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A comparative study on the tubes and feeding behaviour of eight species of corophioid Amphipoda and their bearing on phylogenetic relationships within the Corophioidea

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SUMMARY

Observations are presented on mouthpart functional morphology, and on feeding, grooming and defaecatory behaviour of eight species of corophioid Amphipoda, viz. *Corophium bonnellii*, *Lembos websteri*, *Aora gracilis*, *A. spinicornis*, *Gammaropsis nitida*, *Ericthonius punctatus*, *Jassa falcata* and *J. marmorata*. These data are considered in relation to tube structure and amphipod posture in relation to the tube. All these species occupy double-ended cylindrical tubes made from 'amphipod silk' secreted by the third and fourth peraeopods, incorporating sediment and other debris to varying degrees. Uniquely among this set of species, however, *E. punctatus* has a tube that is architecturally distinct. It tapers along its length and has a distinctive oblique main entrance at its widest end. This end is used preferentially. The other species studied use either opening with equal facility. Such a feature is adaptive in facilitating deployment of the antennae and shielding the head of *E. punctatus*.

Two groupings of species are proposed: group A which feed inside their tube using pleopod-induced through-tube currents, and group B which feed outside or at the entrance to their tube using external water currents. Group A includes *C. bonnellii*, *L. websteri* and the *Aora* spp. Group B includes *E. punctatus* and the *Jassa* spp. *Gammaropsis nitida* exhibits traits from both groups, adding weight to its perceived status as a genus representative of the stem corophioid. The ischyrocerid habit of externalizing food-gathering may be regarded as the first step along an evolutionary line leading to the rod-building podocerid types and ultimately towards the caprellids. All species examined show a degree of flexibility in their feeding habits which helps to explain the success of this taxon, which has radiated into a great diversity of aquatic biotopes.

1. INTRODUCTION

Accounts of feeding behaviour in corophioid amphipods generally relate to common intertidal or fouling species, with emphasis on members of the genus *Corophium*; most notably on *C. volutator* (Hart 1930; Trusheim 1930; Meadows & Reid 1966; Ingle 1969; Mossman 1977; Icely & Nott 1985; Bärlocher *et al.* 1988; Gerdol & Hughes 1994). Other studies include those of Enequist (1949), Shillaker (1977), Foster-Smith & Shillaker (1977), Shillaker & Moore (1987*a*) on *C. bonnellii*; Lakshmana Rao & Shyamasundari (1963) on *C. triaenonyx*; Hughes (1975) on *C. sextonae*; Nair & Anger (1979*a*) on *C. insidiosum*, and Miller (1984) on *C. spinicorne*, *C. insidiosum* and *C. salmonis*.

Accounts of feeding behaviour in other tube-dwelling corophioid genera comprise work on *Amphithoe longimana* (Holmes 1901); *A. rubricata* (Skutch 1926); *Unciola irrorata* and *U. inermis* (Schaffner 1980); *Lembos longipes* (Enequist 1949); *L. websteri* (Shillaker 1977; Foster-Smith & Shillaker 1977; Shillaker & Moore 1987*a*, *b*); *Leptocheirus pilosus* (Goodhart 1939); *Ericthonius brasiliensis* (Zavattari 1920); *E. difformis* (Greze 1970); *E. punctatus* (Hughes 1975, as *E. brasiliensis*); *E. rubricornis* (Schaffner 1980); *Jassa falcata*/*herdmani* [identification uncertain; see taxonomic revision by Conlan 1989] (Hughes 1975, as *J. falcata*); *J. marmorata* (Nair & Anger 1979*b*, as *J. falcata*); and *Jassa falcata*/*herdmani*/*marmorata* [identification uncertain; see above] (Boero & Carli 1979, as *J. falcata*). Although Schellenberg (1929) reported certain life history details for the isaeid *Microprotopus maculatus* and Enequist (1949) speculated on the likely method of food capture for *Gammaropsis sophiae* (as *Podoceropsis*) and *Protomedeia fasciata*, no details of feeding behaviour have been published for representatives of the Isaeidae.

All species, except *Amphithoe* spp. (which are mostly phytophagous; Skutch 1926), feed on suspended or deposited particles including microflora and detritus.

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No study has described the activity of the food handling limbs and the process of food transfer between them in such detail as did Dennell (1933, 1934) for the haustoriid *Haustorius arenarius*. Such information, if available, would greatly facilitate the interpretation of comparative morphology (Moore 1981; Fryer 1988; Lauder 1990; Barnard & Karaman 1991) and possibly provide direct evidence of any selectivity in food gathering. It would also assist in the deduction of evolutionary patterns and systematic relationships within this polyphyletic group (Myers 1981; Barnard & Barnard 1983; Barnard & Karaman 1991).

The study of mouthpart function in these amphipods is handicapped by their small size, the rapidity of their movements and their close juxtaposition; most of the functionally significant elements being directed medially and hidden from view ventrally.

Our objectives were to observe and describe, as far as possible, how the limbs and mouthparts of each species were used in the processes of food capture, sorting and ingestion and, in addition, to assess the importance and interrelationship between tube form, tube hydraulics and the amphipod's position relative to its tube during feeding.

2. MATERIAL AND METHODS

Most species were collected from kelp holdfasts (mainly *Laminaria hyperborea* with some *L. saccharina*) from the shallow sublittoral zone by SCUBA diving at coastal sites around Great Cumbrae Island, Firth of Clyde (54° 45′ N; 4° 54′ W) and Linne Mhuirich rapids, Loch Sween, Scotland (55° 59′ N; 5° 39′ W). *Jassa marmorata* was obtained from scrapings of constant-head standpipes draining the seawater holding tanks in the Specimen Supply Department at U.M.B.S. Millport. *Gammaropsis nitida*, an associate of hermit crabs, was obtained by divers collecting *Pagurus bernhardus* off Keppel Pier, Millport. *Aora spinicornis* was obtained from red algal turf (mostly *Laurencia platycephala* and *Gigartina acicularis*) by diving in Lough Hyne, Ireland (50° 31′ N; 9° 18′ W)(for full details, see Dixon 1992).

The experimental methods used broadly followed those outlined by Shillaker (1977) and Shillaker & Moore (1987*a*), and most observations took place with the aid of a stereo-dissecting microscope and a fibre optic cold-light source. Although a long time was spent underwater in attempts to follow feeding behaviour *in situ*, most species were never visible. Occasional exceptions were *Ericthonius punctatus*, *Gammaropsis nitida* and *Jassa falcata*.

Kelp holdfasts (or whatever) were placed in large white trays filled with sea water. Amphipods which swam out were sorted to species, picked out by pipette, and transferred to 9 cm glass crystallizing dishes containing sea water. They were either allowed to build tubes on the dish floor (sometimes with the aid of added detritus), or were persuaded to take up residence in tube substitutes made from glass capillary tubing. The readiness of most species to live in glass tubing (Shillaker 1977; Shillaker & Moore 1987*a*) facilitated observations of behaviour and mouthpart movements. Mature *Corophium bonnellii* were most often installed in tubes of 1.2 mm internal diameter: larger species preferred tubes of 1.5 mm internal diameter. Information was also gained through watching the animals living in their own tubes, whether in complete or sectioned kelp holdfasts, on hermit crab shells (with or without the hermit crab occupant), or in sections of tube matting scraped from seawater supply pipes as appropriate.

Video recordings were made, using a Burle TC 1504X low light camera with C-mount adapter on the microscope phototube, so that behavioural sequences could be observed repeatedly if necessary. Fast-frame video photography was also used to help analyse details of food-handling in all species, except *A. spinicornis*, utilizing either naturally occurring or artificial suspensions to visualize water currents. The high-speed systems used were a Kodak Spin-Physics unit (Kodak Ectapro 1000 imager and 1000 processor), hired from and used at the National Engineering Laboratory in East Kilbride, and an NAC HS 400 camera and VCR system kindly made available for use by the Dunstaffnage Marine Laboratory at Oban, Scotland. With the Kodak system, recording took place at tape speeds of 60–125 frames s^{-1} (pps), and was transferred onto VHS tape for viewing. The NAC system was used at a tape speed of 200 pps and a shutter speed of 1/2500 s. Recordings were again edited, using a variable speed playback facility, onto VHS tape.

Observations and video-recording took place at room temperature, with the exception of some of the high-speed video work done in a cool-room facility at 15 °C. Currents through the glass tubes and around the mouthparts during feeding were usually visible due to the motion of naturally-occurring suspended silt and detritus particles. Suspensions of carmine red, starch granules and fluorescein were also used; introduced into the vicinity of the tubes by finely drawn-out Pasteur pipettes. Measurements were made using a calibrated eyepiece micrometer, and observations were timed with either a stopwatch or the video screen time display. Estimates of current speed through the tube, obtained by timing suspended detritus particles over measured distances, were converted from units of mm s^{-1} to ml h^{-1} (based on the known sectional area of the glass tubes used) for comparison with data obtained by Foster-Smith & Shillaker (1977).

Illustrations are provided of the habitus, mouthparts and gnathopods of *C. bonnellii*, using it as a model corophioid to assist in visualizing the behaviour we describe (for detailed comparative illustration and description of mouthpart morphology of all species, see Dixon 1992).

3. RESULTS

(*a*) *Observational conditions*

Each species studied reacted differently in the laboratory which affected the way in which they were observed and treated. Such differences also affected the quality and interpretation of the behavioural observations. All the aorid species and *Corophium bonnellii*

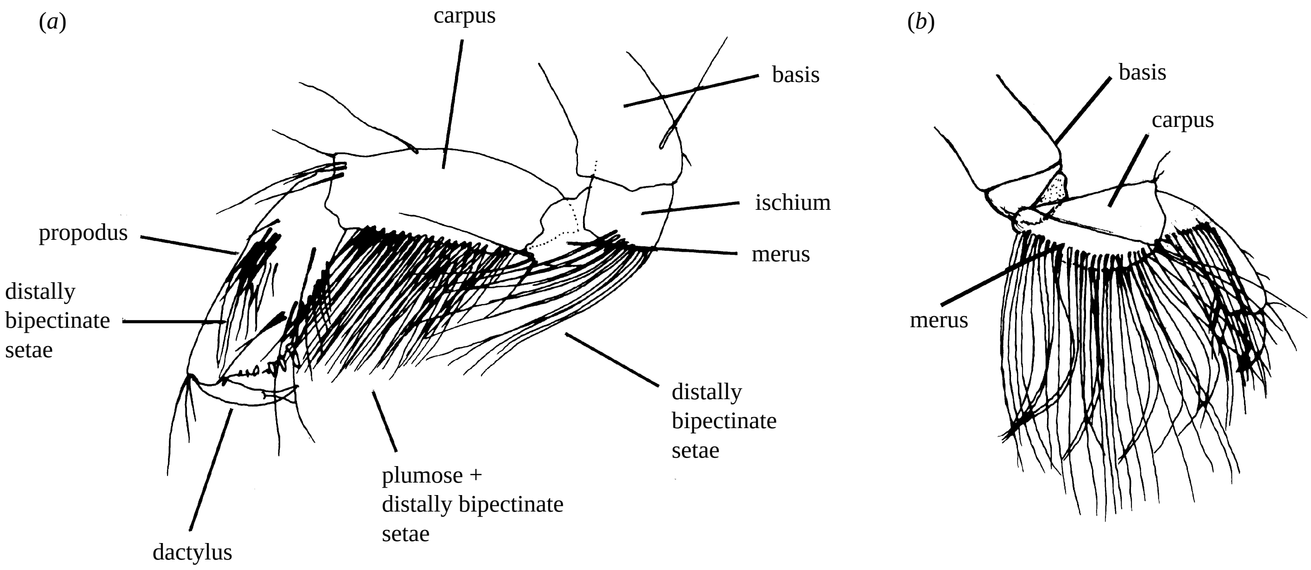

Figure 1. *Corophium bonnellii* (female), distal articles of gnathopods. (*a*) Gnathopod 1 (right, medial view). (*b*) Gnathopod 2 (left, medial).

settled down quickly and, if deprived of their tubes, would quickly build new ones or enter the glass substitutes provided. Once established, however, aorids were more reactive to microscope lights and sudden movement or shadows than *C. bonnellii* and abandoned their tubes more readily. The use of bright lights was therefore avoided except during photography. *Gammaropsis nitida* and the ischyrocerid species were more irritable still, and only rarely settled down in observation dishes. If placed in the dish without its pagurid host, *G. nitida* usually lay quiescent, on its side, on the dish floor. Both *Jassa* spp. swam rapidly around the dish before clinging to the walls, whilst *Ericthonius punctatus* swam vertically upwards and became caught in the surface film. All could be coaxed into glass tubes, but would often abandon them, especially if disturbed by lights or movement. Much observational work was therefore accomplished with these more reactive species installed in their natural tubes, in which they were not so responsive to external stimuli.

(*b*) ***Tube form and feeding behaviour***

(i) Corophium bonnellii (*figures 1–4*)

Tubes of this species were the longest, relative to the occupant's body length, of the species studied (1.5–2 × body length). They were sometimes unattached to a hard substratum (such as holdfast haptera) for much of their length, were rarely straight and the openings at each end were always narrower than the rest of the tube. When living in its own tube, *C. bonnellii* was rarely visible; the only evidence of its occupancy being water moving in or out of the tube openings. All information on feeding was obtained from animals installed in glass tubes. Within these, *C. bonnellii* quickly spun a closer-fitting inner tube, complete with restricted entrances, which often tended to spiral around the inner glass surface if the tubing diameter was much larger than that of the amphipod. A current was drawn through the tube constantly (in an anteroposterior direction) by the metachronally beating pleopods. Suspended particles passed through the tube of one individual at from 2.9–6.4 mm s^{-1} (11.8–26.1 ml h^{-1}) at 10 °C (no. obs. = 14). Pleopod activity was highest during feeding, or when the amphipod was disturbed. Depending on the beat rate of the pleopods, the position held by the abdomen varied from flexed vertically downwards from the peraeon (at low activity levels), to straightened-out behind the body (at the highest beat rates). The abdomen was only curled ventrally during rare quiescent periods.

Whilst feeding, *C. bonnellii* could position itself anywhere within the tube. Water-borne detritus was trapped and ingested with or without the use of the long setulate setae on the second gnathopods.

When the second gnathopods were not in use, the two rows of long setae which line the posterior margins of each merus (left and right, see figure 1) were held close to the underside of the peraeon, out of the through-tube current. When deployed they were fanned out to form a funnel-net (figure 2*a*, *b*). The left and right lateral rows of setae formed the main (ventral and lateral) parts of this net; the tips of these setae were applied to the inner circumference of the tube, so the net occluded its entire lumen ventral to the amphipod (figure 2*b*). The left and right medial rows of setae together formed the uppermost part of the net; the tips of these setae rested on the first gnathopods which, in turn, were held close beneath the maxillipeds. When the net was fully deployed, virtually all the water drawn through the tube passed through it. However, it was often not fully extended and then only sampled a fraction of the seston passing through the tube.

When the gnathopod 2 setal net was in use, it was periodically groomed by the first gnathopods and the intercepted seston collected and passed to the mouthparts (figures 3 and 4). The net was first closed, i.e. the meral setae of the second gnathopods were folded into their respective left and right bundles against the underside of the amphipod. The second gnathopods then moved forward slightly towards the mouthparts while the first gnathopods swung back between the

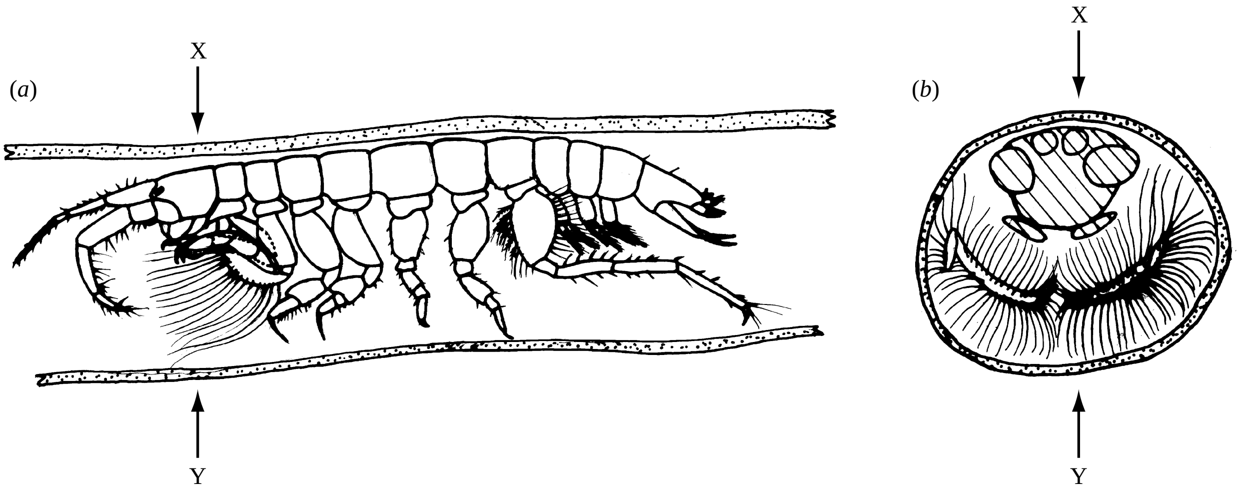

Figure 2. *Corophium bonnellii* (female), habitus. (*a*) Longitudinal section of tube; (*b*) transverse section of tube at XY, showing degree of lumen occlusion by gnathopod 2 filter.

second pair. The first gnathopods were then held so that the left and right ischial articles met medially and the carpi projected anterolaterally just in front of, and parallel to, the fused merus and carpus of the second gnathopods. In this position, the first gnathopod ischial setae (distally bipectinate) were aligned to comb along the medial edges of the folded gnathopod 2 setal bundles; the first gnathopod carpal setae (both fine plumose and robust distally bipectinate types) were positioned to brush through the net bundles from the dorsal side; and the first gnathopod propodi, with medially-directed arrays of bipectinate setae, were crooked ventrally around the lateral edges of each gnathopod 2 net bundle. During the combing process, the second gnathopods moved posteriorly; pulling their setae through the combs of gnathopod 1. At the same time, the first gnathopods also moved forward, pulling their combs in a proximal to distal direction through the gnathopod 2 net bundle. As they pulled forward, the first gnathopods extended and straightened anteriorly over the mouthparts. They then brushed each other alternately back and forth (usually 3–5 times) to assemble the detritus into a bolus. During this process, the gnathopod 2 net was sometimes redeployed across the tube. A single net-grooming operation took *ca.* 1.0–1.5 s, and the efficiency was such that a net clogged with *Dunaliella* sp. could be cleared with one sweep of the gnathopod 1 combs. The gnathopod 2 net also retained old faecal pellets and barnacle cyprid larvae borne in on the current. These were ingested.

The first gnathopods and maxilliped palps kept the detrital material in a bolus as it was fed between the mouthparts. This was achieved by mutual grooming between the ventral setulate setae of the maxilliped palps and the carpal setae of the first gnathopods. The first gnathopods thus served as ventral containment for dropped particles. Ingestion of detritus from the bolus was regulated by the maxilliped outer plates which operated with a rapid scissoring action at up to 20–30 beats s^{-1}. (The maxilliped palp carrying out its grooming functions at the same time.) Subsequent treatment of detrital food was difficult to ascertain, although the apically spinous outer plates of the first maxillae appeared to assist in pushing food between the mandibular spine rows or molars (figure 4). The first maxilla palps, still apparently in their resting position to the sides of the mandibles, were seen moving as if in passive response to workings of inner mouthparts, but had no visible function at this point. The second maxilla was mostly hidden, though the terminal setae on the outer plate could sometimes be discerned interdigitating with the distal spines of the first maxilla outer plates. The filtering role, if any, of the finely plumose setae fringing the medial margins of the inner plates of the second maxillae (figures 3 and 4) could not be determined directly. There was no visible evidence of a systematic rejection of particles whilst feeding (i.e. which would imply some type of sorting procedure, perhaps based on particle size or other qualities), and neither was a posterior–anterior counter-current over the mouthparts observed. However, when particles were rejected (e.g. whole clumps of detritus, faecal pellets, mineral grains too large to ingest) they were flushed out with the anteroposterior through-tube current between the bases of the gnathopods. Alternatively, particles or detritus not ingested were sometimes affixed to the rim of the tube by a brief flurry of 'knitting' activity from the second and third pairs of peraeopods.

Corophium bonnellii also obtained detrital food by regular grooming of other limbs. The importance of food obtained from these sites is not known, but is probably small in relation to the catch of the second gnathopod filter. Most frequently groomed were the first gnathopods and the antennae.

The first gnathopods were usually held close to the underside of the mouthparts, medial faces uppermost, and with the setae on the carpal posterior margins directed medially and towards each other. The two rows of finely plumose setae on the ischia, which are structurally distinct from the net setae of gnathopod 2 (see Dixon 1992) were not seen erected to form a smaller version of the gnathopod 2 net. Seston passing through the tube nevertheless accumulated on these setae (as well as on the mouthparts) and was collected

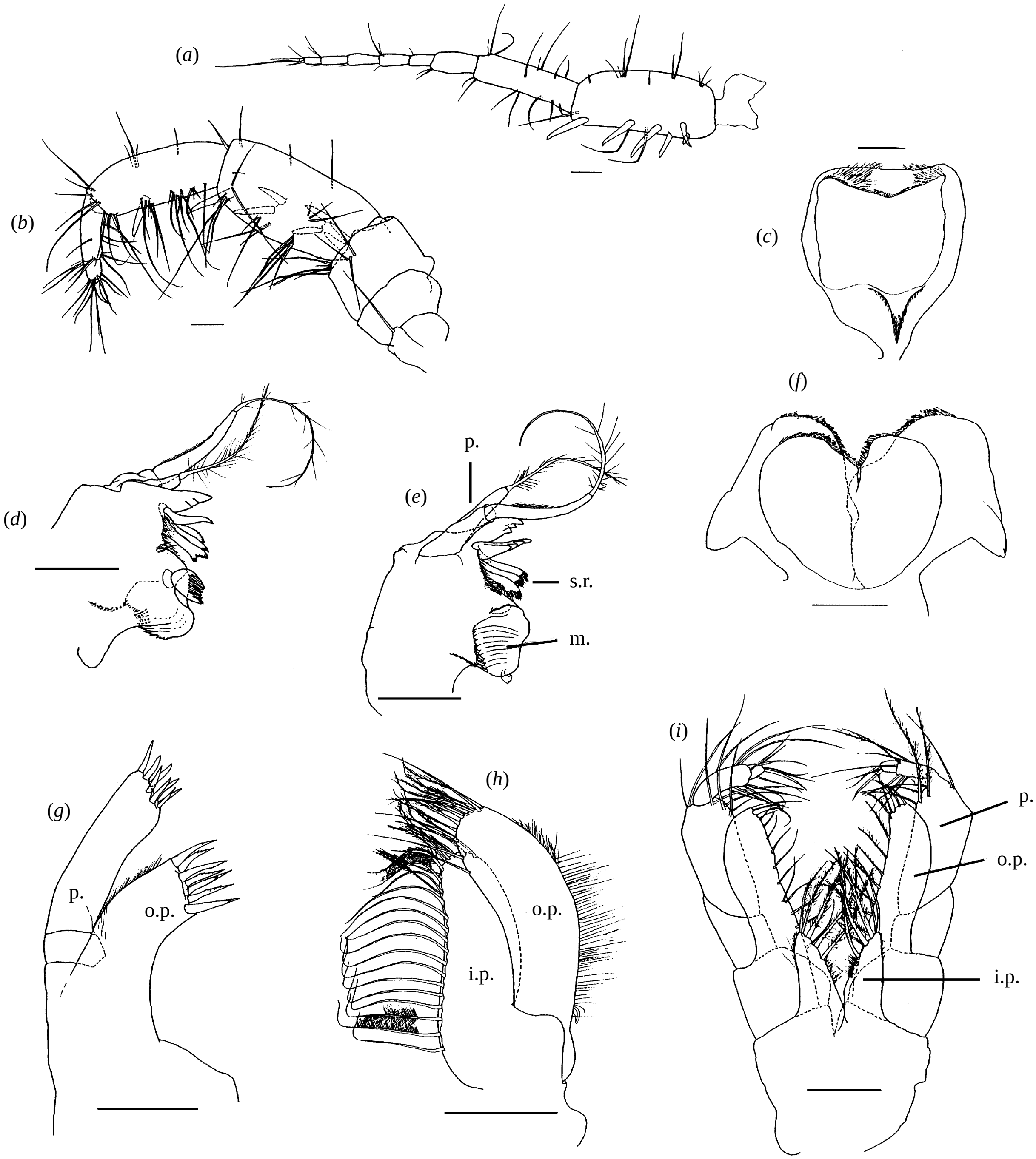

Figure 3. *Corophium bonnellii* (female), antennae and mouthparts. (*a*) Antenna 1 (left, ventral), (*b*) antenna 2 (left, lateral), (*c*) upper lip (posterior), (*d*) mandible (right, posterior), (*e*) mandible (left, anterior), (*f*) Lower lip (posterior), (*g*) maxilla 1 (right, posterior: inner plate missing), (*h*) maxilla 2 (left, posterior), (*i*) maxillipeds (anterior). Abbreviations: p., palp; i.p., inner plate; m., molar; o.p., outer plate; s.r., spine row. Scale bar, 100 μm.

for ingestion by periodic mutual brushing between the left and right gnathopods and the maxilliped palps as described above.

Antennal grooming involved the first gnathopods only. The antenna to be cleaned was flexed back towards the mouthparts, and the first gnathopods reached forward to hold it between the left and right propodi. The gnathopods then pulled back, scraping the proximal antennal articles clean with their dentate propodal setae. As the distal-most flagellar articles were reached, the antenna was reflexed so that the terminal joints were cleaned by being pulled through the grasp of the gnathopods. The whole length of both pairs of antennae was groomed in this way. Alternatively, the slender flagella were sometimes cleaned by being pulled between the dactyli and the dentate propodal palms of gnathopod 1.

Detritus occasionally became trapped in the epistomial space above the upper lip, between the bases of the antennae. The medial margins of the first peduncular segments of the first antennae carry short posteriorly-directed spines (recurved posteriorly in *C. bonnellii*) (figure 3) that retain material in this position. On one occasion the specialized (2-articulate) man-

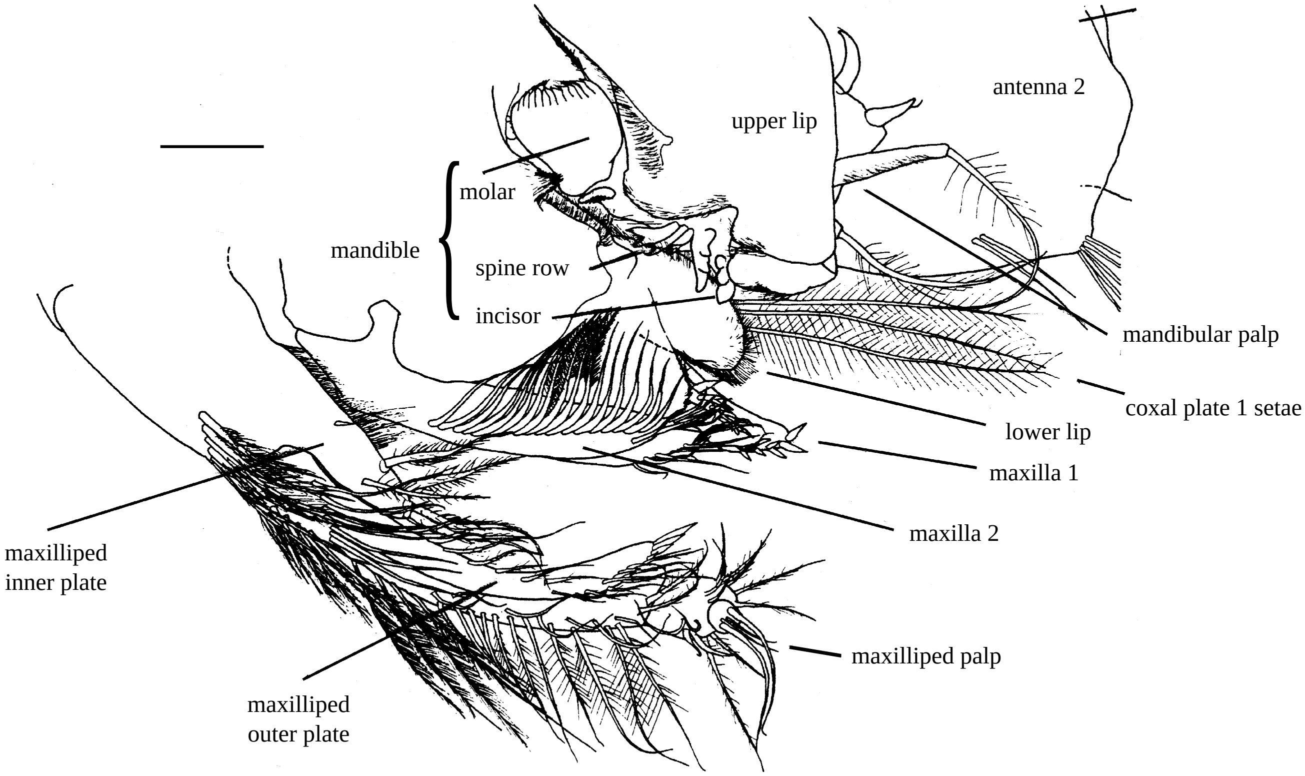

Figure 4. *Corophium bonnellii* (female), sagittal section of mouthparts (left, medial aspect). Scale bar, 100 µm.

dibular palps (figure 3) assisted in dislodging such an accumulation so that it could be reached by the first gnathopods and transferred to the mouthparts. On another occasion, the mandibular palps pushed such an accretion from between the antennae to within the reach of the palps of the maxillipeds and first maxillae. These mouthparts then broke-up the bolus and pushed the pieces between the mandibles. Other pieces were dropped into the through current and either swept out of the tube or recaptured by the gnathopod 2 setal net.

The first gnathopods (carpi mainly) also occasionally groomed the sides of the cephalon and urosome, the brood pouch, the peraeopods and pleopods. They reached back between the second gnathopods in order to clean the posterior parts of the body. Other potential sites for accumulating detritus were the bases of peraeopods 5–7, which are fringed with long pappose setae (especially peraeopod 7). Although the through-tube currents flowed around and between these basal segments, these sites were subject only to occasional grooming. *Corophium bonnellii* can also pick up and ingest settled particles from around its tube entrances. This behaviour was most apparent under calm conditions and when the water in the observation dish had not been changed regularly. If small quantities of sediment were then placed outside either tube entrance, the amphipod would emerge rapidly (always retaining a hold on the tube by the dactyli of peraeopods 5–7), pick up a clump of detritus with its antennae, and retreat into its tube. Here, the detritus would be passed back to the first gnathopods which would hold it against the mouthparts. At this point, violent 'scissoring' activity of the maxillipeds and first maxillae would often disrupt the clump, and also appeared to cause some of the material (including the larger particles) to drop out of the cup formed by the first gnathopods. Some, or all, of the retained detritus would then be ingested in the same manner as if it had been trapped from suspension by the gnathopods or antennae. Any dropped or uningested material would be subsequently flushed from the tube. If *C. bonnellii* was left, without water changes, in dishes with a scattering of detritus on the bottom, within a period of 5 h cleared circular patches, centred on one or both entrances and with a radius approximately equal to one body length, would appear. If, under these conditions, currents around the dish were induced by jetting water from a Pasteur pipette, flurries of activity usually began which included movement along the tube (with somersaulting) to investigate each entrance, energetic pleopod beating, deployment of the second gnathopod setal nets, and renewed antennal grooming.

Although *C. bonnellii* would consume old faecal pellets (both its own and those of other species), the refection of freshly produced pellets was rarely observed. On defaecation, the urosome was normally straightened out, and the faecal pellet ejected and immediately flushed out of the tube with a burst of pleopod activity. On one occasion, a non-ovigerous female half-somersaulted and, with the first gnathopods, collected a pellet as it emerged from the anus. This was then investigated by the mouthparts, in the manner characteristic of all other corophioids studied. The maxilliped palps and first maxilla palps manipulated the pellet, passing it forward over the second maxillae, first maxillae and mandibular incisors, then rotating it end-over-end and returning it to be passed forward again over the biting mouthparts. When viewed from the animal's left side, the pellet was invariably rotated in an anticlockwise direction. During this process, the pellet gradually disintegrated presumably because the peritrophic membrane was disrupted. Some ingestion of faecal material may have taken place, but the bulk of the pellet was dropped into the through-tube current and swept away posteriorly.

Refection of fresh faecal material, however, was observed in two individuals which had been kept in filtered seawater for 72 h previously.

Defaecation rates varied with feeding conditions. In fresh sea water (15 °C) over a period of 6 h, three animals between them produced pellets at a rate of $4.8–14.3\ h^{-1}$. Four animals which had been kept in 0.45 μm-filtered seawater for 72 h previously did not defaecate at all over the same 6 h period. Two animals which had been transferred from fresh to 0.45 μm-filtered sea water produced pellets at rates of $6.5–6.7\ h^{-1}$ over the first 2 h, then stopped defaecating for the following 2 h, and for 4 h thereafter, defaecated at rates of $0.5–2.8$ pellets h^{-1}. Following transfer to filtered sea water, the pellets produced by *C. bonnellii* tended to increase in length, becoming less compact as the gut emptied. Ultimately, animals voided empty peritrophic membrane strings almost as long as the gut. Such pellets were not helped out by the gnathopods and tended to trail from the anus. Even under these conditions, pellets were rarely investigated or consumed.

Corophium bonnellii was seen to capture and consume barnacle cyprid larvae whilst feeding on seston using the filtering setae of the second gnathopods. However, it could not be induced to eat larger items of animal origin, such as dead or moribund amphipods of various sizes. Small pieces of the filamentous red alga, *Ceramium* sp., were either investigated and rejected, or ignored completely.

(ii) Lembos websteri

This species was not observed living within its own tubes in natural kelp holdfasts. However, when it constructed tubes on the detritus-strewn floor of glass observation dishes, the resultant open-ended cylindrical structures were very similar to those of *Aora gracilis*, *Gammaropsis nitida* and *Jassa falcata*. They were made of 'amphipod silk' and fine detritus, with thin elastic walls, and were attached to the substratum for their full length (approximately 1–1.5 × body length of the builder). *Lembos websteri* would live in the tubes of other species (though aggressive take-over of an occupied tube was not witnessed) and, in dissected holdfasts, was often found residing in the distinctive tubes (see below) of *Ericthonius punctatus*.

Like *C. bonnellii*, *L. websteri* spent most of its time within its tube, unless disturbed or induced to forage by stagnating seawater conditions. In both self-built tubes and their glass analogues, it usually adopted a central position with its antennae just protruding from the anterior entrance, and with the dactyli of peraeopods 6 and 7 hooked into the opposite rim. The long flagella of the first antennae probed the immediate environs, whilst the shorter second antennae remained hooked around the rim of the tube entrance. On the first antenna, the articulation between the flagellum and the peduncle permitted the flagellum to reach and probe the sector immediately behind the tube entrance without the animal revealing its head. The abdomen was usually flexed under the peraeon and the pleopods induced an anteroposterior current through the tube. A resting amphipod often lay still without any pleopod-beating, in which case the abdomen could be tightly tucked-up ventrally. At progressively increasing activity levels, the angle between the abdomen and peraeon increased, allowing a greater amplitude of pleopod beating, to the point of maximum reflexion at an angle of approximately 150° from the peraeon. Current speeds through the tube (in an anteroposterior direction for an adult male) varied from $< 0.8\ mm\ s^{-1}$ up to $3.1\ mm\ s^{-1}$ ($5.1–19.7\ ml\ h^{-1}$) at 12.5 °C. However, *L. websteri* can reverse the flow without somersaulting. Currents thus generated by both sexes reached $1.1–1.2\ mm\ s^{-1}$ ($7.0–7.6\ ml\ h^{-1}$). The highest flow rates were achieved in an anteroposterior direction through the tube, and were used when suspension-feeding or when flushing unwanted material from the tube.

In both sexes, the larger first pair of gnathopods (an aorid characteristic) can either be cupped ventrally to, or held to either side of, the mouthparts. To accommodate the latter position, large males have their first gnathopod basal articles and the first coxa, sculpted to receive the distal articles reflexed in this way; although these gnathopods are not normally tucked up into the sides so tightly. The smaller second gnathopods are sometimes thrust forward between the bases of the first pair, but are more usually held cupped together beneath them.

Whilst centrally positioned and drawing a current through the tube, grooming of both pairs of gnathopods and antennae was the most frequent activity shown by both sexes of *L. websteri*. As with *C. bonnellii* (see above), suspended material entrained by the tube irrigation current was the main source of food: it was trapped particularly by setae on the gnathopods and mouthparts. The sexual dimorphism of form and setation of the gnathopods did not appear to influence the process of food capture, but it was reflected in how the gnathopods were used subsequently in grooming and food handling.

In females, the first gnathopods were used for manipulative tasks and in all grooming activities. The posteromarginal distally bipectinate setae arising from the meral, carpal and propodal articles of the first gnathopods were used to groom the long plumose setae fringing the equivalent articles of the second gnathopods. In this procedure, the second gnathopods (either as a pair, or singly and alternately) were brought up ventrally between the first pair, and then pulled backwards and sideways so that the setae of gnathopod 2 were pulled through those of gnathopod 1. These actions were repeated as many times as necessary. The setae of the first gnathopods were apparently cleaned by brushing against the ventrally-directed setal arrays of the maxilliped palps. The propodi and dactyli of the first gnathopods also occasionally assisted the mandibular palps in grooming the antennae. In this process, the gnathopods were parted laterally as the antenna to be cleaned was flexed towards the mouthparts and held between the maxilliped palps. The mandibular palps then flicked down and gripped the antenna between their setose terminal articles. At this point the dactyli of the first gnathopods were sometimes pressed against either side of the antenna as it was then reflexed and pulled between them. The subchelate gnathopods did not hold the antenna within the angle of the dactylar insertion, as was the case in some other species. Scanning electron microscopy of the dactyli (Dixon 1992) revealed a central field on the medial face that was minutely spinose, which would assist this method of antennal grooming.

In males, the first gnathopod is massively enlarged. Although more setose than that of the female, it lacks the short to medium length, ventrally and medially directed meral, carpal and propodal setae that are used by the female for grooming and manipulating. In the larger males especially, the first gnathopods were not used routinely in manipulative tasks or grooming activities. The male second gnathopods are also more setose than in the female, but retain the shorter medially pointing setae of the meri, carpi and propodi that the females possess. The anterior margins (principally) of the male carpi and propodi in both pairs of gnathopods carry a dense range of long, curved, sparsely plumose setae. These can be erected (cf. the meral setae of gnathopod 2 in *C. bonnellii*) but, in their normal resting position, they lie in a compact curved bundle along the anterior margins of each gnathopod. Unlike the gnathopod 2 setae of *C. bonnellii*, however, the erected setae of *L. websteri* are not regularly arranged and the short, sparsely distributed setules do not form a mesh (see Dixon 1992). Such setae would appear to be ideally adapted for trapping seston when erected. However, they were seen erected only very occasionally, and then only momentarily, and were never deployed during any of the observations on feeding or grooming.

In males, the second gnathopods were groomed directly against the maxilliped palps, rather than against the first gnathopods as they are in females. When the second gnathopods moved forward to the mouthparts, the first pair was moved laterally out of the way. (During this process it was possible that the posteromarginal setae of the second gnathopods brushed against those of the first pair, although this was not clearly visible.) The second gnathopods came into contact with the maxilliped palp setae and were cleaned as they were pulled back into their resting position behind and below the first gnathopods. Grooming of the long plumose setae arising from the anterior carpal and propodal margins of both pairs of gnathopods was not observed.

Antennal cleaning in males was similar to that in females though the dactyli of the first gnathopods, obscured as they were by the long propodal setae and possessing no dentate patches medially, did not appear to assist the mandibular palps, as they do in females.

Though normally groomed singly, in both sexes the left and right antennae were occasionally cleaned simultaneously. Then, the gnathopods were parted so that the antennae could be flexed right back and laid against the maxillipeds. The gnathopods were then pressed against the maxillipeds, the mandibular palps deployed, and the antennae then both reflexed and pulled between them.

Females used their first gnathopods for collecting deposited sediment and detritus, as well as for cleaning-off seston trapped on anterior limbs and setae. Males were not seen doing this, but both sexes used both their pairs of antennae to pick up sediment or clumps of detritus from outside their tube entrances. The collected material was carried into the tube using these limbs, with ventral support from the first gnathopods, which also then held it up against the maxillipeds for sorting and ingestion or rejection. Large clumps of detritus received additional support from the mandibular palps, but the second gnathopods were not seen to be used in these instances. Small clumps were held by the palps of the maxillipeds only. The function of these palps was purely manipulative, whilst the toothed palps of the first maxilla served as biting tools to break-up detrital particles. The mandibular incisors were not used in this feeding procedure. The second maxilla (outer plates) operated with a wide 'scissor-like' action, whilst the outer plates of the first maxilla moved with both a scissor action and also vertically up and down. Although not seen directly, the function of the first maxilla outer plate appeared to be to push food particles between the mandibular spine rows and molars.

Defaecation was always followed by manipulation and investigation of the faecal pellet by the mouthparts. Other activities, including feeding, were halted for this process. Consumption of an entire freshly produced pellet, however, was rare. During defaecation, *L. websteri* flexed its urosome ventrally to come within reach of the gnathopods. Each side of the urosome was massaged by short repeated back and forth motions of the gnathopods (either first or second pairs in the female; second pair only in the male). As the pellet emerged, it was caught by the second gnathopods and then passed forward to the mouthparts for investigation and disruption in exactly the same way as described for *C. bonnellii*. If the pellet was wholly consumed, however, investigation was brief or absent and the pellet was simply fed directly between the mandibles via the cutting teeth of the maxilliped outer plates.

As well as ingesting detrital or finely particulate matter, *L. websteri* was also capable of browsing material from the surfaces of mineral grains too large to ingest. One adult female held and manipulated a particle 275 μm in diameter between the first gnathopods and the maxilliped palps. The palps of both the first maxilla (specifically the subterminal distally bipectinate setae on the ventral surface) and the apical setae on the outer plates of the second maxilla were used to scrape the particle. Similar rasping movements of these limbs, together with the rasping and cutting actions of the maxilliped outer plates and the mandibular incisors, were used when *L. websteri* grazed material directly off the substratum (cf. McGrouther 1983). This was observed in the laboratory when, in increasingly stagnant conditions, animals sometimes left their tubes to graze the surfaces of adjacent holdfast haptera.

Lembos websteri was never seen to attack other macrofaunal animals for food although defensive encounters to prevent tube invasion were occasionally witnessed in holdfasts. However, animal food (live or dead) proffered by forceps to one of the tube entrances was nearly always eagerly accepted. Such items included harpacticoid copepods, amphipods (including conspecifics) and nematodes. On one occasion a juvenile mussel (that remained tightly shut) was subjected to prolonged investigation. Such offerings were grabbed by the antennae and gnathopods, and taken into the tube for eating. Prey was held against the mandibles by the first gnathopods, without any particular orientation, and steadily gnawed. Harpacticoid copepods were completely ingested in *ca.* 15 min, whilst a wriggling nematode was threequarters consumed in 90 min. No prior attempt was made to subdue struggling prey. *Lembos websteri* also captured and ingested ciliates from a dense culture placed outside a tube entrance. Small pieces of filamentous red algae (mainly *Ceramium* sp.) were also accepted and eaten in the same way as faecal pellets, by being processed through the chopping action of the toothed outer plates of the maxillipeds and thence between the mandibles.

(iii) Aora gracilis

This species was observed in tubes within kelp holdfasts on two occasions. The tubes were flimsy, and constructed mainly of 'amphipod silk' with a small amount of fine detritus and a few pieces of algae incorporated. Both were open-ended and slightly longer than the body length of the occupant. One was constructed firmly on a single hapteron, whilst the other was suspended between two haptera so that the gap was bridged by the 'roof' and 'floor' of the tube. In observation dishes, *A. gracilis* would build new tubes, using the fine transparent secretions from peraeopods 3 and 4 ('amphipod silk') supplemented by any other materials available. Tubes were indistinguishable from those of the other corophioids studied except for *Ericthonius punctatus* (see below). Within the tubes, the positioning and behaviour of *A. gracilis* was similar to that of both *A. spinicornis* (below) and *L. websteri* (above). It would usually sit centrally in the tube with the pleon folded ventrally, the tips of each antenna just visible at one entrance, and the dactyli of the sixth and seventh peraeopods visible at the other. The pleopods drew an anteroposterior current through the tube at speeds of <0.1–>2.0 mm s^{-1} (0.6–13.0 ml h^{-1}) at 15 °C. As in all the corophioids studied, the fastest flow rate was achieved when the pleon was stretched posteriorly, allowing the maximum amplitude for pleopod-beating. Occasionally, *A. gracilis* would move towards an entrance so that the first antennae could probe around outside the tube. As in *L. websteri*, the first antenna can reach dorsally behind the tube entrance whilst the animal remains hidden. *Aora gracilis* regularly somersaulted within the tube and checked each entrance in this fashion. 'Knitting' movements of silk-generating peraeopods 3 and 4 were also common. Both sexes remained with the first pair of gnathopods cupped together ventral to the mouthparts, whilst the slightly smaller second pair were held beneath, and slightly behind, them. Neither gnathopod pair, in either sex, carries any erectable setae.

In both sexes, the first gnathopods were raised against the mouthparts during antennal grooming. In this position, either they simply helped to retain any detritus scraped-off, or the medial setae of the propodi assisted in cleaning the antenna as it was pulled between the gripping mandibular palps. As in *L. websteri*, the dactyli were not used directly in this procedure. Once the antenna had returned to its normal position, the mandibular palps stayed down and were brushed by the terminal setae of the maxilliped palps before returning to their resting position. The second gnathopods groomed the peraeopods by reaching behind and brushing either individual, or paired, limbs with a repeated proximal-to-distal sweeping action. As the second gnathopods were swung forward again, the first pair moved back to receive the collected detritus on the setae fringing the posterior margins of the meral, carpal and propodal articles. Transfer was accomplished with four or five opposing medio-lateral sweeps between the first and second gnathopods on each side. The first gnathopods then passed the detritus forward to the maxilliped palps with a series of abduction movements.

During defaecation, both pairs of gnathopods engaged in stroking the sides of the urosome. Then, as the faecal pellet emerged, it was caught by the gnathopods and transferred to the mouthparts. There, the pellet was rotated against the mandibular incisors, in typical corophioid fashion, by the maxilliped palps with help from the first gnathopods. Usually, faecal pellets were only consumed when other food was scarce. On one occasion a male, actively feeding on Sephadex® particles over a period of 35 min. (at 16 °C), was observed to defaecate at rates varying between 7.6–11.1 pellets h^{-1}. It took 28 min 50 s, and five pellets, to replace the entire gut contents with Sephadex. Although the pellets were investigated, and broken-up by the mouthparts of their producer, none was ingested. Another male, feeding rapidly on a suspension of the diatom *Skeletonema costatum* and observed for 72 min (at 17.5 °C), defaecated at a rate of between 6.4–21.2 pellets h^{-1}. Of the 16 pellets produced, six were investigated and broken-up, while the remainder were flushed out of the tube without investigation.

Hyperadult males, with their spectacularly enlarged and elongated first gnathopods, make less use of these limbs as tools in grooming than do females. The basal articles are angled sharply back, inside the bases of the second gnathopods, reaching as far as the third coxal plates. The main limb flexure occurs between the ischial and meral articles and, from here, the distal articles extend forward and are held to either side of the mouthparts. In large males, the propodus and enlarged dactylus project well beyond the cephalon. The second gnathopods lie outside the bases of the first pair, with the distal segments held ventrally. From here the distal articles of the second gnathopods can be swung medially and upwards, between the first gnathopods, to the mouthparts. However, in the case of large males, the size of the first gnathopods severely impeded access to the mouthparts by the second pair. Antennal cleaning was usually done by the mandibular palps, often assisted by the maxilliped palps, whilst the first gnathopods were held out of the way. During defaecation, urosome-massaging by the gnathopods was rare, and the pellet was ejected straight onto the mouthparts by the flexed abdomen. Subsequent pellet manipulation was by the maxilliped and first maxilla palps only.

Detritus placed outside the tube entrance was usually investigated immediately, collected by the antennae and first gnathopods, and drawn into the tube for further investigation and ingestion. Clumps of detritus were held up to the mouthparts by the first gnathopods or, if small enough, by the maxilliped palps only. Sediment particles, up to 0.85 mm in diameter, were also held up to the mandibles by the first gnathopods and manipulated by the maxilliped palps. These large particles were later stuck to the rim of the tube and it was unclear whether the amphipods were actually browsing the particles, or simply covering them with a sticky secretion prior to their incorporation into the tube. Under stagnating conditions with no suspended food available, *A. gracilis* explored the area immediately around its tube entrances for detrital particles and old faecal pellets. One emerged completely from its tube (in a kelp holdfast) in order to graze on adjacent haptera surfaces in the same way as described for *L. websteri*.

Aora gracilis accepted and ingested both live and dead amphipods offered by forceps to a tube entrance. An adult female took *ca.* 2 h to half-consume a similar sized *Ericthonius punctatus*. Adults and juveniles would also accept and eat 1 mm long pieces of the red alga *Ceramium* sp. As with detritus, all such offered food was collected at the tube entrance by the antennae and first gnathopods, and dragged inside before consumption commenced.

(iv) Aora spinicornis

The tubes built by this species were similar to the flimsy open-ended structures of its congener, *A. gracilis*. The stance taken up within the tube, including the positioning of the antennae, gnathopods and peraeopods and the flexure of the abdomen in relation to the peraeon was also similar to that of *A. gracilis*. Currents through the tube, always in an antero-posterior direction, varied between < 0.1–3.5 mm s^{-1} (0.6–22.3 ml h^{-1}) at 15 °C but for normal feeding and grooming activities, were maintained at *ca.* 1.0 mm s^{-1} (6.4 ml h^{-1}).

Females rested with the first gnathopods cupped ventrally beneath the buccal mass and with the second pair held just behind them. The first gnathopods of the males were usually positioned to either side of the mouthparts. They are not enlarged to the extreme extent attained in *A. gracilis*, are more setose, and are also used more for routine grooming and other manipulative tasks than in *A. gracilis*. They assisted in antennal grooming, peraeopod grooming and also cleaned the second gnathopods. The setae of both pairs of gnathopods were extended permanently and were not movable.

In antennal grooming, the antennae were pulled, usually one at a time, between the setose grip of the ventrally-flexed mandibular palps. The postero-marginal setae on the propodi of gnathopod 1 also swept along each antenna as it was reflexed. In males, the enlarged dactyli of the first gnathopods were sometimes also hooked around the antenna during this process. Two antennae may be cleaned at the same time (cf. *A. gracilis* and *L. websteri*). As a separate procedure, the setose carpal and propodal articles of the first gnathopods were also used to groom the proximal antennal peduncles and the sides of the cephalon.

The peraeopods were periodically brushed simultaneously by both pairs of gnathopods. They grasped an anteriorly extended limb and cleaned it with a series of short, proximal to distal-directed, brushing actions. The second gnathopods were then groomed by the first pair, and the detritus passed forward to the maxillipeds just as in *A. gracilis*. In addition, the first gnathopod was occasionally unfolded and extended so that the basal and ischial articles could be brushed by the setose carpi and propodi of the second gnathopods. The setae of the first gnathopods were groomed against those of the maxilliped palps both by adduction/abduction and by repeated backward or forward brushing motions. The most frequently groomed appendages were the antennae (by the mandibular palps and the first gnathopods), the second gnathopods (by the first gnathopods only) and the first gnathopods themselves (by the maxilliped palps and the second gnathopods).

Prior to defaecation, in a process similar to that described for other aorid species, the ventrally-flexed urosome was often stroked by the gnathopods. As the pellet was ejected, it was caught by either the first or second pair of gnathopods and passed forward to the mouthparts. It was manipulated against the biting mouthparts by the maxilliped palps, with a characteristic end-over-end rotation (anticlockwise when viewed from the left side). The broken pellet was usually dropped into the pleopod-induced current and flushed from the tube, but occasionally it was partially or wholly consumed; especially if suspended detrital food was scarce. Of two males observed feeding in fresh sea water (15 °C) over a 34 min period, the defaecation rate for one varied between 7.0–14.6 pellets h^{-1}, the other from 12.2–12.8 pellets h^{-1}. None of these pellets was eaten. After 24 h in 0.45 μm-filtered sea water (15 °C) the rates had declined to 2.1–3.8 pellets h^{-1} and 3.6 pellets h^{-1} respectively (over a 44 min period). Pellets produced by this time were wholly consumed, apart from one which was only partly consumed.

Aora spinicornis displayed similar flexibility in feeding (and the same range of manipulative abilities) to the other aorid species, in that both sexes readily accepted and ingested a range of particulate material, live or dead crustaceans and finely chopped pieces of algae.

(v) Gammaropsis nitida

This species builds its tubes in and on whelk shells inhabited by the hermit crab *Pagurus bernhardus*. On nearly all the pagurid-inhabited whelk shells observed, *G. nitida* tubes were concentrated in, or immediately around, the siphonal canals. Tubes were also found within the shell in locations not likely to be abraded by movements of the pagurid, such as near the apex or amongst protective fouling growth, if present, within the main whorl. They were also found on the outer shell surfaces, either in the sutures, or amongst encrusting epifauna. The tubes were flimsy, open-ended structures built flat against the substratum, made of 'amphipod silk' and fine detritus, and with an overall length approximately the same as that of the amphipod. As with the tubes of the three aorids above, the walls were flexible so that the amphipod could somersault and move freely inside.

Whether quiescent in its tube *in situ*, or in glass tubes, *G. nitida* usually positioned itself midway within it with the tips of the antennae showing at one entrance, and the dactyli of peraeopods 6 and 7 hooked around the rim of the opposite opening. The abdomen was flexed ventrally under the peraeon and the beating of the pleopods induced a slow anteroposterior through-tube current. This current was often jerky; stopping and starting with the slow rhythm of the pleopods (a reflection of the high viscosity regime at this small scale). At faster velocities, the pleon was reflexed to a maximum angle of *ca*. 135° from the peraeon. *Gammaropsis nitida* could also reverse the direction of the current through the tube without first somersaulting. In an adult male (3.4 mm in length) anteroposterior velocities varied from 0.1 to 1.3 mm s^{-1} (0.6–8.3 ml h^{-1}) at 13 °C while the reverse currents were slower, varying from 0.1 to 0.2 mm s^{-1} (0.6–1.3 ml h^{-1}).

In both sexes the enlarged second pair of gnathopods was held slightly wide of the body, enabling the first gnathopods to work freely between them. The first gnathopods, with their medial and posteromarginal arrays of dentate setae, were normally held directly beneath the maxillipeds, medial faces uppermost. In this cupped position under the mouthparts, they intercepted some of the incoming seston, and were frequently groomed by the maxilliped palps. The mandibular palps were often flexed towards the first gnathopods and maxillipeds during this grooming activity, although whether to be cleaned themselves or to assist in the gnathopod grooming, could not be determined. The antennae, meanwhile, were usually held straight out to the front. In this position, the distinctive setal arrays of both pairs (similar to those found on the ischyrocerid species below) did not appear to be deployed to their best advantage, in terms of maximizing a potential catch of seston. Nevertheless they were groomed occasionally by the setose terminal articles of the mandibular palps and, occasionally, also by being pulled through the angle between the dactyli and propodi of the first gnathopods.

At intervals, the amphipod would partly emerge from its tube and adopt a stance with antennae and gnathopods spread wide. The first antennae were directed anteriorly, the second pair were stretched out to either side at *ca*. 90° from the body, and the first gnathopods were held wide to either side of the mouthparts. Sometimes the animal emerged far enough to reveal the second gnathopods, which were also held out wide to either side; sometimes only the antennae were emergent. In these positions, the setose antennae appeared to be more effective at capturing suspended material from currents external to the tube. In the still conditions of observation dishes, however, this stance was not usually maintained for more than a few seconds after which the amphipod would resume its mid-tube position. Currents induced around animals in glass tubes, by squirting Pasteur pipettes, occasionally elicited partial emergence, accompanied by spreading the antennae.

Gammaropsis nitida emerged from either tube entrance to pick-up settled detritus using both the first gnathopods and the antennae. Material was dragged into the tube, held up to the mouthparts by the cupped first gnathopods, and either partially ingested (the remainder being ejected anteriorly by pleopod beating and body movements) or added to the structure of the tube accompanied by 'knitting' movements of peraeopods 3 and 4.

Individuals generally rejected animal material (crustacean remains) and suspensions of either carmine red or *Dunaliella* sp. out of the anterior tube opening with the aid of the pleopod-generated current. One individual accepted a small fragment of the red alga *Plocamium cartilagineum*. This was grabbed from the forceps by the antennae and first gnathopods, manipulated against the mouthparts by the first gnathopods, but ejected anteriorly from the tube after 2 or 3 s.

As in the aorid species studied, faecal pellets were always brought forward to the mouthparts by the gnathopods following a 2 or 3 s period of massaging the flexed pleon by both pairs of gnathopods. The pellet was then manipulated against the mandibles by the maxillipeds and first maxillae (often also with the assistance of the first gnathopods) with the end-over-end rotation already described, and then ejected. In contrast to the Corophiidae and Aoridae, however, disrupted pellets were ejected anteriorly from the tube. Complete refection of freshly produced pellets was never observed.

No other grooming movements were seen, apart from the brushing of the seventh peraeopods with the second pair of gnathopods.

(vi) Ericthonius punctatus

Tubes of this species were usually built on the more exposed haptera of kelp holdfasts, or on the stipe, often in high densities. They were always straight (*ca*. 1.5 × body length), semicircular in transverse section and attached to the substratum along their whole length. Uniquely amongst the Corophioidea studied, the tube tapered slightly along its length and its two entrances were architecturally distinct. The widest entrance formed an oblique arch (figure 5) whilst the opposite opening was smaller, simpler and comparatively ragged-edged. When closely packed, around a

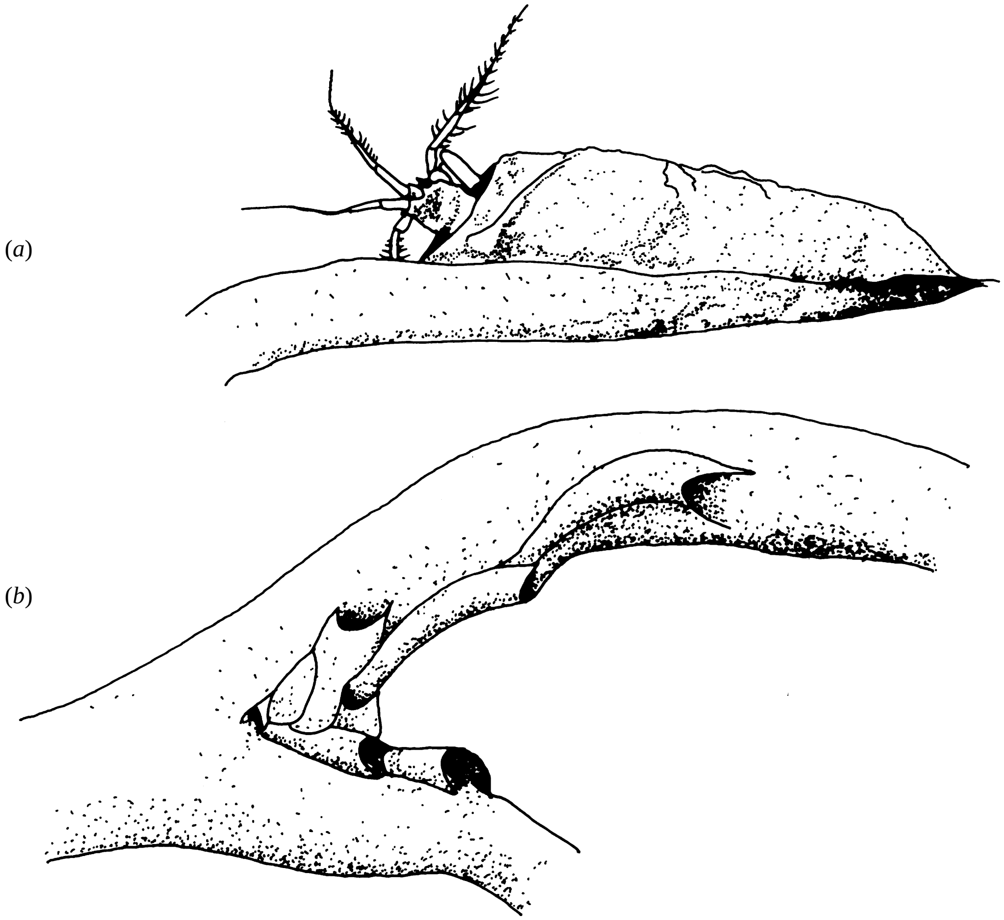

Figure 5. Tube morphology of *Ericthonius punctatus*. (*a*) An occupied tube, (*b*) a cluster of empty tubes on a kelp hapteron.

kelp stipe for instance, the tubes often overlaid each other but the main entrances were always uppermost and in open water. The occupant usually lay with its head towards the main entrance. If sufficiently provoked from the front, it would simply reverse down the tube or, in extreme cases, somersault and swim out of the other entrance.

In characteristic feeding stance, *E. punctatus* lay with its dorsum to the substratum in the main entrance, with only the antennae, eyes and mouthparts emergent. In this position, the sloping tube entrance to each side, together with the underlying substratum, provided maximum protection to the sides and back of the head, whilst (a) giving the characteristically protuberant eyes an unobstructed field of view to the front and sides, and (b) providing ready access to the mouthparts for the reflexed antennae. The antennae, with their arrays of long setae, were extended out of the tube entrance to cover as large a surface area as possible. The first antennae were extended anteriorly whilst the second pair projected laterally at right angles to the body. At intervals, each antenna was curled back towards the mouthparts. At the same time, both mandibular palps were flicked ventrally so that the setose terminal articles pressed against either side of the antenna. The antenna was then pulled back between these setae which retained any adhering particles, after which the outstretched feeding position was resumed. The mandibular palps themselves were groomed by the maxillipeds (using the long distally bipectinate setae on both the palps and the outer plates) and the resultant bolus of detritus pushed between the mandibles by the combined action of the first maxillae and the forward-pointing setae of the maxilliped inner plates. The mandibular palps probably trapped suspended material independently, since they were often groomed by the maxillipeds (sometimes with the aid of the first gnathopods) without any antenna cleaning having previously taken place.

In still, filtered sea water *E. punctatus* used its antennae to generate water movement around the tube entrance. The first antennae were flexed and reflexed rhythmically together, whilst the second antennae were rotated with a clockwise sculling action (when viewing the animal's right side). Unlike *C. bonnellii* or the aorids studied, pleopod-induced currents through the tube were barely detectable using fine suspensions of detritus or carmine red. Amphipods installed in glass tubes were always observed to lie with the abdomen curled ventrally under the peraeon (rather than stretched out along the tube) restricting the amplitude of pleopod movement. Reverse currents (i.e. in a posteroanterior direction) were, however, seen momentarily when unwanted material in the tube was ejected anteriorly.

Upon defaecation, faecal pellets were always transferred from the anus to the mouthparts by the first gnathopods, and investigated briefly in the manner common to nearly all the species studied. The faecal material thus released was partially reingested, after which the pellet remains were pushed out of the main entrance by a combination of concerted pleopod activity, helped by the use of both pairs of gnathopods and the mandibular palps. Complete refection of newly produced faecal pellets was not observed. However, in still clear water, individuals sometimes advanced partially from their tubes to gather-up loose detritus and old faecal pellets for investigation and/or consumption. Such material was picked up by the gnathopods (primarily), sometimes with assistance from the antennae, and carried into the tube. Here, it was passed to the maxillipeds and first gnathopods for collation, subsequent investigation and ingestion or rejection. This proceeded in the same way as described for all other species dealing with a clump of detrital material. *Ericthonius punctatus* was also seen browsing on larger sand grains ($> 250\ \mu m$ in diameter). These particles, supported and manipulated by the first gnathopods and maxillipeds, were scraped by the mandibular incisors and the distal spines on the palps of the first maxillae. Although not clearly visible, the distal setae of the second maxillae, and possibly those on the outer plates of the maxillipeds, also appeared to be involved in this process.

Ericthonius punctatus was also seen on several occasions to ingest animal prey. It accepted dead conspecifics placed outside the tube main entrance. Offerings were picked-up by the gnathopods during a rapid foray (contact with the tube always being maintained by the seventh peraeopods), and drawn back into the tube for inspection and consumption. During feeding, the carcass would be supported by the first and second gnathopods whilst it was gnawed by the steady rhythmic action of the mandibular incisors and the palps of the first maxillae. A small carcass was usually eaten from end to end; feeding on larger bodies began at any site. *Ericthonius punctatus* was twice seen to attack live animals passing close to the main tube entrance. Once, a nematode was captured and, after considerable struggle, partially eaten. Another individual reached out of its tube and grabbed a passing nudibranch, *Favorinus branchialis*. It grasped the tip of one of the cerata so that as the seaslug moved away, it became stretched. At the point where the amphipod could hang on no longer without leaving its tube, it let go.

Pieces of the filamentous macroalga *Ceramium* sp., offered by forceps, were always accepted, and eaten in a manner similar to that described above for animal food. Under poor feeding conditions, *E. punctatus* individuals sometimes left their tubes and grazed epiphytic material from the surfaces of the nearby kelp stipe or haptera. These grazed patches were easily visible by their lighter colour than the surrounding kelp surfaces.

(vii) Jassa falcata

Tubes of this species, as built in kelp holdfasts, were never fully revealed. Whilst the animals themselves were often visible in the crevices amongst the haptera, their tubes remained hidden amongst fouling growth and proved impossible to extricate. On occasion, *J. falcata* was observed living in tubes similar in structure to those described for *Lembos* and *Aora* species. Whether these were self-built, or taken over from the original aorid occupants was never clarified. However, in a glass dish with scattered detritus on the bottom, *J. falcata* would build double-ended tubes (either in a corner or on the open floor) indistinguishable from those of the Aoridae under study. (Natural tubes of this species have, however, been seen whilst diving at other sites in northern British waters, including Orkney, Rona, St Kilda and Rockall. At these sites, double-ended tubes, 1–1.5 × body length, were constructed in high densities (often contiguous) on hydroids and on the thalli of foliose red algae. They were indeed similar to aorid tubes in appearance except that, when occurring at fouling densities, they overlay each other in the same fashion as described for *Ericthonius punctatus*).

Jassa falcata fed mainly at its tube entrance, using its outstretched setose antennae to trap suspended material. Unlike *E. punctatus*, however, it protruded directly into open water and therefore did not usually gain protection of its rear from the substratum. In holdfasts, it fed with equal facility at either tube entrance, and readily somersaulted within its tube. (However, when observed in high densities, with tubes overlapping each other, it displayed a distinct preference for feeding at the raised opening.) The usual posture, whether feeding at an entrance or quiescent within the tube, was with the abdomen curled ventrally beneath the peraeon. Pleopod movements caused a weak water current (velocity range $0.2–0.4\ mm\ s^{-1}$, or $1.3–2.5\ ml\ h^{-1}$; $n = 6$ at 17 °C) to pass through the tube in a posteroanterior direction. This current was maintained whilst feeding, when the position of the amphipod ranged from having only the antennae emergent to having the head and body, as far as gnathopod 2, protruding. In the latter case, the gnathopods were also held wide, like the antennae. However, in still-water conditions with little or no seston available, it emerged still further, to the point where the pleopods and part of the ventrally-flexed abdomen were also exposed. This stance was facilitated by peraeopods 5–7 remaining hooked into the tube wall. In this position the through-tube current ceased, and the pleopod activity caused water to be drawn in from the sides, and from the front and rear instead.

The antennae were groomed periodically, one at a time, by the maxillipeds, the first gnathopods and, sometimes, by the mandibular palps. Only the flagella received this treatment from the mandibular palps; possibly due to the flexibility of the antennae being limited by their heavy build. The antennal peduncles were groomed in a separate movement by the first gnathopods. The rate at which the antennae were flexed towards the mouthparts varied from $< 6\ min^{-1}$ on average (range: $2–10\ min^{-1}$, $n = 10$) in still water, to a mean of almost $12\ min^{-1}$ (range: $2–28\ min^{-1}$, $n = 10$) in moving water. These being preliminary investigations only, no account was taken of food quality, satiety or other possible influences.

The degree to which, under natural conditions, a suspension-feeding *J. falcata* orientated its outstretched antennae with respect to water movement was not rigorously ascertained. However, in glass dishes, the orientation of a feeding individual never changed in response to alterations of current direction (as induced by jetting water from a Pasteur pipette). Field observations showed that amphipods living distally on flexible substrata such as algae or hydroids, were automatically swung into optimal alignment for feeding by currents or wave surge. Detritus passing close to the antennae, and associated setae, rarely elicited an active feeding response. Furthermore, fine detritus descending past a downward-facing *J. falcata* did not cause it to turn over in order to maximize the potential food catch. Similarly, antennal flexing and grooming followed by feeding was only induced if detritus actually fell into the antennal nets.

This species fed on clumps of detritus and old faecal pellets, holding them up to the mouthparts with the first gnathopods initially, and then the maxillipeds. Rapid scissor-like actions of the first and second maxillae (combined with a steady lateral rocking motion of the mandibles) broke up the clump in readiness for swallowing. Its own fresh faecal pellets were rarely consumed. Following ventral flexure of the abdomen, sometimes accompanied by the stroking of the urosome by the gnathopods, the faecal pellet emerged from the anus and was passed forward to the maxillipedal palps by the first gnathopods. The maxillipedal palps rotated the pellet end-over-end against the incisors and first maxillary palp, which disrupted it somewhat, and it was then usually dropped and ejected anteriorly from the tube.

Jassa falcata occasionally accepted and consumed live or dead animal material (amphipods, copepods and nematodes) offered on forceps, but was never observed to attack other animals. Large items were held primarily by the first gnathopods, but also by the second gnathopods if necessary. Pieces of finely chopped *Ceramium* sp. were often seized from the forceps by the antennae and gnathopods, but after investigation by the mouthparts were dropped.

(viii) Jassa marmorata

This species constructed a turf of tubes around the inner surfaces of drainage stand-pipes in the Marine Station's seawater system. Such turf can completely occlude the pipes and constitute a virtual monoculture of this species, along with some harpacticoid copepods and numbers of the small sabellid polychaete *Fabricia sabella*. The tubes of *J. marmorata* were closely packed (*ca*. 30 animals cm^{-3} of turf) and overlay one another so that the 'main' entrance, was uppermost and gave immediate access to the overlying water. This arrangement is similar to that described for clusters of *Ericthonius punctatus* tubes and fouling densities of *Jassa falcata*. When introduced to the observation dishes, *J. marmorata* become extremely active, individuals distributing themselves over the dish floor and walls, where over a period of two or three days they built flimsy open-ended tubes that were regularly spaced *ca*. 5–10 mm apart. These tubes were roughly one body length long, constructed of 'amphipod silk' secretion supplemented by any other material available (mainly detritus captured from suspension) and they looked similar to the tubes built by most of the other species studied. Individuals moved freely inside the tube, and somersaulted to appear at either entrance. Individuals remaining on the original pieces of tube-matting were predominantly large mature males and females.

Like *J. falcata*, the typical stance adopted by *J. marmorata* in its tubes was one of partial emergence from the main entrance with abdomen curled ventrally, peraeopods 5–7 hooked securely into the tube, and antennae outstretched. In still water pleopod beating induced water flow over the amphipod, but the pattern of flow depended on how far it had emerged from the tube. When totally enclosed by the tube, the pleopods induced a slow ($< 0.5\ \mathrm{mm\ s^{-1}}$ or $3.2\ \mathrm{ml\ h^{-1}}$ at 13.5 °C) current through the tube in a postero-anterior direction. As it protruded progressively further from the tube and the beating pleopods approached the entrance, more water was drawn in from the front and sides. If the gnathopods were revealed, then they too were held wide, like the antennae. As with *J. falcata*, in still conditions, this species emerged from its tube to the point where the pleopods and part of the ventrally flexed abdomen were exposed. In this position the through-tube current ceased, and pleopod activity caused water to be drawn in from the sides, and from the front and rear instead.

The antennae, with their setal net arrays, were the main appendages used to capture material from suspension, both for food and for tube-building. Setal arrangement on the antennae, and on the terminal articles of the mandibular palps, was similar to that seen in *J. falcata*. On the antennae, the setae of each article are graded in length (longest distally) so that interference between the arrays of each segment during antennal flexure is minimal. The outstretched antennae were periodically flexed back towards the mouthparts, one at a time, and groomed by the first gnathopods and maxillipeds. At the same time, both mandibular palps were flicked down to assist the gnathopods in cleaning the flagellar articles. These were, in turn, brushed by the maxilliped palps and first gnathopods. As with *J. falcata*, the stoutness of the antennae restricted their flexibility so the mandibular palps were only able to reach and groom the more distal (flagellar) regions. The first gnathopod propodi gripped the flexed antenna proximally between them and pulled as the antenna was reflexed. Any detritus collected by the propodal setae was transferred to the maxilliped palps by repeated abduction sweeping actions. This procedure was not influenced by differences in the setation of the flagellar articles associated with maturation in the males. The rate of antennal flexing and grooming in glass tubes in still water (13.5 °C), varied from $< 1\ \mathrm{min^{-1}}$ on average (range 0.4–1.0 $\mathrm{min^{-1}}$, $n = 5$) for animals wholly within the tube, to a mean of almost 3 $\mathrm{min^{-1}}$ (range 1.1–12.0 $\mathrm{min^{-1}}$, $n = 18$) for animals with their antennae emergent.

Jassa marmorata readily fed upon suspensions of ciliates or polystyrene particles introduced to one or other of the tube entrances, collecting them from suspension with its antennae as described above and also by grooming other parts of the body, including the mouthparts and gnathopods. However, unlike *J. falcata*, it ignored large items of potential food offered by forceps such as dead amphipods, copepods and pieces of algae. Occasionally these items were held by the gnathopods for a few seconds before being allowed to drop to the bottom of the dish.

Defaecation was preceded by ventral flexure of the abdomen, the sides of the urosome were sometimes 'massaged' by the gnathopods, and the ejected faecal pellet was usually transferred to the mouthparts by one or other of the gnathopod pairs. As in large males of *A. gracilis*, the pellet was sometimes moved straight to the maxillipeds without assistance from the gnathopods. The pellet was rotated against the mandibles by the maxilliped palps and usually dropped into the pleopod current and flushed out anteriorly. Fresh faecal pellets were consumed rarely. Three females, maintained in unfiltered sea water, were induced to ingest a small amount of carmine red to act as a gut marker. In each case 85 minutes elapsed before the marker first appeared in a pellet. Two of these amphipods had full guts to start with, and over the 85-min period each produced four pellets at rates varying from 2.2–2.5 pellets h^{-1}. The other had an empty gut at the start of the observations, but took the same time as the others to pass the red stain. None of these pellets was eaten.

4. DISCUSSION

(*a*) *Tubes and their utilization by corophioid amphipods*

Our descriptions of the tubular homes of each species studied are in accord with the few available accounts for the same species (Enequist 1949; Shillaker & Moore 1978; Boero & Carli 1979). Two-entrance, cylindrical tubes are typical constructs of other tube-building corophioid amphipods (Holmes 1901; Zavattari 1920; Skutch 1926; Goodhart 1939; Enequist 1949; Barnard *et al.* 1988). However, *Ericthonius punctatus* appears to be unusual amongst the Corophioidea in constructing tapering tubes with entrances which are architecturally distinct; the main entrance being oblique. This is not the case in *E. brasiliensis* (Zavattari 1920). The tubes of *Corophium bonnellii* were the longest (relative to body size) of the species studied, and were also the most carefully tailored to suit the sectional dimensions of the occupant. This accords with the perceived status of this species as a fine-particle suspension-feeder (Shillaker & Moore 1987*a*). Interestingly though, the tubes of *Leptocheirus pilosus* - another fine particle suspension-feeder with a gnathopod filter system similar to that of *Corophium* spp. (Goodhart 1939) - are more comparable to those of other aorid species, e.g. in structure and size relative to occupant, than to those of *C. bonnellii*. However, like those of *C. bonnellii*, the tube entrances of *L. pilosus* are smaller than the bore at the tube's mid-point.

The species studied were divisible into two groups on the basis of how the tube was used during feeding: (A) those which fed inside their tube, and (B) those which fed outside it, or at the tube entrance. Group A included *C. bonnellii*, *L. websteri*, *A. gracilis* and *A. spinicornis*. These species use their pleopods to draw currents through the tube, in an anteroposterior direction, for respiration and food capture. Of these, *C. bonnellii* generated the most rapid through-tube currents, and was the only species to deploy a specially adapted filtering apparatus to collect suspended food. *Lembos websteri*, the only other studied species to possess long erectable setae on the gnathopods, was not seen to use them in suspension-feeding; nor did Shillaker & Moore (1987*a*) do so. They saw suspended detritus trapped by the short medially- and ventrally-directed setae of the gnathopod carpi and propodi, but not by the long erectable setae. In a brief report on the related species, *Autonoe* (= *Lembos*) *longipes*, Enequist (1949) saw suspended detritus caught on the gnathopod setae, but did not mention the deployment of specialized erectable setae for this purpose. Goodhart (1939), however, reported that *Leptocheirus pilosus* (both sexes) deploys a gnathopod 2 setal net for suspension-feeding in a fashion similar to that of *C. bonnellii*. Nevertheless, both some aspects of tube construction and stance adopted within the tube by *L. pilosus* were similar to that reported for the aorids in the present study.

Group B included *Jassa falcata*, *J. marmorata* and *Ericthonius punctatus*, which feed at the tube entrance using their setose antennae (and possibly mandibular palps also) to capture seston from extrinsic currents. In still water, these species generated slow through-tube currents, but in a posteroanterior direction. Under increasingly stagnant conditions the jassids would emerge from their tubes almost completely, so that pleopod beating caused water to be drawn to the animals both laterally and ventrally. *Ericthonius punctatus*, however, used its antennae to induce water movement outside the tube entrance, in the same way as described for *E. brasiliensis* by Zavattari (1920). Enequist (1949, p. 380) denied Zavattari's observation, presumably because he did not observe the behaviour of *E. brasiliensis* under stagnating water conditions.

It was noted in the field, that *E. punctatus* often occurred in such densities that their tubes overlapped each other, and that amphipods tended to favour one tube opening (the open-water end) for feeding. This was also noted in *J. falcata* at sites subject to rapid tidal currents or long wavelength surge. In such environments, amphipods in their tubes, either on algae or fouling on mooring ropes, were automatically orientated to trap suspended detritus with their setose antennae. *Jassa marmorata* also lived in extremely high densities in the laboratory's piped seawater system where, although its tubes were attached to an inflexible, unmoving substratum, the extrinsic water current was unidirectional.

Interestingly, *Gammaropsis nitida* showed morphological and behavioural characteristics of both groups A and B. Its antennal setation patterns are similar to those of ischyrocerids, and like them, it was observed to feed at the tube entrance and to generate posteroanterior currents. However, it could also feed from an anteroposterior water flow induced by the pleopods in the manner of species in group A. The assumption is that, at times, *G. nitida* may suspension-feed passively in the currents generated past, or inside, the shell occupied by the hermit crab (Conover, 1979). If or when, for whatever reason, these currents become slack, then it can feed from its self-generated through-tube current (cf. *C. bonnellii* and the aorid species studied).

Rates of pleopod-generated water movement through amphipod tubes have previously been estimated only for *C. bonnellii* and *L. websteri* (Foster-Smith & Shillaker 1977). Using a pressure transducing apparatus, and by recording over a range of conditions, they obtained flow rates of 3.6–7.4 ml h^{-1} for *C. bonnellii* and 0.54–1.3 ml h^{-1} for *L. websteri*. For the same species we obtained ranges of 11.8–26.1 ml h^{-1} and 5.1–19.7 ml h^{-1}, respectively calculated on the rates at which suspended particles moved through tubes. Our measurements are likely to be overestimates since they are based on flow rates along the centre line of the cylindrical tube, and drag forces reduce water flow near tube walls. In addition, our estimates represent instantaneous rates whilst those of Foster-Smith & Shillaker (1977) were averaged over *ca*. 60 min. These factors may account for our estimates being elevated by an order of magnitude above those reported by Foster-Smith & Shillaker. Nevertheless, they confirm that *C. bonnellii* pumps water through its tube more quickly than *L. websteri*. In our study, species of *Aora* and *L.websteri* generated anteroposterior currents at approximately the same rate, whilst the pleopod-generated water movements of *Gammaropsis nitida* and the ischyrocerid species were the slowest recorded. At present, comparative data on the respiration rates of representatives of different corophioid groupings are lacking, so our understanding of the respiratory significance of different tube types and irrigational behaviours by corophioids is nil (cf. Williams *et al*. 1987 on caddisfly larvae).

Most species studied showed flexibility in dealing with different foods. All could pick up particles deposited within reach of either tube entrance (except for *E. punctatus* which was only seen to feed in this way from one entrance) and trap suspended detritus for feeding. All, except *J. marmorata* and *G. nitida*, were seen to eat animal material of conspecific, meiofaunal or planktonic origin (either dead or alive) as offered by forceps or delivered by pipette. Unprompted carnivory was only witnessed in *E. punctatus* which was once seen to attack and eat prey that happened to be passing the tube entrance. Similar behaviour was also noted for this species by Hughes (1975).

All species, except *C. bonnellii*, regularly investigated their own freshly produced faecal pellets. This ritual, previously reported for *C. bonnellii* and *L. websteri* by Shillaker & Moore (1987*a*), interrupted other activities and usually involved at least partial disruption of the pellet (coprochaly and/or coprohexy, *sensu* Noji *et al*. 1991) before its ejection from the tube. *Corophium bonnellii* was only seen once to investigate, and partially ingest, one of its own freshly produced faecal pellets. Total consumption of the pellet occurred under poor feeding conditions (e.g. if the sea water was not changed regularly) or when the amphipods were unsettled, as when adjusting to new conditions (e.g. when first introduced to the dishes or new glass tubes). This was observed for all species, although only rarely in the case of *C. bonnellii*. All, including *C. bonnellii*, would ingest old faecal pellets along with other detritus (cf. Hargrave, 1970). The process of fresh faecal pellet investigation by amphipods was previously reported by Holmes (1901) for *Amphithoe longimana* and by McGrouther (1983) for *Paracalliope australis*.

Four species (*E. punctatus*, *L. websteri*, *A. gracilis* and *J. falcata*), were seen browsing the surfaces of mineral particles too large to ingest. Nielsen & Kofoed (1982) discussed the probability of particle browsing in *C. volutator*; a process in which the distally bipectinate setae on the distal articles of gnathopod 1 (similar to those described for *C. bonnellii* by Dixon 1992) were used. To judge from the grooming motions of gnathopods 1 in all species, together with the general ubiquity of distally bipectinate setae on limbs involved with grooming, it is likely that particles of all sizes are browsed by the rasping actions of these setae during transfer of material to the mouthparts. This process presumably dissociates aggregates and loosens the biofilm of microorganisms and organic matter around mineral particles.

Furthermore, *E. punctatus*, *L. websteri* and *A. gracilis* left their tubes and grazed epiphytic growth off kelp stipes and haptera when the supply of suspended food was low. These species also accepted and ate pieces of fresh macroalgae (*Ceramium* sp.) although none was seen to eat any of the macroalgal species growing around their natural tubes, even under conditions of prolonged starvation.

(*b*) *Grooming by corophioid amphipods*

As suspension-feeders, all species used the brushing action of limbs to transfer detritus to the mouthparts from wherever on the body it was captured or became trapped. In spite of the obvious specific adaptations shown for trapping seston (using setal arrays on either the antennae or the second gnathopods), all species displayed a similar repertoire of grooming movements in which the gnathopods (especially the smaller pair), maxillipeds and mandibular palps (except in *C. bonnellii*) were the primary tools. These limbs are equipped with distally bipectinate setae, which appear to fulfil a scraping rôle in this process (but see Factor 1978). These observations largely concur with those of Holmquist (1982, 1985) who observed that talitroidean amphipods (lacking mandibular palps) use their mouthparts and both pairs of gnathopods for grooming. Interestingly, he commented on the fact that of six species studied (Holmquist 1982), none was seen to close opposed gnathopods on an appendage and pull the latter between them. This contrasts with some of the observations herein (see also Coleman 1989), although the significance of this difference is not immediately apparent.

As described by Dixon (1992), the carpal and propodal articles of at least one pair of gnathopods in all the species we studied are equipped with ranges of distally bipectinate setae along their medial and posterior margins. In the males, the development and enlargement of the dominant gnathopod pair with increasing maturity usually entails the disappearance of such setae and these gnathopods can lose their grooming rôle (although they can still be used, for example, to hold large food items against the mouthparts). The first gnathopods of *Corophium bonnellii* are adapted to cope with the comparatively large amounts of detritus collected by the filtratory setae of gnathopod 2. Thus their carpal posterior margins and propodal medial faces are furnished with robust distally bipectinate setae (first described for the genus by Ingle, 1969), which probably function both as combs and rasps; in addition to which the ischia and carpi bear rows of long plumose setae, the main function of which is to hold the detritus combed from gnathopod 2 by the pectinate setae.

Corophium bonnellii is exceptional amongst the species studied in that the posterior (i.e. ventrally directed) setae on the maxilliped palps are densely plumose, whereas in the other species studied they are distally bipectinate. These setae function similarly in all species studied, i.e. in assisting in the transfer of particulate food from the gnathopods to the mouthparts. As speculated above for the gnathopods, it is possible that this distinction in setal morphology reflects the potential volume of detrital food captured from suspension by the gnathopod 2 filter setae, as well as the predominantly fine nature of any particles diverted from the external water column into the tube by the pleopodal current.

All species studied, except *C. bonnellii*, used their mandibular palps for grooming the antennae (often in conjunction with the maxilliped palps and first gnathopods). *Corophium bonnellii*, with its reduced mandibular palp, used only its first gnathopods and maxilliped palps in this task. A function for the reduced mandibular palp of *C. bonnellii* was not conclusively determined. Grooming the interantennal space would probably be accomplished more efficiently by the basic mandibular palps of the other species (Barnard 1969; Barnard & Karaman 1991) which, being longer and more setose, would be more likely to prevent material from becoming trapped there in the first place. Shillaker (1977) and Shillaker & Moore (1987*a*) conjectured that the interantennal space represents an additional detrital food collection site. *Corophium* and related genera are adapted to feed from fast through-tube currents using voluminous gnathopod filters. As such, we conjecture, they have no requirement to utilize mandibular palps as additional food-collecting limbs (cf. Ischyroceridae), and/or as additional antennal grooming tools (cf. all other species in this study). Instead, the mandibular palps may serve primarily as forks to dislodge the larger, compacted clumps of material that inevitably accumulate in the interantennal peduncular 'dead' space, which would tend to be retained in that position by spines on the antennal peduncle. Interference with the primary feeding mechanism could therefore be minimized. Compacted material dislodged could also serve as a source of tube-building material: so, although *C.bonnellii* can deal with both large and small particles effectively, in this way it may segregate the two activities for efficiency. Interestingly, *Leptocheirus pilosus*, which deploys a setal net for suspension-feeding (Goodhart 1939), retains basic setose mandibular palps. This tallies, however, with its different reported feeding stance, with antennae protruding from the tube in the same way as observed for the aorids studied.

(*c*) *Grazing by corophioid amphipods*

This category included those feeding activities in which the biting or rasping action of the mandibular incisors, maxilla 1 palps (apical spines), maxilla 2 outer plates (apical setae) and maxilliped outer plates (spinose medial margins) were brought to bear directly on the food. Examples of such activities include particle-browsing, the disruption of detrital boli (including faecal pellets) and the consumption of large prey items, in addition to the grazing of microbiota from algal or other substrata. *Corophium bonnellii*, with its comparatively small and slightly built mandibular incisors, and weakly spinose first maxillae and setose maxilliped outer plates, was less inclined to tackle large or tough food items than the other species studied. Gerdol & Hughes (1994), however, have testified to the effectiveness with which the molars of *C. volutator* grind up diatom frustules.

(*d*) *Sorting and transfer of detritus through the mouthpart bundle of corophioid amphipods*

This aspect of feeding behaviour was obscured from direct observation by the tightly packed nature of the mouthparts and their medially oriented activity. As reported by Miller (1984) the mandibles, hinged proximolaterally, operated with a slow (*ca.* 1–3 Hz) adduction/abduction action. This was true both when the incisor portion was being used or when the molar portions only were in use). Movements of the upper and lower lips could not be followed. Both pairs of maxillae moved with a rapid (< 30 hz) scissor-like action. The first maxilla palp is primarily a biting and manipulative organ. The rôle of the first maxilla outer plate, however, in addition to biting, appeared to be to push food particles between the mandibular spine rows and molars. The second maxillae could rock back and forth, but it was not possible to determine whether the motion of the inner plates had any axial rotatory component, as reported for *Haustorius arenarius* during maxillary filter-feeding (Dennell 1933). As mentioned above, the primary rôle of the apical setae on the second maxilla inner and outer plates is probably a rasping one, though they may also assist in grooming the first maxillae. As discussed by Dixon (1992), the setae fringing the maxilla 2 inner plate medial margins almost certainly have a filtratory function but, although interspecific structural differences may be linked with filtratory efficiency, this was not evident from external observation of the mouthparts or from behaviour. The maxillipeds can be rocked back and forth which causes the anteriorly-projecting plumose setae on the medial margin of each inner plate to be pulled and pushed between the lower lip inner lobes whilst, at the same time, brushing against the filtratory setae of the second maxillae. The potential for such activity to move particulate material forward through the mouthparts and between the mandibles is obvious. This type of motion could also be used to force water through the maxillary filter system. In all species observed, the maxillipeds also operated with a scissor-like action. It was not clear if the basal articles were thus parted in those species in which the maxilliped inner plates bear interlocking spines (cf. Dennell 1937; Nicolaisen & Kanneworff 1969; Dixon 1992). When used in this scissor-like fashion the maxilliped outer plates, with their mediomarginal spines (in all species except *C. bonnellii*) were effective as cutters and assisted in breaking-up long thin food items such as algal filaments and faecal pellets. In all species, including *C. bonnellii*, the scissoring action of the maxilliped outer plates and palps (or rather the setae thereon) was used to break up clumps of detritus prior to ingestion.

(*e*) *Phylogenetic implications of differences in feeding behaviour between corophioids*

The evolutionary lineages within the complex superfamily Corophioidea are currently unclear. Myers (1981) contended that there is a basic dichotomy in primitive corophioideans in relation to the structure of the head and its appendages. In a domicolous animal, the greatest environmental pressures will be on the exposed, in this case head, region. In one evolutionary line, both pairs of antennae retained a sensory function, becoming elongate and slender, thereby extending the range for collection of sensory information around the habitation without the necessity for exposure of the body. In the other lineage, the first pair of antennae retained their sensory function, while the second pair lost it, becoming shorter and stouter and used in food gathering. *Gammaropsis* appears to be a primitive member of the first line, *Protomedeia* a primitive member of the second (note also Conlan 1988). Both genera exhibit an enlarged second gnathopod pair in the male. Myers (*loc. cit.*) identified these as independent events, with both lines producing forms with enlarged first gnathopods in the males, represented today by neomegamphopids (first line) and aorids (second line). Lyons & Myers (1990) have conjectured as to why in some corophioids the second pair of gnathopoda has been converted to an accessory feeding structure, bypassing the first pair. In their opinion, the anterior-most thoracic appendages are required as agonistic or epigamic structures in a tube-dweller to permit interaction with other individuals without having to extend far from its habitation.

Evidence for such a split within the Corophioidea comes also from our behavioural and functional morphological investigations of feeding. As shown above, the ischyrocerid species project their setose antennae from the tube to capture seston borne on extrinsic water currents. The other species studied (and, by structural inference, genera like *Xenocheira*, *Kuphocheira*, *Haplocheira*, *Leptocheirus*, *Anonychocheira*, *Janice*, *Microdeutopus* [*versiculatus*, *gryllotalpa*], *Paracorophium*, *Lemboides*, *Bemlos* [*leptocheirus*]) use their pleopods to generate through-tube currents, from which seston is captured by setose appendages concentrated anteriorly (especially the gnathopods and mouthparts). Confirmatory studies (cf. Goodhart 1939 on *Leptocheirus*) on the feeding stance of representatives of these genera would be desirable. *Gammaropsis nitida* was able to feed in either fashion. All the species we studied used the propodal and carpal medioventrally-orientated setation of the gnathopods (only the smaller pair in large mature males) in subsequent grooming and food transfer activities.

Our work on *G. nitida* supports the suggestion that the genus *Gammaropsis* is a stem corophioid (Barnard 1969, 1973; Myers 1981; Barnard & Karaman 1991), since its feeding behaviour contains elements of both the ischyrocerid and the aorid/corophiid lineages, and as such is presumed to be primitive. Further information, however, is required on the life style and feeding habits of other *Gammaropsis* species to establish how general is this finding: *G.nitida*, after all, occupies a rather unusual habitat and Conlan (1988) considered this genus to be polyphyletic.

It would be interesting to examine feeding and water-current production in amphipods which inhabit tubular structures open at one end only. For instance, both siphonoecetines (Gauthier 1941; Just 1988) and *Photis conchicola* (Carter 1982) inhabit small gastropod shells (the former are free-roaming, the latter attach the shells to algae), and both have setose antennae similar to those of the jassids studied here, and are largely epifaunal in habit. In siphonoecetines the antennae have an important additional function as swimming appendages (Steele 1988; Just 1988).

The ischyrocerid habit of externalizing food gathering at the tube entrance, might now be regarded as one step along the line leading to clinging, rod-building podocerid types (see Barnard *et al.* 1988; Mattson & Cedhagen 1989), which, it has been suggested, have generated the caprellids (Laubitz 1979; but note Barnard & Karaman 1991). A parallel exists with the Isopoda, in that one direction of evolution has been towards climbing, suspension-feeding types (Ohlin 1901; Brandt & Wägele 1990) with setose antennae, mouthparts and anterior peraeopods.

That all corophioids examined retain flexibility in feeding abilities in spite of the various specializations shown by individual species helps to explain why representatives of this major amphipod taxon have been so successful in colonizing benthic habitats the world over. Hassack & Holdich (1987) have commented upon the fact that colonies of tubicolous tanaids can attain very high population densities, and have pointed out the protective role of tubes against predators, as also during reproduction and moulting. That similar closely-packed colonies characterize both epifaunal and infaunal corophioid populations (Connell 1963; Thorson 1971; Moore 1985) reflects the fact that, as in sessile colonial taxa, particulate food in abundance – in the form of seston or depositing particles – is brought to their vicinity, and continually replenished, by external agencies.

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