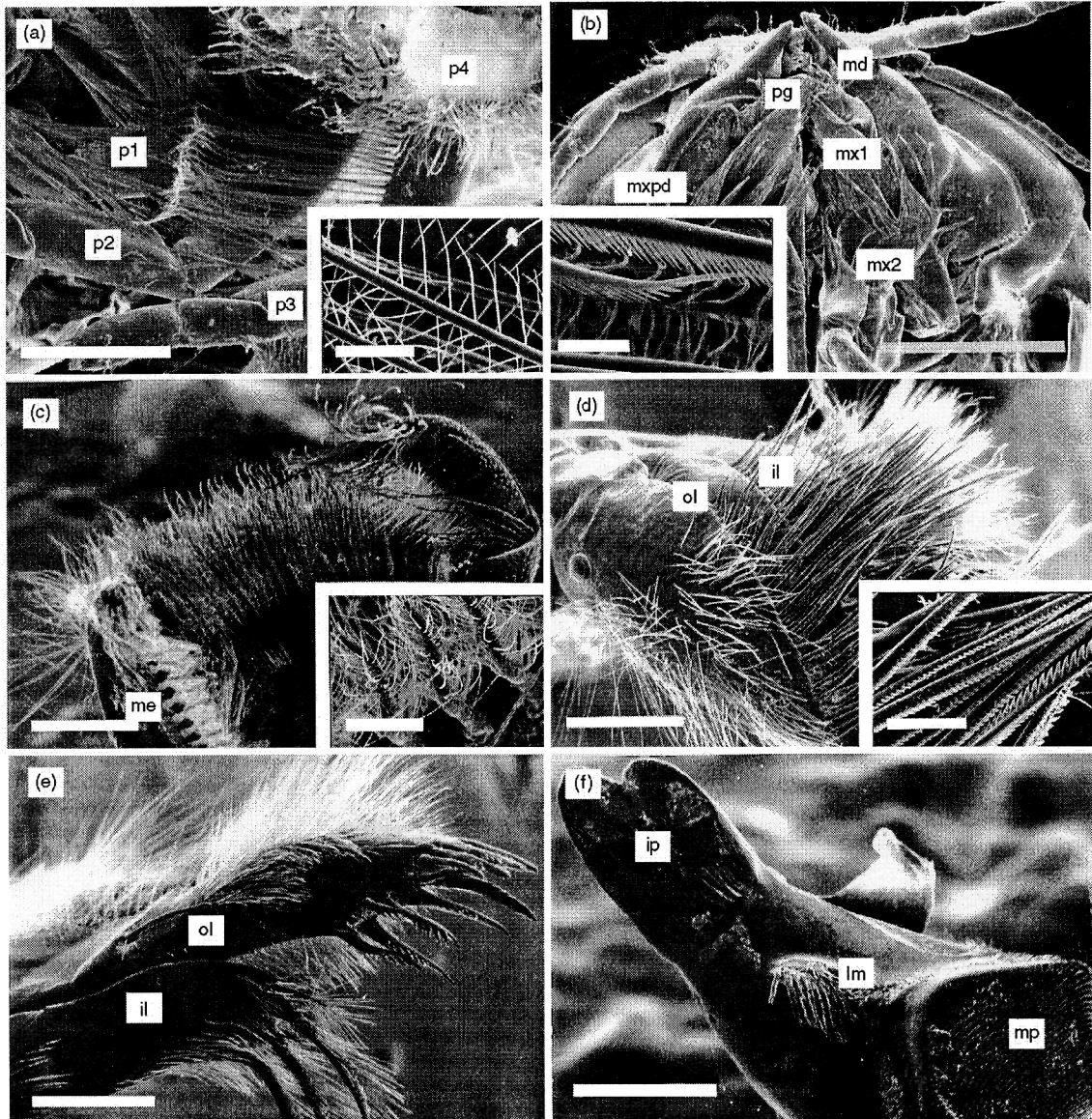
Fig. 1. Scanning electron micrographs (SEM) showing the feeding structures of *Sphaeroma terebrans*. **(a)** SEM of the first four pereiopods of *S. terebrans* from a ventro-lateral aspect. Inset: setae on the dorsum of the first pereiopod. Scale bar = 500 μ (Inset: 20 μ) **(b)** SEM of the oral region of *S. terebrans*, showing the position and relations of the mouthparts *in situ*. The animal's left maxilliped has been reflected inferiorly to reveal the second maxillae underneath. Inset: setae on the maxilliped. Scale bar = 1 mm (Inset: 10 μ) **(c)** Dorsal (inner) surface of the right maxilliped. Inset: setae on the inner margin of the maxilliped endite. Scale bar = 200 μ (Inset: 40 μ) **(d)** SEM of the left second maxilla. Inset: setae on the outer lobe. Scale bar = 200 μ (Inset: 40 μ) **(e)** SEM of the right first maxilla. Scale bar = 200 μ **(f)** SEM of the right mandible. Scale bar = 200 μ. Abbreviations: il, inner lobe; ip, incisor process; lm, lacinia mobilis; md, mandible; mx1, first maxilla; mx2, second maxilla; me, maxilliped endite; mp, molar process; mxpd, maxilliped; ol, outer lobe; p1–p4, pereiopods 1–4; pg, paragnath.

Functional morphology of the gut

As in many Crustacea, the proventriculus is the most complex part of the alimentary canal, with both the oesophagus and the hindgut being no more than a relatively simple and straight tube with slight folds in the wall. All parts of the isopod gut are lined with cuticle of varying thickness. The terminology employed by Storch (1987) and Storch & Štrus (1989) is used below to describe structures in the proventriculus of *S. terebrans*.

Proventriculus

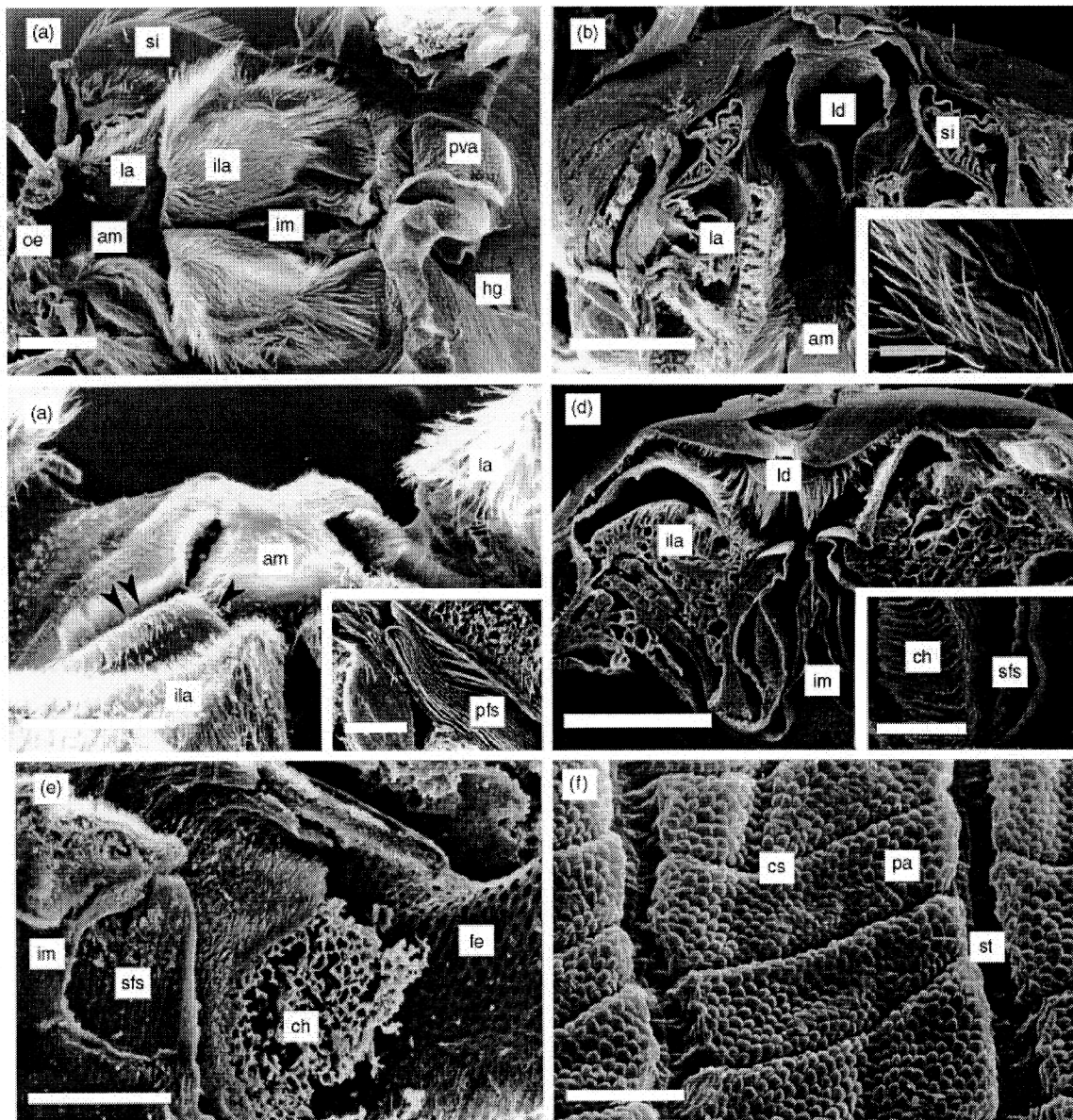The most complex part of the proventriculus of

Fig. 2. Scanning electron micrographs (SEM) showing structures within the proventriculus and hindgut of *Sphaeroma terebrans*. **(a)** SEM of the floor of the proventriculus of *S. terebrans*, showing the various protuberances rising from the ventral and lateral surfaces of the proventriculus. The left of the micrograph is anterior. Scale bar = 200 μ. **(b)** SEM of a section through the anterior proventriculus. Inset: Multi-pronged setae on the antero-inferior surface of the lateralia. Scale bar = 200 μ (Inset: 20 μ) **(c)** SEM of the superior surface of the primary filter apparatus, showing its relation to the lateralia. Double arrowheads indicate a primary filter channel; single arrowhead indicates a transport channel. Inset: section through a primary filter channel. Scale bar = 100 μ (Inset: 40 μ) **(d)** SEM of a section through the proventriculus at the level of the secondary filter. Inset: transverse section through the medial wall of the inferolaterale, showing the presence of channels formed by fused setae. Scale bar = 200 μ (Inset: 40 μ) **(e)** Para-sagittal section through the secondary filter apparatus, including the inferomedianum and the medial wall of the inferolaterale. Scale bar = 50 μ **(f)** SEM of the inner wall of the anterior hindgut. Scale bar = 20 μ. Abbreviations: am, anteriomedianum; ch, channels formed by fused setae; cs, cross striations; fe, fenestrations; hg, hindgut; ila, inferolaterale; im, inferomedianum; la, laterale; ld, lamella dorsalis; oe, oesophagus; pa, papillae; pfs, primary filter setae; pva, posterior ventral ampulla; sfs, secondary filter setae; sl, superolaterale; st, striations.
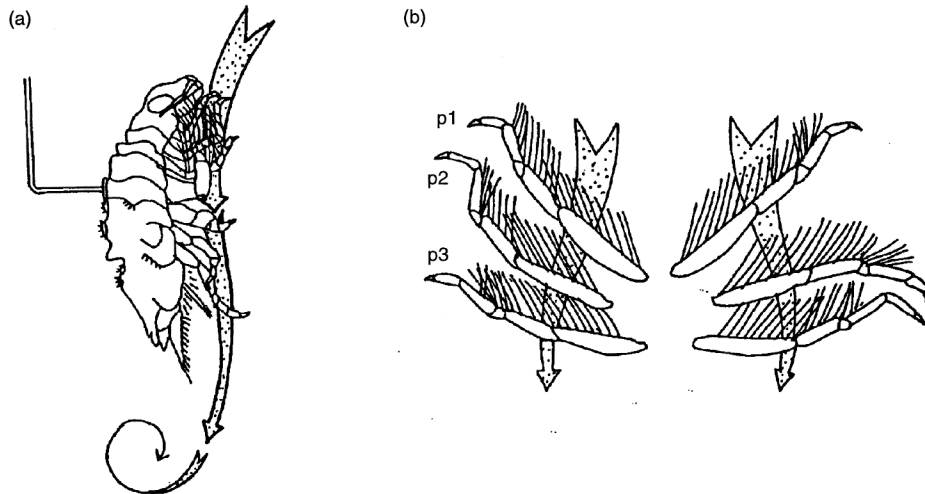
Fig. 3. (a) Diagram showing the direction of the water current generated by the beating action of the pleopods, as evidenced by the movement of algal culture added to the water column above the tethered animal's head. **(b)** Diagram showing the orientation of the first three pereiopods in relation to the water current. Abbreviations: p1–3, pereiopods 1–3.

S. terebrans is the ventral floor (Fig. 2a). The dorsal surface, or roof of the proventriculus is much simpler, bearing only a flattened, unpaired and setose structure called the lamella dorsalis, which is oriented posteriorly (Fig. 2b). On the lateral walls of the proventriculus are two large and heavily setose protuberances called the lateralia (Fig. 2b), which lie closely pressed against the filtering setae of the primary filter apparatus. The lateralia bear on their anterior surface several multi-pronged spines $\approx 20\,\mu m$ in length (Fig. 2b). These spines are the only evidence of a masticatory apparatus within the proventriculus. Lateral to and slightly above the level of the lateralia is another pair of flattened protuberances called the superolateralia (Fig. 2b); they have along their lateral margins a row of long, cylindrical spines. The superolateralia extend posteriorly, and form a broad shelf reaching the junction of the hindgut and proventriculus (Fig. 2a).

Between and ventral to the lateralia lies the primary filter apparatus, which consists of an upward and anteriorly directed protuberance (the anteriomedianum) rising from the floor of the proventriculus (Fig. 2c), on either side of which are two rows of fringed filtering setae. The rows of setae are oriented at approximately 60° to the midline of the proventriculus, and form the antero-dorsal wall of a filtration channel running along the length of each side of the primary filter (Fig. 2c). The gap between two adjacent setae is $\approx 2\,\mu m$, which is therefore the maximum size of the particles that can pass through this filter. A transportation channel leaves the mid-point of each filtration channel at approximately right angles, and leads to the groove lying between the two remaining paired structures of the proventriculus floor, the inferolateralia (Fig. 2c).

A median ridge (the inferomedianum) runs along the length of this groove (Figs 2a & d), and forms part of the secondary filter apparatus. In cross-section, the medial border of each inferolaterale is seen to project medially into the adjacent groove, and form a shelf-like structure over the apex of the inferomedianum (Fig. 2d). The medial walls of the inferolateralia within the groove form the outer valves of the secondary filter, and are lined with a dense (up to $30\,\mu m$ thick) layer of fused setae, which form outward-radiating channels (Figs 2d & e).

The cuticle lining the medial wall of the inferolateralia has a reticulate appearance, with fenestrations of up to $2\,\mu m$ in diameter leading to the epithelium beyond (Fig. 2e). The surface of the inferolateralia immediately bordering the central groove has numerous short, and closely packed setae (Figs 2d & e). The dorsal surfaces of the inferolateralia have numerous long and slender setae, which give this area a bushy appearance. Their most posterior portions extend deeply into the hindgut, and form the posterior ventral lamellae (Fig. 2a). The inferomedianum rises as a pyramidal projection with an onion-shaped apex from the floor of the central groove between the inferolateralia. On either side of the inferomedianum rises a row of flattened, fringed setae, which point posteriorly and form the secondary filter *sensu stricto* (Fig. 2d).

Hindgut

The hindgut is a simple tube with shallow folds along its dorsal and ventral walls. A thin cuticle lines the lumen of the hindgut, and carries numerous striations running in a more-or-less circular manner around the gut for its entire length (Fig. 2f). These striations are regions where the cuticle is very thin; also visible at this magnification are numerous cross-striations running almost perpendicular to the larger, circular striations, as well as the presence of copious amounts of papillae on the
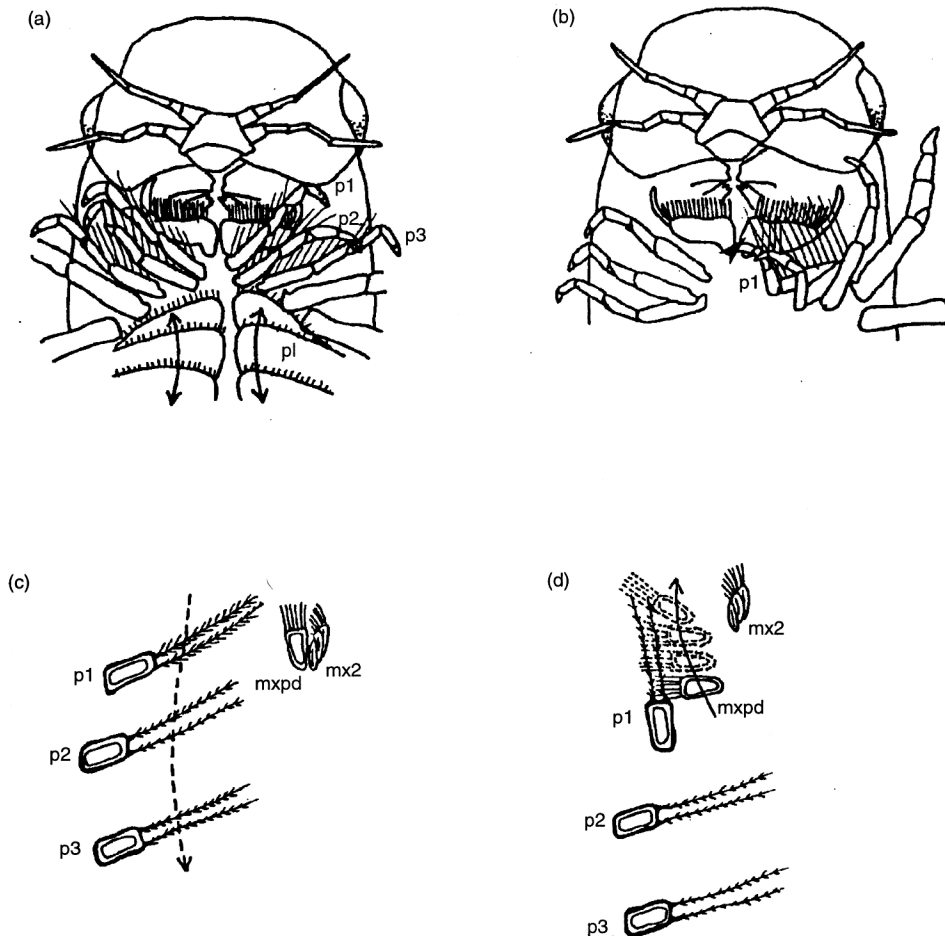
Fig. 4. Sequence of events obtained from video observations of live tethered animals. **(a)** Typical position of appendages while filter feeding. Arrows indicate beating action of pleopods. **(b)** Comb setae of left maxilliped (arrowhead) removing food particles trapped on the setae of the left first pereiopod. **(c)** Schematic sagittal section through the first three pereiopods, a maxilliped and a maxilla, showing their relative positions as water flows through the setae on the pereiopods. **(d)** Schematic sagittal section through the first three pereiopods, a maxilliped and a maxilla, during the 'combing' action of the maxilliped on the first pereiopod. Abbreviations: mx2, second maxilla; mxpd, maxilliped; p1–3, pereiopods 1–3; pl, pleopods.

surface of the raised regions demarcated by intersecting striations.

Behavioural observations

Following the introduction of a few drops of algal culture into the water, a feeding current was generated by the rapid beating action of the pleopods at a rate of $\approx 329 \pm 26$ (mean $\pm$ SE) beats per min. The feeding current passed posteriorly along the ventral surface of the animal and through the anterior three pairs of pereiopods (Fig. 3a). Figures 4a and c show the typical position of the three pairs of anterior pereiopods during the feeding process. The setae on these pereiopods are oriented perpendicular to the water current, forming a wide, shallow U-shaped filter with the arms pointing upstream, and the base pointing in the direction of the water current (Fig. 3b).

Feeding activity is sporadic, and occurs subsequent to a bout of filtering activity. During feeding, each pereiopod is moved downwards, and the filtering setae are brought to lie parallel to the ventral surface of the animal (Figs 4b & d). Food particles trapped on the setae of the pereiopod are then removed by the mouthparts. The maxillipeds are rotated through 90° ventrally, allowing the tufts of setae to comb through the setae on a pereiopod of the corresponding side. The second and third pereiopod of the same side are also brought into the same position as the first, and combed through in quick succession. The pereiopods on the opposite side are then combed in an identical manner.

Figures 5a & b show the passage of food material collected by the setae of the maxilliped into the mouth.
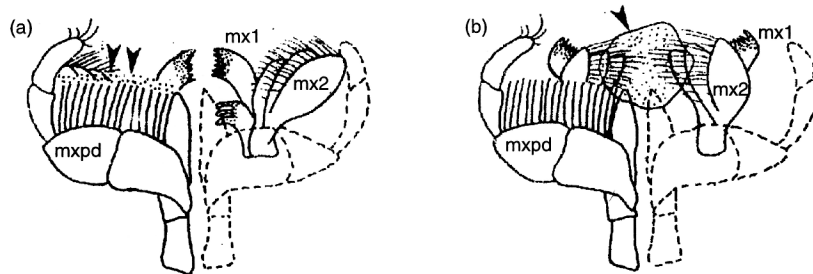
Fig. 5. Sequence of events obtained from video observations of live tethered animals, showing processing of food collected by the comb setae of the maxillipeds. The left maxilliped and its setae have been omitted for clarity. **(a)** Position of mouthparts following the combing of the pereiopod setae by the maxillipeds. Double arrowheads indicate food particles collected by the maxilliped. **(b)** Formation of a loose bolus of food and mucus (arrowhead) by the medial movement of the second maxillae. Abbreviations: mx1, first maxilla; mx2, second maxilla; mxpd, maxilliped.

The food material removed from the setae on a pereiopod collects at the distal ends of the comb setae of the maxillipeds. This allows the long setae on the outer two lobes of the second maxilla, which are close to the inner surface of the maxilliped, and protrude above the ends of the comb setae, to scrape the collected food off the ends of the comb setae. Thus, as the second maxillae move medially, the food material on the ends of the comb setae would also be transported medially by the long setae. Simultaneously, the first maxillae open to receive the food material. At this stage, the food material can be seen as a loose bolus held together in mucus (Fig. 5b). The second maxillae then open up while the first maxillae move medially and push the bolus into the mouth. This simultaneous opening of the first maxillae and closing of the second maxillae (and *vice versa*) is repeated for a few seconds following each 'combing' session, until all the collected food material is removed from the comb setae. Once this action ceases, the maxilliped endites rapidly jerk upwards (towards the mouth) a few times to ram food material into the mouth by means of the stout, plumose setae on the inner surface of the endite described earlier.

DISCUSSION

The gross morphology of the mouthparts was found to be generally similar to the description given by Harrison & Holdich (1984) for *S. terebrans*. Behavioural observations and electron microscopy provide evidence of the filter-feeding capability of *S. terebrans*. The means by which the isopod filters out particles suspended in the water column seems to be similar to the 'aerosol filtration' mechanism suggested by LaBarbera (1984), wherein particles of a wide range of sizes can be effectively captured by the filtering device. Electron microscopy has shown that the filter setae on the pereiopods are well suited to trap particulate food material of a size $> 5 \mu m$. Several types of phytoplankton including *P. salina*, offered to *S. terebrans* during the course of the video observations, fall within this size range.

Several types of algal species could form an important part of the diet of *S. terebrans*. While much has been learned about the taxonomy and distribution of phytoplankton in the seas surrounding Australasia in the past decade (Jeffrey & Hallegraeff, 1990), there have been relatively few studies of phytoplankton species diversity in mangrove habitats anywhere in the world (Robertson & Blaber, 1992). Species such as *Asterionella japonica*, *Chaetoceros abnormis* and *Coscinodiscus* spp. are commonly encountered in Australian waters (Jeffrey, Vesk & Hallegraeff, 1990), and could form important constituents of the diet of *S. terebrans*. In addition to these larger (20–200 μm) phytoplankton, smaller species of 'nanoplankton' (2–20 μm) may also figure prominently in the diet of *S. terebrans*.

Further evidence of a microphagous feeding habit may be obtained from observations on the structure and functioning of the mouthparts of *S. terebrans*. The paragnaths, the first and second maxillae, and the maxillipeds are well endowed with long (200–400 μm) setae, ideal for transporting particulate food material into the mouth. This contrasts sharply with the structure of corresponding mouthparts of *Limnoria* spp., where the setae are shorter and stouter in relation to the appendage on which they are borne (Menzies, 1959). Furthermore, the mandibles of *Limnoria* are equipped with a sharp point and toothed edge on the right appendage, and a denticulate flat surface on the left appendage (Qayle, 1992). While this would allow the animal to remove thin slivers of wood small enough to be ingested, it seems unlikely that the blunt incisor processes of the sphaeromatid mandibles would be able to achieve the same effect. The mandibles of *S. terebrans* are held motionless during the process of filter feeding, and are probably brought into use only during the process of digging or extending a borehole when, as Messana *et al.* (1994) noted, pieces of wood removed from the borehole wall are ejected by means of the water current produced by the beating pleopods.

Movements of the first maxillae, during the passage of food material from the comb setae of the maxillipeds to the mouth indicate that these appendages might perform a preliminary triturating action on the food

before it is ingested. The repeated opening and closing of thc first maxillae following each bout of filtering and 'combing' would allow the incisiform spines of the outer lobe of the first maxilla to partially break open any large phytoplankton cells, such as some diatoms.

The water current generated by *S. terebrans* within its borehole as postulated by Rotramel (1975) and observed by Messana *et al.*, (1994) has been partially verified by video observations of tethered animals. As the isopods are oriented with their anterior end facing the blind end of the boreholes, and as the water passes posteriorly through the filter setae on the pereiopods along the ventral surface of the animal, water entering the borehole would do so over the dorsal surface of the animal and pass anteriorly. It is worth noting that this pattern of water flow is in essence similar to the inhalent and exhalent currents produced by molluscan wood borers such as *Teredo* and *Bankia*, where phytoplankton containing water is drawn in through an incurrent siphon and filtered by the gills, before being ejected through an excurrent siphon (Qayle, 1992).

The structure of the gut of *S. terebrans*, and in particular the proventriculus or stomach, was found to resemble closely that of terrestrial herbivorous isopods such as *Porcellio scaber*, *Tylos latreillei* and *Ligia italica*, as described by Storch (1987), Hames & Hopkins (1989) and Storch & Štrus (1989). A primary and secondary filter apparatus, as well as the protuberances on the lateral walls of the proventriculus, namely the lateralia and superolateralia, are features common to all these species. One major difference, however, was the absence of a distinct masticatory apparatus in the anterior proventriculus of *S. terebrans*. Such a structure has been observed only in terrestrial isopods, where it consists of a region of stout cuticular spines on the ventral surface of the lateralia, as well as lateral to the primary filter setae on the floor of the proventriculus. As the regions bearing these spines oppose each other, it has been suggested that ingested food is triturated between these regions before passing through the filter systems (Storch, 1987).

While such a masticatory apparatus would be ideal for an organism feeding on tough plant material such as wood, its absence in *S. terebrans* suggests a diet consisting predominantly of finer, easily processed food such as bacteria, fungal hyphae and phytoplankton. The only structures in the gut of *S. terebrans*, which could possibly have a triturating function, are the multi-pronged spines present on the anterior surface of the lateralia. These spines are of an ideal size and in an ideal location to rupture all but the largest of phytoplankton cells. Fluids and particulate material of a size < 2–$3\,\mu m$ are forced into the filtration channels by the pressing action of the lateralia against the setae of the primary filter, following which the filtrate is transported to the secondary filter. Only particles of a size $< 1\,\mu m$ can be admitted between the setae of the secondary filter and transported to the digestive glands. This is brought about by the contraction of the intrinsic muscles within the inferolateralia. It is therefore evident that the primary function of the proventriculus has been to reduce the dimensions of ingested particulate matter, from an initial size of $> 5\,\mu m$ to a final size of $< 1\,\mu m$, thus facilitating the digestion of food material within the digestive glands.

The channels and fenestrations observed in the cuticular lining of the medial surface of the inferolateralia have never been described previously from the proventriculus of any isopod. The dense setae at the medial extremities of the channels closely resemble the 'filter press setae' on the outer valve of the pyloric filter of *Penaeus merguiensis* as described by King & Alexander (1994), and probably do not allow the passage of solid particles into the channels beyond. These channels on the medial surface of the inferolateralia were reported by Nicholls (1931) in *Ligia oceanica* as a 'network of fine fibres', while the cuticle bearing fenestrations was described as a 'plate with many minute holes'. It seems likely that fluids would be able to enter these channels, and be absorbed directly by the epithelium of the proventriculus *via* the fenestrations in the cuticular lining of the inferolateralia. High amounts of glycogen were reported from the epithelium of the proventriculus of the terrestrial *Tylos latreillei* (Storch & Štrus, 1989) and *Porcellio scaber* (Storch, 1987), as well as the amphibious *Ligia italica* and *Ligidium hypnorum* (Štrus, Drobne & Ličar, 1995), although no mention was made of either the channels on the medial walls of the inferolateralia, or the fenestrations in the cuticle in the same region.

The morphology of the gut therefore complements that of the mouthparts; the structures present in the proventriculus would not be able to process ingested fragments of wood effectively, especially since a masticatory apparatus is not present. While recent studies suggest that cellulose digestion is possible in *S. terebrans* (Benson, Rice & Johnson, 1999), the evidence presented in this study point to the strong likelihood that *S. terebrans* derives its nutrition from a microphagous filter-feeding habit, with the wooden substrate into which it bores serving only as a source of shelter. These findings call for a reassessment of the possible interactions between *S. terebrans* and their mangrove habitat, and in particular, the live mangrove trees into which they bore. It has been suggested that marine borers such as *S. terebrans* can both harm (Rehm & Humm, 1973; Rehm, 1976; Perry & Brusca, 1989) and benefit (Simberloff, Brown & Lowrie, 1978; Barkati & Tirmizi, 1991) coastal mangrove ecosystems. The fact that boring activity by *S. terebrans* is not continuous (Becker, 1968), and the fact that the isopod does not appear to consume the mangrove tissue, indicate that the effect of borers on mangrove trees might not be as straightforward as is commonly thought.

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